Historia de vida temprana e inversión reproductiva de invertebrados bentónicos: integración al manejo y conservación a través de modelos de dispersión

Early life and reproductive investment of benthic invertebrates: integration to management and conservation throught dispersal models

Marta Blanco Sánchez

Historia de vida temprana e inversión reproductiva de invertebrados bentónicos: integración al manejo y conservación a través de modelos de dispersión

Marta Blanco Sánchez

Tesis presentada para la obtención del título de Doctorado por la Universidad de Barcelona

2018

Fotos de Portada y Contraportada: Alejandro Pérez Matus, Cristina Ruano, V. Häussermann & G. Försterra
Fotos Interior: Marta Blanco Sánchez
Dibujos interior: Andrés Julian
Diseño y edición: Marta Blanco Sánchez

Early life history and reproductive investment of benthic invertebrates: integration to management and conservation through dispersal models

Historia de vida temprana e inversión reproductiva de invertebrados bentónicos: integración al manejo y conservación a través de modelos de dispersión

FACULTAD DE CIENCIAS BIOLÓGICAS
PONTIFICIA UNIVERSIDAD CATÓLICA DE CHILE
CENTRO DE **conservación marina**
NÚCLEO **MILENIO**

UNIVERSITAT DE BARCELONA

Facultad de Biología

Departamento de Biología Evolutiva, Ecología y Ciencias Ambientales
Universidad de Barcelona

Tesis presentada para la obtención del título de doctorado por la Universidad de Barcelona

Programa de doctorado en Biodiversidad (HDK04)
Línea de investigación: Conservación y Gestión de la Biodiversidad (101113)

Marta Blanco Sánchez
Doctoranda
Universidad de Barcelona
CCM-UB

Dra. Miriam Fernández
Directora
Pontificia Universidad Católica de Chile
CCM-PUC

Dra. Creu Palacín Cabañas
Tutora
Universidad de Barcelona
UB

Dr. Andrés Ospina-Álvarez
Co-Director
Pontificia Universidad Católica de Chile
CCM-PUC

2018

Mariscos resbalados en la arena,
brazos resbaladizos,
estómagos del agua,
armaduras abiertas a la entrada
de la repetición y el movimiento,
púas, ventosas, lenguas,
pequeños cuerpos fríos,
maltratados
por la implacable eternidad del agua,
por la ira del viento.

Pablo Neruda

Agradecimientos

En primer lugar, agradecer a Miriam Fernández y Andrés Ospina por el apoyo y paciencia durante todo el proceso de aprendizaje que ha supuesto esta tesis doctoral, siempre han estado disponibles para aconsejarme y darme su opinión, tanto durante los primeros años en Chile como estos últimos años desde la distancia. Este trabajo no hubiese sido posible sin vuestra ayuda y dedicación y me alegro de poder haber tenido el gusto de aprender y trabajar con vosotros.

Este trabajo tampoco hubiese sido posible sin la ayuda de todas las personas que acompañaron mi estancia de dos años y medio en la Estación Costera de Investigaciones Marinas, me ayudaron a resolver dudas en todo momento e hicieron de esta etapa un período enriquecedor y divertido. A Ricardo Calderón y Randy Finke que siempre estuvieron disponible para ayudarme a preparar el material para todos los muestreos, a Mayra Figueroa que siempre me pedía las boletas y rendir las cuentas! a Mª Dulce Subida que siempre estuvo disponible para resolver mis dudas con R, a Bryan Bularz, Joan Escobar y Jessica Bonicelli que fueron mis compañeros de despacho de doctorandos durante el último año en Chile. A Manuel González, Catalina Ruz y Sebastián López que siempre estaban dispuestos para echarme una mano en los buceos. A Nacho González por ayudarme a diseñar y acompañar mis primeros experimentos con larvas. A Tito Santis que además de ayudarme con su experiencia como buzo mariscador siempre me abrió las puestas de su casa junto a Edith para compartir buenos ratos con ellos.

Pero seguro mi estancia en Chile no hubiese sido lo mismo sin los asaditos con vistas al mar y los carretes interminables en las Cruces! y claro estos no hubiesen sido lo mismo sin el rey del confort Fran Carollo y sin mi vecina gaditana Teresa Fernández. Tampoco hubiesen sido lo mismo sin compartir esos pisco-sours y chelitas con vosotros: Yolanda Sánchez, Cristina Ruano, Alba Medrano, Elliott Ramos, Alejandro Pérez, Sergio Carrasco, Loes Vandercasteele, Rodrigo Urbe, Simon Karythis, Itziar Burgués, Miguel Andreu, Jenna Shinen, Silvia De Juan, Montse Rodríguez, y tantas otras personas con las que he compartido y seguro me olvido. Y como no a las dos poliquetas más divertidas de Madrid, Patricia Álvarez y Aida Verdes.

Gràcies a la Creu Palacín per deixar-me un despatx on escriure la tesi un cop vaig tornar de Xile i aconsellar-me en tot moment sobre tots els tràmits i paperassa, gràcies també a l'Àlex García per compartir despatx i experiències de l'etapa final de tesi.

Gràcies als meus pares, germans i nebots per fer-me sempre costat i animar-me a fer allò que m'agrada encara que suposés marxar molt lluny, gràcies per estar sempre a l'altre banda de l'skype i portar-me el caliu de casa allà on fos.

Per últim, a la boleta de pel taronja que em vaig emportar de Xile, la Taneta que amb el seu runruneig i careta dolça sempre em fa baixar l'estrès. I com no al Quim Molina Colomina que m'ha aguantat durant tot aquest llarg procés, m'ha animat en tot moment, inclús m'ha ajudat a processar mostres, i sobretot gràcies per fer-me costat cada dia, sense tu no hauria estat possible.

Esta tesis ha estado financiada por una beca de postgrado de la Fundación Mutua Madrileña, y por los proyectos Fondecyt 1130976 y la Iniciativa Científica Milenio (CCM RC 1300004) del Ministerio de Economía, Fomento y Turismo del Gobierno de Chile.

Índice

Acrónimos y Abreviaturas

ALA: Áreas de Libre Acceso

AMERB: Áreas de Manejo de Explotación de Recursos Bentónicos

AR: de las siglas en inglés “Allochthonous Recruitment”, reclutamiento alóctono

CCC: Corriente Costera de Chile

CTP: Captura Total Permitida

DVM: de las siglas en inglés “Dial Vertical Migration”, migración vertical diaria

ESBA: Estudio de Situación Base del Área

GSI: de las siglas en inglés “Gonadosomatic Index”, índice gonadosomático

IBM: de las siglas en inglés “Individual Based Model”, modelos basados en individuo

LGPA: Ley General de Pesca y Acuicultura

LR: de las siglas en inglés “Local Retention”, retención local

MPA: de las siglas en inglés “Marine Protected Areas”, áreas marinas protegidas

OAA: de las siglas en inglés “Open Access Areas”, áreas de libre acceso

PLD: de las siglas en inglés “Planktonic Larval Duration”, duración de la etapa larval planctónica.

PMEA: Plan de Manejo y Explotación del Área

RLR: de las siglas en inglés “Relative Local Retention”, retención local relativa

SEIBM: de las siglas en inglés “Spatialy Explicit Individual Based Model”, modelos basados en individuo espacialmente explícitos

SR: de las siglas en inglés “Self-Recruitment”, auto-reclutamiento

TURF: de las siglas en inglés “Territorial Users Right for Fisheries”, derechos territoriales de uso para la pesca

Part I
Primera parte

Resumen de la tesis

Las zonas costeras son uno de los ecosistemas que sufre mayor impacto antrópico a nivel mundial. La sobreexplotación de los recursos marinos es una de las actividades humanas que genera mayor impacto, reduciendo la abundancia y tamaño de las especies objetivo. Una de las medidas para proteger estos ecosistemas consiste en el establecimiento de áreas marinas protegidas. En Chile, el sistema actual de manejo de las pesquerías artesanales de especies bentónicas está basado en áreas parcialmente protegidas, las Áreas de Manejo y Explotación de Recursos Bentónicos (AMERBs), lo que ha supuesto una mejora en la sostenibilidad de una actividad de larga tradición en el país. Estas áreas entregan derechos de usos territoriales, conocidos mundialmente como TURF (sigla en inglés de Territorial Use Right for Fisheries). Sin embargo, actualmente estas áreas se gestionan de forma individualizada, de tal manera que la escala espacial de manejo no está acoplada a la escala de la dinámica de las poblaciones de invertebrados bentónicos. El objetivo de esta tesis es identificar áreas de alto valor para la producción, exportación y llegada de larvas en base a los patrones de historia de vida temprana, considerando variables y/o condicionantes relevantes de la fase adulta bentónica, como (a) la inversión reproductiva, (b) la densidad y talla de los adultos reproductores, variables determinantes de la distribución espacial de la producción de huevos y larvas, así como también variables que intervienen en la fase larval planctónica, como (c) los rasgos biológicos larvales, para acoplarlo con los patrones de circulación costera con el fin de contribuir a un mejor entendimiento de la dispersión y conectividad larval. Para este fin se seleccionaron dos especies relevantes social, comercial y ecológicamente: el erizo rojo (*Loxechinus albus*) y la lapa (*Fissurella latimarginata*). En primer lugar, se evaluó mediante muestreos de campo el efecto de la protección (relacionada con el régimen de explotación) y afloramiento costero sobre la inversión reproductiva y la condición individual de los adultos reproductores. Esta información sumada a los datos empíricos de distribución de tallas, densidad de individuos y fecundidad de las hembras reproductoras se utilizó para desarrollar un modelo de producción potencial de huevos en la costa central de Chile. Para el estudio del reclutamiento y dispersión se desarrolló un modelo biofísico de dispersión larvaria que permite evaluar el efecto de la variabilidad oceanográfica y los rasgos biológicos (migración vertical de las larvas y desarrollo dependiente de la temperatura) en la distancia de dispersión, el éxito del reclutamiento, y los patrones de conectividad larval. Los resultados sugieren que, para ambas especies, la protección y el afloramiento costero no tienen un efecto sobre la inversión reproductiva y la condición de los individuos. Sin embargo, la protección sí tuvo un efecto sobre la talla y densidad de individuos generando claros patrones espaciales de producción de gametos. Se observó que la variación geográfica y temporal de los procesos de circulación dominan el transporte y la dispersión de las larvas en la región, independientemente de los rasgos biológicos evaluados. La mayoría del reclutamiento fue alóctono, con niveles bajos de auto-reclutamiento y retención local, incluso para la especie con un tiempo de vida planctónica corto (*F. latimarginata*). Los patrones geográficos de salida y llegada fueron similares para ambas especies, observándose una mayor importancia relativa de la región norte del dominio de estudio. Estos resultados permiten identificar los principales determinantes de la producción de huevos, el éxito del reclutamiento y la distancia de dispersión para dos especies de gran interés comercial en Chile, información que podría guiar recomendaciones para el manejo y la conservación en una de las regiones costeras más productivas pero también más explotadas del mundo.

Palabras clave

Conectividad, Áreas Marinas Protegidas, Invertebrados Bentónicos, Pesca artesanal, Inversión Reproductiva, Modelos de Dispersión Larvaria

Thesis Abstract

Coastal zones are one of the ecosystems receiving higher anthropic impact. Fishing is a major source of human impact, reducing density and size of exploited species. Marine protected areas are one of the strategies established to control fishing impacts. The current artisanal fisheries management system in Chile is based on partially protected areas, TURFs (Territorial Use Right for Fisheries). This system enhances sustainability of one of the traditional activity in the country. However, these areas are individually managed so the scale of resource management is not coupled with the scale of exploited population dynamics. The objective of this thesis dissertation is to identify areas of high value for propagule production as well as source and sink areas based on early life history patterns, considering variables relevant for the adult phase such as (a) reproductive output, (b) density and size of reproductive adults as both variables define the spatial distribution of eggs and larvae, as well as variables that affect the larval phase such as (c) larval biological traits, coupling these pieces of information with coastal circulation models to reach a better understanding of dispersal and larval connectivity. Two benthic invertebrates species exploited by artisanal fisheries in Chile, the red sea urchin (*Loxechinus albus*) and keyhole limpet (*Fissurella latimarginata*) were used as models. First, I evaluated the effect of protection and coastal upwelling on reproductive output and individual condition of reproductive adults. Based on size distribution, density of individuals and fecundity data I developed an egg production model along the central coast of Chile. Finally, I developed a biophysical larval dispersal model to assess the effect of oceanographic variability and larval biological traits (larval diel vertical migration and temperature-dependent larval development) on dispersal distance, recruitment success and connectivity patterns. These results showed that fishing regime and coastal upwelling did not affect individual reproductive output either individual condition for both species. However, fishing regime had an effect on size and density of individuals. I found that the geographic and temporal variation in circulation processes dominate transport and effective dispersal of larvae in the study region, regardless of larval biological traits. Most recruitment to local population was allochthonous, with low levels of self-recruitment and local retention even for the species with short planktonic larval duration. Similar geographic patterns of source and destination strengths were observed in both species, with the northern region of the studied domain showing relatively higher importance. These findings allow identifying primary determinants of recruitment success and dispersal distance for two important exploited species in Chile, and to provide the bases to advance recommendations for management and conservation in one the most productive, but also exploited, coastal regions in the world.

Key words

Connectivity, Marine Protected Areas, Benthic Invertebrates, Artisanal fisheries, Reproductive Output, Larval Dispersal Models

Introducción General

Introducción general

Ciclos de vida en invertebrados bentónicos

Ciclos de vida complejos

La mayoría de invertebrados bentónicos presentan un ciclo de vida complejo, con una fase larvaria planctónica y estadios juvenil y adulto bentónicos (Thorson 1950). Un ciclo de vida complejo típico se inicia con la liberación de los gametos, embriones o larvas a la columna de agua por parte de los adultos reproductores, de vida bentónica. En muchos casos, la fertilización y el desarrollo larvario completo ocurren en la columna de agua. El período de desarrollo planctónico puede durar desde horas a meses, dependiendo de la especie, y mostrar desde uno a varios estadios de desarrollo larval (Mileikovsky 1971). Durante esta fase, las larvas pueden alimentarse activamente en el plancton (larvas planctotróficas) o utilizar las reservas del huevo para completar su desarrollo (larvas lecitotróficas). Dado este complejo ciclo de vida, la dinámica espacial y temporal de las poblaciones de estos organismos está afectada por varios procesos, destacando: (a) la inversión reproductiva y la fecundidad de los adultos, (b) el éxito de fecundación, (c) el crecimiento, comportamiento, duración y mortalidad en la etapa larvaria, (d) la dispersión y transporte por las corrientes en el plancton, y (e) procesos que afectan las fases bentónicas. Estos procesos, a su vez, no son independientes entre sí. Por ejemplo, la duración de la vida larval depende de la inversión materna en la reproducción, y a su vez afecta la mortalidad larval. Por otro lado, estos procesos están determinados por una amplia variedad de factores condicionantes, entre los que destacan (a) la temperatura, (b) la disponibilidad de alimento, (c) la presión pesquera, (d) la dinámica oceanográfica y (e) el hábitat disponible (Figura 1.1).

Inversión en reproducción

Este cuerpo teórico fue formalmente inicializado por Fisher (1930), quien demostró que la inversión individual en reproducción es un proceso de importancia evolutiva, sujeta a la selección natural. El éxito reproductivo al final de la existencia de un individuo debe ser estimado considerando la inversión o el gasto actual en el cual cada individuo debe incurrir para poder reproducirse y como dicha inversión

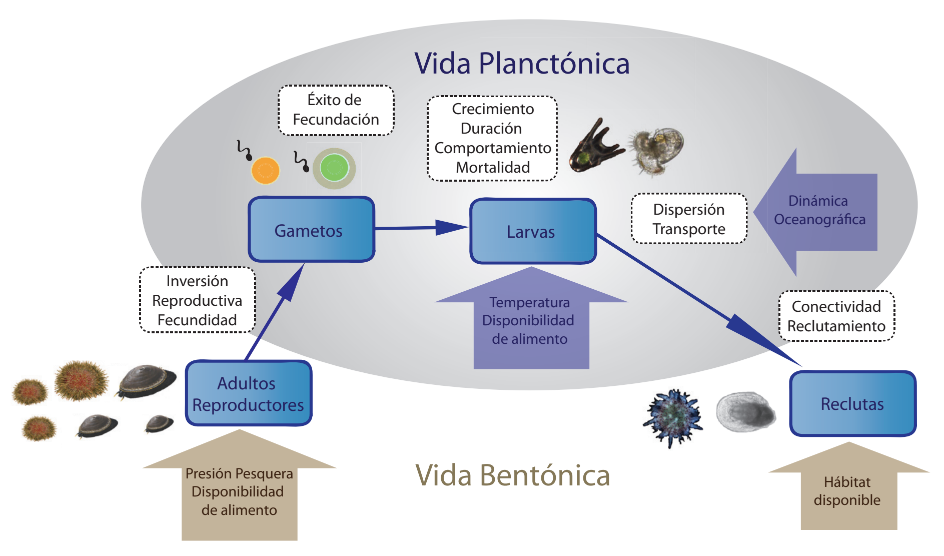


Figura 1.1. Ciclo de vida de invertebrados bentónicos.

afecta su éxito reproductivo futuro (Fisher 1930, Brommer 2000). Los individuos que a lo largo de su existencia asignan recursos a la reproducción en función de los costos y beneficios de las oportunidades reproductivas actuales y futuras son favorecidos evolutivamente mediante selección natural (Houston & McNamara 1999). Se espera entonces que la interacción y variación temporal y espacial entre los factores ambientales, tales como la temperatura y la disponibilidad de alimento, determinen la inversión en reproducción impactando la distribución y abundancia de organismos, considerando la variabilidad espacial del hábitat (Spicer & Gaston 1999). Estudios recientes sobre la inversión en reproducción de algunas especies de herbívoros marinos sugieren mayores tasas de crecimiento gonadal en localidades influenciadas por la surgencia o afloramiento costero en comparación con zonas de sombra de surgencia (Pulgar et al. 2013, Aldana et al. 2017). Las diferencias oceanográficas en temperatura y disponibilidad de nutrientes (Wieters et al. 2003) ocasionadas por la variabilidad en la intensidad y persistencia de dicho proceso (Thiel et al. 2007) afectan directamente el crecimiento de las macroalgas (Nielsen & Navarrete 2004, Aldana et al. 2017) que son fuente de alimento de numerosas especies de herbívoros de interés comercial en Chile, tales como Fissurella spp. y *Loxechinus albus* (Moreno 2001, Garcia-Huidobro et al. 2015). Este patrón da cuenta de la importancia de considerar explícitamente la variabilidad espacial de la inversión individual en la reproducción para alcanzar un mejor entendimiento de la dinámica espacial de las poblaciones marinas. Sin embargo, no solo los factores oceanográficos pueden condicionar el potencial reproductivo de una especie en una determinada localidad. En el caso de especies de interés comercial, el régimen de explotación pesquera es un determinante fundamental de la abundancia de adultos, la que a su vez influye en el potencial reproductivo de una localidad (Castilla & Durán 1985). La pesca no solo influye sobre la abundancia de adultos, sino que también selecciona los individuos más grandes, por dos razones. Primero porque tienen mayor valor en el mercado pero además porque la regulación vigente impide la extracción de individuos pre-reproductores. Dado que las hembras más grandes tienen proporcionalmente gónadas de mayor tamaño (Kido & Murray 2003), es claro que la explotación pesquera es un factor clave en determinar el potencial reproductivo local. Por ende, resulta interesante relacionar el potencial reproductivo individual con la abundancia de los recursos bentónicos de interés comercial, a fin de estimar el potencial reproductivo de las poblaciones locales a lo largo de un gradiente de explotación pesquera, como es el que ofrece la costa de Chile, con un extenso mosaico de áreas total y parcialmente protegidas y áreas de libre acceso.

Fase larval

Las condiciones oceanográficas también afectan la fase larval, de diversas maneras. (Metaxas & Saunders 2009). En muchas ocasiones las condiciones ambientales (e.g., temperatura, disponibilidad de alimento) interaccionan con los rasgos biológicos (e.g., la tasa de crecimiento; Sanford & Menge 2001, Talmage & Gobler 2011). Sin embargo, el efecto es más complejo en especies con fase planctónica ya que la duración de la etapa planctónica está fuertemente influenciada por la temperatura experimentada por las larvas durante su desarrollo (Gillooly et al., 2002; Hoegh-Guldberg, 1995; O'Connor et al., 2007). Se ha observado, que a temperaturas más altas, la duración de la etapa larval se reduce significativamente (O'Connor et al. 2007). Esto puede afectar la abundancia de larvas, al condicionar la mortalidad durante esta fase. Pero además, puede condicionar el transporte y la dispersión de las larvas y con ello, la conectividad de las poblaciones (Ayata et al. 2010). En baja California, Hart and Scheibling (1988) mostraron la correspondencia entre las fluctuaciones interanuales de la temperatura del océano y las variaciones en el reclutamiento del erizo de mar Strongylocentrotus droebachiensis, relacionando temperaturas elevadas con mayor reclutamiento. Este hecho, pone en relevancia la necesidad de estudiar las ventanas de tolerancia térmica de las larvas para poder evaluar los patrones de conectividad.

Otro condicionante fundamental del desarrollo y sobrevivencia larval es el comportamiento exhibido por las larvas. El comportamiento larval interactuando con las condiciones ambientales puede alterar la duración de la etapa planctónica y, en consecuencia la dispersión y el reclutamiento de las larvas (Paris & Cowen 2004, Woodson & McManus 2007). Muchas especies presentan fases larvales que tienen la capacidad de desplazarse verticalmente entre masas de agua que exhiben diferentes temperaturas, y que viajan a diferentes velocidades y distintas direcciones (Metaxas & Saunders 2009, Ospina-Álvarez et al. 2012), por eso se denomina migración vertical. Algunas especies tienen la capacidad de migrar verticalmente en la columna de agua, ya sea con una periodicidad determinada (Marta-Almeida et al. 2006, Ospina-Alvarez, Parada, et al. 2012) o de acuerdo a su edad o etapa de desarrollo (i.e., migración ontogénica) (Butler IV et al., 2011). La migración vertical diaria o migración nictimeral consiste en el patrón de desplazamiento vertical que realizan los organismos planctónicos durante el ciclo diario, durante el día se sitúan en profundidad y durante la noche ascienden a aguas superficiales (Rudjakov 1970). El comportamiento de migración vertical es particularmente importante en zonas influenciadas por condiciones oceanográficas que favorecen la advección, como por ejemplo el afloramiento costero (Poulin et al. 2002, Aiken et al. 2011). En las zonas de afloramiento costero se ha relacionado la alta concentración de larvas bajo la capa de Ekman al fenómeno de migración vertical (Aiken et al. 2011). Presumiblemente, este fenómeno previene el transporte de las larvas fuera de la zona costera durante los eventos de afloramiento y favorece el transporte de las larvas hacia la costa durante los eventos de relajación del afloramiento costero (Roughgarden et al. 1991, Peterson 1998, Morgan et al. 2009), aumentando la retención de las larvas de especies costeras (Morgan et al. 2011). De hecho, existen evidencias de que la migración vertical incrementa la retención de las especies costeras y la probabilidad de auto-reclutamiento (Cowen et al. 2000, Aiken et al. 2011). La inclusión de rasgos biológicos larvales tales como las respuestas específicas a la temperatura y el comportamiento de migración vertical en los modelos de dispersión larval pueden mejorar nuestra comprensión de la dinámica y los patrones de conectividad, para poder desarrollar planes de manejo adaptados a cada especie.

Conectividad y dinámica de poblaciones

Dinámica de las metapoblaciones

Una metapoblación se define como un sistema en el que las poblaciones locales habitan parches de hábitats discretos conectados demográficamente entre sí, donde la dispersión entre parches no es lo suficientemente baja como para negar una dependencia de la dinámica regional ni suficientemente alta como para eliminar cualquier independencia de la dinámica de la población local (Kritzer & Sale 2006) (Figura 1.2). Siguiendo esta definición podemos decir que la mayoría de invertebrados bentónicos constituyen metapoblaciones ya que mayoritariamente se distribuyen en hábitats frecuentemente fragmentados, y además presentan ciclos de vida complejos, caracterizados por una fase larval planctónica, que contribuye a una dispersión efectiva entre parches de hábitat favorables.

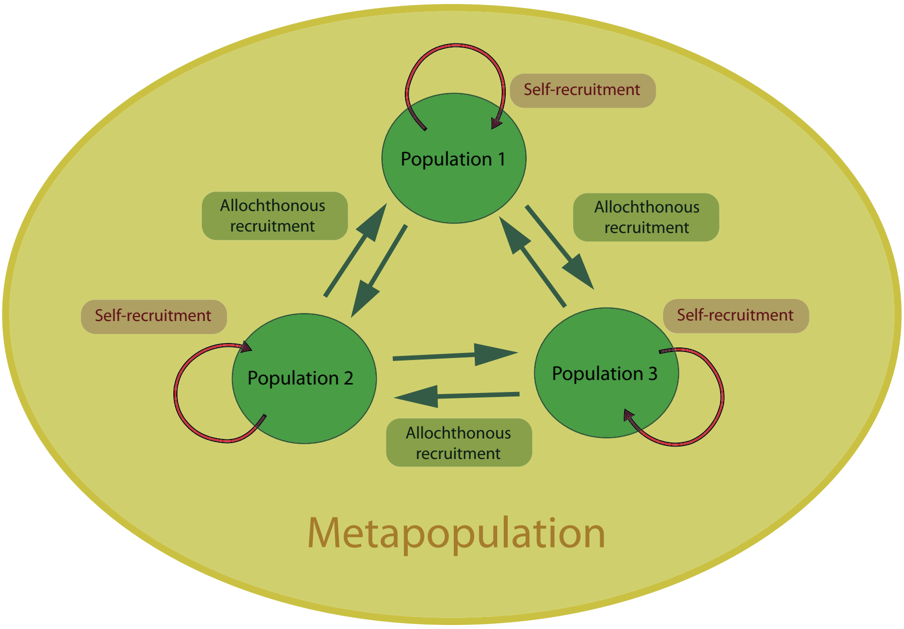


Figura 1.2. Adaptación de Kritzer and Sale (2004). Representación de una metapoblación. Los círculos representan poblaciones locales discretas dentro de la región más grande delimitada por un óvalo exterior. Las metapoblaciones pueden verse como una red de poblaciones parcialmente cerradas donde existe un cierto grado de auto reclutamiento (flechas rojas) y dinámica independiente, pero esto se combina con un suministro no menor, de otras poblaciones distantes (flechas verdes).

La inclusión del concepto de metapoblación en el manejo y conservación de las poblaciones de especies marinas es fundamental desde hace varias décadas. Sin embargo, antes de los años 80 la gestión de los recursos marinos se centraba en examinar las poblaciones localmente, prestando poca atención a la interacción entre subpoblaciones distantes de la misma especie (Kritzer & Sale 2006). Esta visión cambió al observar la importancia de la dispersión larval y el impacto de la dinámica del reclutamiento en la estructura de las poblaciones locales (Caffey 1985, Roughgarden et al. 1985, 1988). Sin embargo, estimar la dispersión larval y el reclutamiento de especies marinas es complejo ya que interactúan múltiples factores, siendo necesario tener un conocimiento de la variabilidad de los procesos hidrodinámicos y del conjunto de habilidades sensoriales y comportamentales que cambian a medida que la vida larval progresa (Sale & Kritzer 2003). En este sentido, numerosos estudios señalan la necesidad de desarrollar técnicas para estimar la conectividad entre las poblaciones marinas que conlleven al planteamiento de estrategias de conservación efectivas (Kritzer & Sale 2004).

Transporte larval

El transporte larval, estrictamente se define como la traslocación de las larvas desde un punto x1, y1 a x2, y2 (Pineda et al. 2007). Esto involucra los movimientos horizontales a los que se ven sometidas las larvas cuando son transportadas a través del océano principalmente por procesos físicos de meso y macro escala. El estudio del transporte larval es una disciplina compleja ya que en la definición de las trayectorias que experimenta cualquier larva en el océano interactúan procesos oceanográficos a diferentes escalas espaciales y temporales (Werner et al. 2007), la topografía y geomorfología costera, pero también el comportamiento larval individual (Pineda et al. 2007) (Figura 1.3).

Dispersión larval

La dispersión larval describe la distribución de las larvas desde las zonas de desove a las zonas de asentamiento (Pineda et al. 2007). De esta manera, la dispersión larval resulta de la suma de todos los desplazamientos que determinan el transporte larval, y puede visualizarse como la probabilidad de que un cigoto o larva liberado en un lugar particular, llegue a su lugar de asentamiento (Pineda et al. 2007). Ese recorrido se conoce como distancia de dispersión, el transporte larval

es un proceso (o suma de procesos) fundamentales en determinar esa distancia; grandes distancias de dispersión requieren de un transporte larval significativo. Sin embargo, otros procesos y factores que actúan a nivel poblacional, asociados al inicio y final de la fase larval dispersiva, son importantes determinantes de la dispersión larval (Pineda et al. 2007). Entre estos se pueden citar el desove, que depende del número, edad (i.e., talla) y fecundidad de los adultos reproductores, los cuales pueden a su vez estar fuertemente condicionados por la disponibilidad de alimento y la explotación pesquera. También son relevantes los que determinan el éxito del asentamiento, como la sobrevivencia larval o la disponibilidad de sitios para el asentamiento, entre otros (Figura 1.3).

Sumado a las dimensiones espaciales de la producción de huevos, y tanto la disponibilidad como la calidad de hábitats para juveniles y adultos, se deben considerar los procesos inherentes al transporte larval. La dispersión larval necesariamente debe considerar la probabilidad de sobrevivencia (Pineda et al. 2007), normalmente asociadas a variaciones ambientales (e.g., exposición a temperaturas letales; advección que transporta las larvas fuera de los hábitats viables), la disponibilidad de alimento (particularmente en larvas planctotróficas que pueden morir por inanición) y la depredación. Es esperable que las distintas fuentes de mortalidad actúen en mayor o menor medida de acuerdo a la edad o al estadio del desarrollo larval (Metaxas & Saunders 2009), y al tiempo de duración del mismo. La duración del período de desarrollo larval en el plancton (PLD) es variable, dependiendo de la especie y también dependiendo de las condiciones ambientales de temperatura experimentada por las larvas en crecimiento. Por lo general, a mayor duración de la etapa pelágica menor es la sobrevivencia (Cowen and Sponaugle, 2009). En muchas especies la menor sobrevivencia es compensada por una mayor fecundidad (Hedgecock & Pudovkin 2011). La evidencia disponible sugiere tasas de mortalidad larval superiores o alrededor del 90% (Rumrill 1990).

Conectividad larval

La conectividad se define como el intercambio de individuos entre poblaciones geográficamente distantes que conforman una metapoblación (Cowen and Sponaugle, 2009), determinando la persistencia y resiliencia de las poblaciones frente a impactos tales como la contaminación y la sobrepesca, y la diversidad genética (Cowen et al. 2007). Para las especies con escasa movilidad en la fase adulta, como son los invertebrados bentónicos, la conectividad es el resultado de la dispersión larval, la que a su vez está determinada por el transporte larval, por ello cuando hablamos de conectividad en las poblaciones de estas especies hablamos de conectividad larval (Figura 1.3). Así, evaluar la conectividad larval es necesario para entender la dinámica de las metapoblaciones.

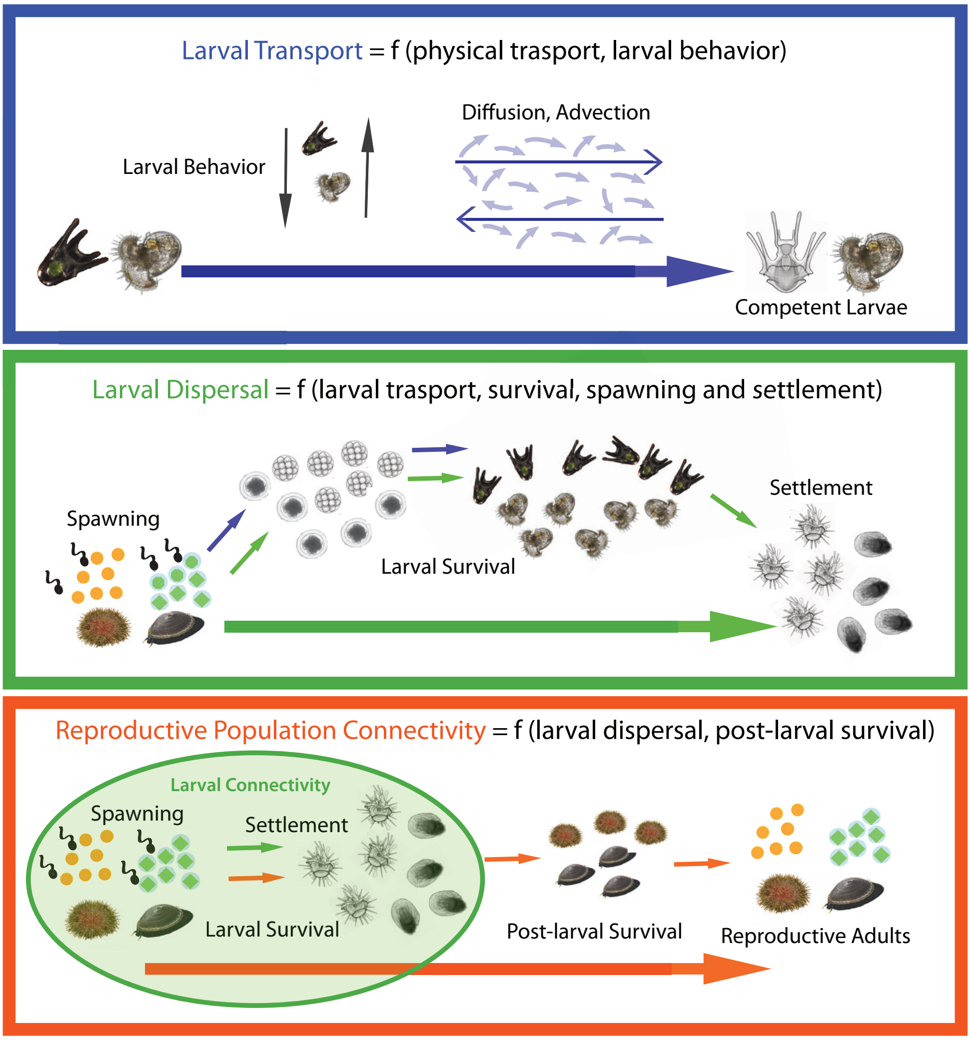


Figura 1.3. Adaptación de Pineda et al. (2007). Esquemas de los conceptos de transporte larval, dispersión larval, y la conectividad larval y poblacional. Cada concepto está representado por flechas de colores: (azul) transporte larval, (verde) dispersión larval y (naranja) conectividad poblacional. El circulo verde indica los procesos incluidos dentro de la conectividad poblacional que intervienen en determinar la conectividad larval que es equivalente a la dispersión larval.

Estimación de la conectividad larval

Existen diversas aproximaciones tanto directas como indirectas para tratar de estimar la conectividad larval (Cowen and Sponaugle, 2009; Munguia-Vega et al., 2014). El estudio de la conectividad mediante métodos directos consiste principalmente en muestreos de campo utilizando trampas de plancton. Mediante estos métodos se ha estimado la retención larval (Paris & Cowen 2004) y la escala demográfica de la conectividad (Lo-Yat et al. 2006). Sin embargo, estos métodos presentan una limitación ya que no permiten evaluar la conectividad en escalas de tiempo amplias, aportando una estimación instantánea de la distribución de las larvas (Leis et al. 2011).

Hasta el momento, pocos estudios empíricos han evaluado el movimiento de las larvas en el océano (Irisson et al. 2015), debido a la dificultad de seguir a los pequeños propágulos altamente diluidos en las masas de agua (ver, sin embargo, Berenshtein et al. 2014, Kough et al. 2014, Leis et al. 2014, 2015, Staaterman et al. 2014, Cresci et al. 2017). Existen otros métodos directos que permiten estimar patrones de conectividad de forma más robusta y en escalas temporales más amplias, como son los métodos basados en la genética y en los marcadores bioquímicos de las estructuras calcificadas (Leis et al. 2011). Uno de los métodos empíricos para estudiar la conectividad consiste en el estudio de marcadores bioquímicos como el bario, el cobre o el magnesio presentes en las estructuras calcificadas de los organismos marinos (ej. otolitos en peces y estatolitos en invertebrados). Estos marcadores proporcionan información del origen de los individuos recolectados para evaluar los patrones de conectividad (Thorrold et al. 2007, López-Duarte et al. 2012). En la costa de Chile, este método ha sido utilizado para evaluar las diferencias regionales en las poblaciones de C. concholepas (Zacherl et al. 2003, Manríquez et al. 2012). Sin embargo, la evaluación de la conectividad a escalas más pequeñas requiere de una mejor comprensión de la variación temporal del entorno químico en la zona de estudio (Manríquez et al. 2012). Los marcadores también pueden ser artificiales, los individuos se marcan mediante la inmersión de huevos en tinta fluorescentes (Jones et al. 2005) o mediante la inyección de hembras reproductoras con isotopos estables de bario, en caso de marcaje de isotopos transgeneracionales (Thorrold et al. 2006). Mediante estas técnicas, estudios realizados en arrecifes de coral han demostrado que las larvas de algunos peces tropicales (ej. Amphiprion polymnus) mayoritariamente reclutan cerca de los hábitats parentales (Jones et al. 1999, 2005, Almany et al. 2007). Sin embargo, la aplicación de estas técnicas en el estudio de la conectividad larval, a pesar de los notables avances, presenta limitaciones tecnológicas ya que las estructuras calcificadas de muchos organismos son insuficientes para las técnicas utilizadas en el análisis de isótopos (Thorrold et al. 2007).

Otro método empírico para evaluar la conectividad es el análisis de parentesco y las pruebas de asignación genética (Leis et al. 2011). El análisis de parentesco permite encontrar padres de un individuo y se ha utilizado para evaluar el auto reclutamiento en larvas de peces (Berumen et al. 2012) y para estudiar los patrones de conectividad larval (Harrison et al. 2012). Alternativamente, se ha propuesto una aproximación para evaluar los flujos de genes para distinguir una población en subpoblaciones discretas y detectar las barreras a la dispersión (Leis et al. 2011). Este método se basa en la varianza de las frecuencias de alelos para diferenciar una subpoblación y la población total estudiada (Weersing & Toonen 2009). Mediantes métodos genéticos se han evidenciado las diferencias en las poblaciones de C. concholepas entre regiones con características topográficas diferenciadas en las costa de Chile (Cárdenas et al. 2009, 2016). Sin embargo, para hacer inferencias sobre la conectividad a partir de datos genéticos se requiere evaluar la variabilidad genética temporal y espacial, ya que no se puede suponer que las poblaciones marinas están en equilibrio para los procesos demográficos y evolutivos (Hedgecock et al. 2007).

También se están utilizando métodos indirectos basados en modelos biofísicos (Werner et al. 2007) es decir, acoplar un modelo hidrodinámico con un modelo basado en individuos (IBMs de las siglas en inglés "Individual Based Models"). Los IBMs permiten incorporar los principales rasgos biológicos que intervienen durante la vida larval planctónica en el estudio de la conectividad. Una clara limitación de los métodos indirectos es la resolución de los modelos hidrodinámicos. Estos modelos están basados en ecuaciones que describen la circulación oceánica, así la resolución espacial y temporal es crucial para resolver los procesos físicos. Solo los modelos hidrodinámicos de alta resolución, del orden de kilómetros, son capaces de resolver los procesos de mesoescala. La resolución de los modelos también depende de la resolución de los datos de la velocidad del viento, la temperatura, la salinidad, las mareas y los aportes de agua dulce, entre otros. Sin embargo, estos modelos presentan la ventaja de permitir evaluar simultáneamente el papel de los diferentes factores que intervienen en la conectividad tanto físicos como biológicos e inferir los patrones de conectividad larval y las escalas temporales y geográficas de estos patrones (Aiken et al., 2007; Cowen and Sponaugle, 2009; Metaxas and Saunders, 2009; Werner et al., 2007).

Los modelos basados en individuos (IBMs)

Los modelos basados en individuos se definen como un modelo de simulación en el que se consideran los individuos como entidades únicas y discretas, las cuales tienen propiedades que cambian durante su ciclo de vida además de la edad (e.g. peso, talla, movilidad, tasa de alimentación, etc.; Grimm and Railsback 2005). Una de las características esenciales de los IBMs es que permiten hacer inferencias poblacionales a partir de simulaciones donde se modelan los individuos. En los IBMs las propiedades de los individuos (comportamiento, tamaño, alimentación, etc.) determinan su sobrevivencia y reproducción. El éxito biológico individual determina cuales de estas propiedades individuales son susceptibles de ser objeto de la selección natural y consiguientemente surgir como propiedades emergentes que forman parte de las características de la población. Este tipo de modelos han sido usados ampliamente en ecología tanto terrestre como marina (Grimm 1999).

Numerosos estudios han utilizado IBMs para estudiar el efecto de factores biológicos sobre la dispersión y los patrones de conectividad de diferentes especies marinas, como por ejemplo el comportamiento de migración vertical (Ayata et al., 2010; Huret et al., 2010; Ospina-Alvarez et al., 2015; Parada et al., 2008), el crecimiento larval (Rochette et al. 2012, Garavelli et al. 2016), la flotabilidad de los huevos y larvas (Mullon et al. 2003, Ospina-Alvarez et al. 2012), la orientación individual de las larvas por medio de sonidos (Wolanski et al. 1997), el comportamiento en la alimentación (Woodson & McManus 2007). Otra aplicación de los IBMs es la evaluación de las escalas espaciales de dispersión y conectividad larval para diseñar redes de áreas marinas protegidas (Treml & Halpin 2012). Otros estudios han usado estos modelos para evaluar el efecto del cambio climático sobre la dispersión y la conectividad (Lett et al. 2010, Aiken et al. 2011). El potencial de estos modelos es mucho más amplio aún, y de importancia para la planificación en manejo y conservación.

La costa central de Chile como modelo de estudio

Patrones de circulación costera

La zona de Chile central es uno de los ecosistemas más productivos del mundo, influenciado por el sistema de la corriente de Humboldt (HCS, de las siglas en inglés “Humboldt Current System”). Este sistema corresponde a una de las principales áreas de afloramiento a nivel mundial, asociada al surgimiento de aguas profundas de la costa del Pacífico sur oriental. La zona costera de este sistema, se caracteriza por la presencia de la Corriente Costera de Chile (CCC), que fluye predominantemente hacia el norte cerca de la costa, forzada por los vientos de componente sur (Strub et al. 1998, Aiken et al. 2008) (Figura 1.4A). La zona de Chile central se caracteriza por presentar varios centros de afloramientos costeros más o menos intensos (Thiel et al. 2007). Los centros de afloramiento costeros están provocados por los vientos de componente sur que provocan el afloramiento o la surgencia de aguas sub-superficiales, más frías y ricas en nutrientes cerca de la costa (Thiel et al. 2007) (Figura 1.5). Sin embargo, este proceso no es continuo a lo largo de la costa, sino que está alterado por la topografía (Strub et al. 1998, Rutllant et al. 2004, Aiken et al. 2008, Tapia et al. 2009). A lo largo de la costa hay centros de afloramiento, intensificados alrededor de cabos y salientes de la costa, donde el agua superficial fluye aguas afuera (Aravena et al. 2014). Asociados a estos centros de surgencia se observan zonas de sombra de surgencia, generalmente asociados a bahías y entrantes de la costa, donde las masas de agua quedan retenidas (Graham & Largier 1997, Aiken et al. 2008). Estos procesos de afloramiento costero están asociados a fenómenos de mesoescala que se observan en la región como los vértices y filamentos que generan una gran heterogeneidad espacial en escalas de pocos kilómetros (Letelier et al. 2009, Aguirre et al. 2012, 2014, Hormazabal et al. 2013). En los centros de afloramiento la circulación de la capa superficial (capa de Ekman), impulsada por los vientos de componente sur, fluye aguas afuera de la costa (Aiken et al. 2007), y por debajo de esta capa, las velocidades de las corrientes se hacen más débiles y el transporte está orientado hacia la costa. Este proceso genera diferencias en la intensidad y dirección de las corrientes en un gradiente vertical. En la región de estudio, el ciclo estacional está muy marcado y el afloramiento costero ocurre predominantemente durante la primavera y verano austral (Narváez et al. 2004, 2006). Sin embargo, los episodios de surgencia no son permanentes en el tiempo, tras episodios de intensificación de la surgencia, que tienen una duración de unos pocos días, se dan episodios de relajación de la surgencia, en la que los frentes de afloramientos transportados aguas afuera durante los episodios de intensificación de este fenómeno se devuelven hacia la costa (Roughgarden et al. 1991), confiriendo a la zona una gran variabilidad temporal en la frecuencia e intensidad de los procesos. Estas características costeras afectan la dinámica de retención y exportación de larvas dentro de áreas geográficas pequeñas. Dentro de Chile central, la región en la que se enmarca este estudio corresponde a la costa central de Chile (desde los 31.50ºS hasta los 36.00ºS y desde los 71.50ºO a los 74.00ºO) (Figura 1.4B).

Características socio-económicas de la región de estudio

La zona de estudio abarca 795 km de costa (regiones: parte de la IV, V, VI y la VII). En esta zona hay un total de 75 Áreas de Manejo de Explotación de Recursos Bentónicos (áreas que asignan derechos territoriales exclusivos de pesca; TURF es la sigla en inglés por Territorial Use Right for Fisheries) operativas (SERNAPESCA 2013) que cubren el 31% de la longitud de costa en la región (ver detalles abajo). El resto de los caladeros de pesca bentónica se denominan áreas de libre acceso donde

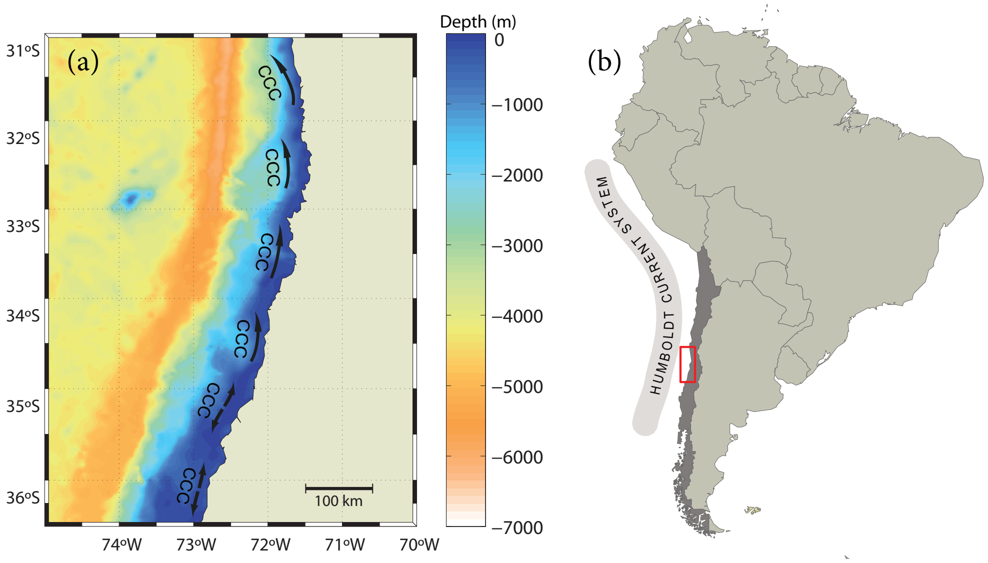


Figura 1.4. Región de estudio y patrones generales de circulación. (a) Patrones de circulación costera, las flechas negras indican la dirección de la Corriente Costera de Chile (CCC). (b) Región de estudio, el recuadro rojo indica el dominio de estudio dentro del ecosistema de la corriente de Humboldt.

además de las medidas regulatorias generales (talla mínima, épocas de veda) se aplica la prohibición de extracción para algunas especies como el loco. En general la fiscalización es pobre, y se permite la pesca recreativa (Godoy et al. 2010). En la región de estudio tan solo hay 4 áreas marinas protegidas que representan menos del 0.001% de la costa. De hecho, es una de las zonas donde coexisten una gran demanda de usos en la costa (turismo, pesca artesanal y recreativa) y por ello hay resistencia al establecimiento de áreas marinas totalmente protegidas (Gelcich et al. 2008).

En los últimos años, los desembarcos en Chile central de los tres recursos bentónicos tradicionalmente explotados más importantes (loco, erizo y lapa) han disminuido, aunque hay variabilidad entre localidades (de Juan et al. 2015). Sin embargo, el desembarco de macroalgas (*Lessonia trabeculata*, *Lessonia nigrescens*) está aumentando en la zona, a pesar de que los precios de este recurso aun son bajos y el volumen de extracción es muy variable entre años (de Juan et al. 2015). Las macroalgas son organismos estructuradores de hábitat y la sobre-explotación de este recurso puede suponer la destrucción del ecosistema (Pérez-Matus et al. 2017) en el que habitan la mayoría de los recursos explotados por el sector

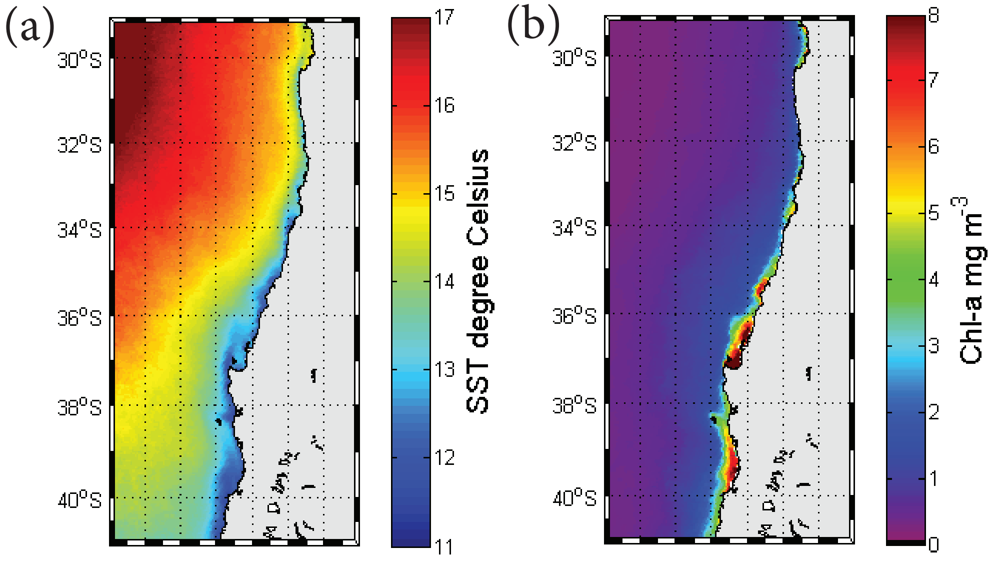


Figura 1.5. Distribución espacial de la temperatura y producción primaria (Clorofila a). (a) Mapa de temperatura interanual acumulada de la superficie del mar durante la noche (18 de Mayo de 2002 - 1 de Marzo de 2015). (b) Mapa de Clorofila-a interanual acumulada (18 de Mayo de 2002 - 1 de Marzo de 2015). Fuente: MODIS-NASA.

pesquero artesanal. La pesca artesanal en Chile es una de las actividades socioeconómicas más antiguas del país (Castilla & Fernandez 1998). Sin embargo, la sustentabilidad de esta actividad está en riesgo por la sobreexplotación de recursos claves (Defeo & Castilla 2005). Para poder preservar de forma sostenible esta actividad es necesario diseñar planes de manejo a gran escala que integren la gestión local del manejo y se coordinen a nivel regional y nacional, para ello es de especial relevancia identificar las áreas críticas para la producción larval y el reclutamiento de las especies costeras.

La pesca artesanal en Chile

Historia de la pesquería de invertebrados bentónicos

La pesca artesanal en Chile opera en más de 100 puertos pesqueros, también llamados “caletas”, y se extiende a 5 millas náuticas (9.3 km) de la costa a lo largo de los más de 4600 km que abarca el país (aproximadamente desde los 18ºS, en la frontera con Perú, hasta los 54ºS en el cabo de Hornos) (Orensanz et al. 2005, González et al. 2006, Gelcich et al. 2010). La pesca artesanal utiliza embarcaciones menores de 18 m de eslora y de 50 toneladas. Las capturas de la pesca artesanal representan un 20% del total de los productos pesqueros exportados en Chile, siendo una de las actividades más productivas, con un gran impacto social y una larga tradición en el país (Gelcich et al. 2005). Es una pesquería multiespecífica que extrae más de 60 especies diferentes de peces e invertebrados, con un gran valor en el mercado tanto interno como externo (Castilla & Fernandez 1998). El volumen de capturas fue de más de 134.000 toneladas el año 2013 (SERNAPESCA 2013), la mayoría se exportan al mercado asiático, Japón y Taiwán (Gelcich et al. 2005). En una franja muy restringida de la zona de operaciones de la pesca artesanal opera la pesquería de invertebrados bentónicos, los cuales son extraídos por mariscadores de orilla y buzos a pulmón libre (apnea), con equipo autónomo (botella) o con manguera (hooka). Los mariscadores de orilla y buzos a pulmón libre, que utilizan las capturas, para consumo propio, en su mayoría, no están oficialmente cuantificados (Durán et al. 1987). Sin embargo, entre los más de 22.000 buzos profesionales, oficialmente registrados, la “hooka” es el tipo de buceo más extendido (Defeo et al. 2016) y es una técnica relativamente extendida entre los pescadores con pequeñas embarcaciones (menores de 10 m, Castilla 2010) (Figura 1.6).

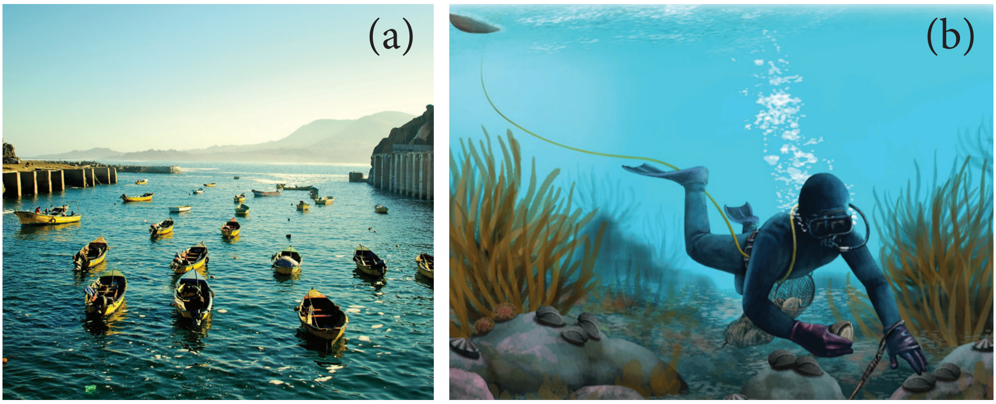


Figura 1.6. Fotografía de la caleta de Chungungo (autora: Cristina Ruano) (a). Dibujo de un buzo recolectando mariscos con hooka (autor: Andrés Julian) (b).

Durante la década de los 70 la demanda del mercado asiático hizo aumentar enormemente las capturas de la flota artesanal, principalmente las de loco (*Concholepas concholepas*), un gasterópodo de la familia Muricidae, endémico de las costas de Chile y Perú (Figura 1.7A). Las capturas aumentaron sustancialmente durante la década de los 80, y para disminuir drásticamente a partir de 1988 evidenciando el colapso de la pesquería (Castilla & Fernandez 1998). El loco es la especie de marisco más apreciada de Chile (González et al. 2006), y el colapso de esta pesquería llevó a una importante crisis económica al sector artesanal. A raíz de esto comenzó una relativa diversificación de la pesca artesanal bentónica (Castilla & Fernández 1998, Orensanz et al. 2005, González et al. 2006), para incluir otras especies de invertebrados, hasta ese momento menos valoradas. Estas contingencias crearon las condiciones necesarias para que al momento de establecerse la Ley General de Pesca y Acuicultura (LGPA, Núm. 18 892) en 1991, se reformara drásticamente la gestión de las pesquerías en Chile y particularmente la de invertebrados bentónicos (Gelcich et al. 2010). La nueva ley LGPA introdujo la herramienta de gestión llamada "Régimen de Extracción Bentónico" para regular la extracción de loco. Esta herramienta establecía una cuota de captura total permitida (CTP) para cada región, dividida en cuotas individuales entre los buzos legalmente registrados (Orensanz et al. 2005). Este nuevo régimen comenzó a implementarse en 1993, y durante el primer año el número de pescadores artesanales se duplicó. Esto tuvo dos consecuencias importantes: se redujeron las ganancias individuales para cada pescador, y no se produjo la recuperación esperada de las poblaciones de loco (Orensanz et al. 2005). Posteriormente (1998) se estableció un nuevo tipo de regulación, también contemplada en la ley LGPA, las Áreas Marinas de Explotación de Recursos Bentónicos (AMERBs, de ahora en adelante TURFs. Las TURFs son zonas costeras geográficamente delimitadas en las que se cede el uso exclusivo a organizaciones de pescadores (sindicatos y cooperativas) en cada territorio o caleta. Para la asignación de las TURFs, los sindicatos legalmente constituidos deben contratar la realización de un Estudio de Situación Base del Área (ESBA) y elaborar un Plan de Manejo y Explotación del Área (PMEA) para el área solicitada, los que son presentados a evaluación del Servicio Nacional de Pesca (SERNAPESCA). El ESBA debe incluir la cartografía de las comunidades bentónicas presentes en el área, además de una estimación de la abundancia de todos los recursos bentónicos objeto de explotación. El PMEA debe incluir un cronograma anual de la previsión de extracción y proponer medidas de manejo adicionales. Las organizaciones de pescadores deben presentar anualmente un informe de seguimiento en el que se incluyen estimaciones de abundancia y biomasa de los recursos explotados, y en base a estos datos se asignan las cuotas anuales de extracción de cada recurso en el área. Las TURFs se asignan por períodos de cuatro años, renovables, si se han cumplido los reglamentos. Para estos estudios (ESBA, PMEA e informes de seguimiento) las organizaciones de pescadores deben contratar consultores certificados por la subsecretaria de pesca. La ejecución de estos estudios está en gran parte subvencionada por el estado a través de agencias y programas de desarrollo. El sistema descrito es un acuerdo de co-gestión en el que las autoridades estatales (SUBPESCA, que forma parte del ministerio de economía y competitividad) negocian la administración de los recursos de las TURFs de forma individualizada con las organizaciones de pescadores de cada territorio o caleta (Orensanz et al. 2005). Las TURFs fueron inicialmente creadas debido al colapso de la pesquería de loco, sin embargo este sistema se ha extendido para la gestión de más de treinta especies bentónicas diferentes (gasterópodos, bivalvos, cefalópodos, crustáceos, equinodermos y algas) independientemente de su historia de vida y valor en los mercados.

Actualmente Chile cuenta con 772 TURFs activas (SERNAPESCA 2013), uno de los sistemas basados en derechos territoriales de uso pesquero más extenso del mundo (Orensanz et al. 2005). Las TURFs suelen estar comprendidas en áreas de menos de 1km de costa, aunque tienen extensiones variables y algunas pueden cubrir varios kilómetros (White & Costello 2011). Una particularidad de las TURFs es que cada sindicato de pescadores está a cargo de su propia TURFs, siendo responsables de la vigilancia y la aplicación de medidas contra la pesca ilegal, ya que solo los pescadores miembros del sindicato pueden extraer recursos en la TURF. En las TURFs, además de las medidas propias del sindicato se deben cumplir con regulaciones nacionales como tallas mínimas legales, vedas reproductivas, etc. En las áreas adyacentes a las TURFs o áreas de libre acceso, se permite el acceso de todos los pescadores de la región, estas áreas están sujetas únicamente a regulaciones específicas de cada recurso (vedas reproductivas y talla mínima). Estudios recientes muestran mayor abundancia y biomasa de organismos en TURFs que en áreas libres, y también individuos de mayor tamaño (Gelcich et al. 2012). Sin embargo, aunque el sistema de TURFs ha permitido gestionar los recursos pesqueros artesanales evitando el colapso local del recurso, cabe destacar que no hay una coordinación de las TURFs a escala comunal ni regional. Dada la naturaleza de los recursos explotados, especies con ciclos de vida complejos (adultos bentónicos y fases larvarias pelágicas), sumado a la elevada heterogeneidad espacial del hábitat, es relevante avanzar hacia un sistema de TURFs integral y coordinado a diferentes escalas geográficas para el manejo y conservación de los recursos bentónicos costeros.

Principales especies explotadas

En Chile, la pesca artesanal de especies bentónicas tiene como objetivo una gran variedad de especies, tanto algas marinas como invertebrados bentónicos (Orensanz et al. 2005). Las especies más importantes son el loco (*Concholepas concholepas*), la lapa (*Fissurella* spp.) y el erizo rojo (*Loxechinus albus*) (Figura 1.7). La pesquería de lapa es una pesquería multiespecífica que incluye 10 de las 13 especies del género *Fissurella* presentes en las costas de Chile (Oliva & Castilla 1992), aunque las más abundantes en la costa central de Chile son: *Fissurella latimarginata*, Fissurella cumingi y Fissurella máxima, siendo *F. latimarginata* la más importante en las capturas de los pescadores artesanales (Oliva & Castilla 1992).

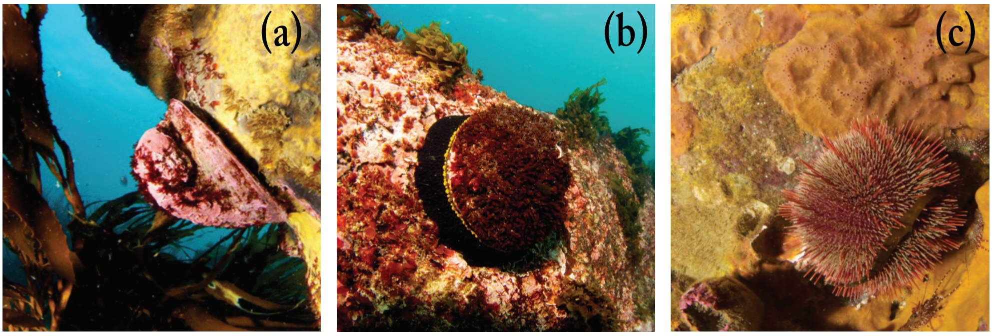


Figura 1.7. Fotografías de las principales especies objetivo del sector pesquero artesanal en Chile, (a) el loco (*Concholepas concholepas*), (b) la lapa (*Fissurella latimarginata*) y (c) el erizo rojo (*Loxechinus albus*).

Hacia una gestión sostenible de las pesquerías artesanales

Las zonas costeras son uno de los ecosistemas que sufren un mayor impacto en el mundo (Halpern et al. 2008). La sobre-explotación de los recursos marinos es una de las actividades humanas que de forma persistente genera un mayor impacto, reduciendo la abundancia y el tamaño de las especies objetivo y causando efectos sobre toda la comunidad (Pauly et al. 1998, Castilla 1999, Myers & Worm 2003). Han sido numerosas las iniciativas conservacionistas para proteger los ecosistemas marinos y los servicios que proveen (Freire & García-Allut 2000, Levin et al. 2009, Afflerbach et al. 2014). Las herramientas son variadas, desde cambios en las regulaciones pesqueras, nuevas estrategias de manejo (e.g., cuotas transferibles, derechos territoriales de uso) así como la creación de áreas marinas protegidas. El beneficio de las áreas marinas protegidas, en sus diferentes formas, se evidencia en la recuperación tanto en abundancia como en tamaño de las especies explotadas tras unos años de cierre de las áreas (Castilla & Durán 1985, Edgar & Barrett 1999, Denny et al. 2004, Shears et al. 2006, Lester et al. 2009). La evidencia también sugiere que los beneficios no solo se dan bajo regímenes de protección total, sino también parcial (Lester & Halpern 2008). Algunos trabajos también señalan los beneficios en las áreas adyacentes, tanto por la exportación de adultos (Goñi et al. 2006) como por la exportación de larvas (Pelc et al. 2009). En este sentido, es relevante evaluar el efecto de las reservas más allá de sus límites para realmente mostrar los beneficios para la pesca.

El establecimiento y éxito de las áreas marinas protegidas con fines pesqueros depende de múltiples factores condicionantes (Gell & Roberts 2002). Por un lado, los factores socio-económicos que condicionan su establecimiento y por el otro el éxito y desempeño que dependen tanto del esfuerzo pesquero en áreas adyacentes como del planeamiento espacial de estas áreas (Halpern & Warner 2003). El establecimiento de áreas marinas totalmente protegidas suele tener una fuerte oposición, principalmente por parte del sector pesquero ya que ve como se reduce el área de pesca. El establecimiento de áreas marinas totalmente protegidas tradicionalmente ha sido impulsado desde las instituciones sin un previo consenso entre las comunidades de usuarios de las áreas (Hilborn et al. 2004, Glaser et al. 2010). Las áreas parcialmente protegidas como es el caso de las TURFs, ofrecen la oportunidad de proteger un área a través del compromiso del sector pesquero. De hecho, el sistema actual de manejo de las pesquerías artesanales de especies bentónicas en Chile, basadas en las TURFs, ha supuesto una mejora en la sostenibilidad del sistema socio-ecológico ya que permite desarrollar dos actividades tradicionalmente antagónicas: la explotación de los recursos marinos y la conservación (Fernández & Castilla 2005, Gelcich et al. 2010). Esto se debe a que las TURFs presentan indicadores biológicos con rendimientos cercanos a los de las áreas totalmente protegidas y superiores a las áreas de libre acceso (Gelcich et al. 2012). Sin embargo, la escala de manejo no está acoplada a la escala de la dinámica de las poblaciones de invertebrados marinos. Actualmente el sistema de manejo de las pesquerías artesanales en Chile, basado en las TURFs, se regula mediante la evaluación de la abundancia de los recursos explotados a nivel local. Estudios recientes señalan la necesidad de coordinar esta gestión a nivel regional, mediante el uso de redes de reservas considerando el actual sistema de TURFs, para acoplar el manejo a la dinámica espacial de las poblaciones explotadas (Gelcich et al. 2005, Tognelli et al. 2009). Uno de los aspectos necesarios para avanzar en este objetivo es tener un conocimiento amplio de todas las fases del ciclo de vida de las especies explotadas. Numerosos estudios en Chile, señalan que la falta de conocimiento sobre las fases planctónicas y el reclutamiento de ciertas especies explotadas por la pesca artesanal, es uno de los principales obstáculos para evaluar el sistema de TURFs (Leiva & Castilla 2002).

Un plan de manejo y conservación basado en una red de reservas (áreas total o parcialmente protegidas) en un paisaje de explotación, debe incluir las áreas de desove (Gell & Roberts 2003). Además, las escalas espaciales de regulación

de los recursos naturales (regulaciones espaciales del esfuerzo pesquero), deben estar acopladas a las escalas espaciales de dispersión y reclutamiento (Botsford et al. 2001, Pelc et al. 2010, White & Costello 2011) para poder contribuir a la persistencia de la población (Kaplan et al. 2006, 2009, Botsford et al. 2009). Una red diseñada considerando la conectividad podría potenciar los beneficios para la conservación, aumentando la resiliencia de las poblaciones frente a impactos emergentes (cambio climático, contaminación, etc.) y contribuir a la sustentabilidad de los servicios ecosistémicos (Cowen et al. 2007, Lowerre-barbieri et al. 2016). Tradicionalmente, los planes de manejo y conservación para las especies objetivo de la pesca están principalmente basados en la abundancia de adultos, y aunque implícitamente consideran la importancia del reclutamiento, explícitamente no se incluyen los patrones espaciales de reclutamiento (Szuwalski et al. 2015). Los procesos que afectan la dinámica de desove y asentamiento de las poblaciones marinas, tales como la fecundidad de los adultos, las áreas con mayor importancia relativa en la producción de larvas, y la dispersión de las larvas están aún poco evaluados. En este sentido, es necesario avanzar hacia la consideración explícita de la interacción de los procesos que operan durante la fase larvaria acoplados con los patrones de distribución y reproducción de adultos (Fernández et al. 2017). Chile ofrece ventajas para avanzar hacia planes de gestión exitosos y sostenibles, debido a la clara heterogeneidad espacial en la distribución de adultos, asociada a áreas protegidas (parciales o totales).

Distribución de las capturas de lapa y erizo

Los datos históricos de desembarcos de erizos se remontan a los años 30. Hasta 1976 las capturas nacionales no sobrepasaron las 5000 toneladas y a partir de 1977, a raíz del incremento de las exportaciones durante esa década, los desembarques del recurso erizo se incrementaron a razón de 2000 toneladas por año, llegando a un máximo histórico en 1999. La pesquería de erizo se extiende a lo largo de todo el litoral de Chile, existiendo dos focos principales, uno en la zona norte, de la Iª a la IIIª región, y otro al sur de la Xª a la XIIª región. Un total de 244 áreas de manejo registradas tienen el recurso erizo como objetivo (SERNAPESCA 2013). En la zona de estudio los mayores desembarcos de erizo se dan en la Vª región (Figura 1.8). Como medidas administrativas para regular la pesquería de erizo se aplica la talla mínima legal de extracción, que en el ámbito nacional es de 70 mm.

de diámetro con espinas, vigente desde 1987 y un período de veda anual, aplicado de la Iª a la XIª región, del 15 de octubre al 15 de enero.

La pesquería de lapa es multiespecífica, la cual tiene como objetivo 10 de las 13 especies del género Fissurella descritas para las costas de Chile. Los datos de desembarques de esta pesquería no distinguen entre las diferentes especies, aunque en la costa central *F. latimarginata* es una de las especies más importantes en volumen de capturas. Para el recurso lapa, entre 1978 y 1983 las capturas no sobrepasaron las 300 toneladas a partir de 1984 los volúmenes de pesca alcanzaron las 1000 toneladas, llegando a 3000 toneladas en 1985. El factor fundamental del incremento de la actividad de esta pesquería, en términos de desembarques, fue motivado por las normas pesqueras a las cuales se sometió el recurso loco, prohibiendo su captura en áreas de libre acceso. Entre 1986 y 2001 los desembarques se mantuvieron estables en un rango de 2159 y 4142 toneladas, a excepción del año 1993 donde la extracción alcanzó las 6034 toneladas debido a la alta demanda del mercado exterior, principalmente asiático. La pesquería de lapa se extiende por todo el litoral Chileno, pero es más intensa entre las regiones I y V, regiones de las que se obtiene más del 60% de las capturas nacionales (Olguín & Jerez 2003). Por otro lado, un total de 119 áreas de manejo tienen inscrito el recurso lapa como recurso objetivo, principalmente en la IVª y Vª región (SERNAPESCA 2013) (Figura 1.8). Como medidas administrativas para regular la pesquería de lapa se aplica la talla mínima legal de extracción, que para *F. latimarginata* es de 65 mm de longitud de concha.

Rasgos biológicos de las especies modelo de estudio: la lapa ojo de cerradura (*Fissurella latimarginata*) y el erizo rojo (*Loxechinus albus*)

Hábitat de los adultos reproductores y patrones de desove

El erizo rojo (*L. albus*) se distribuye a lo largo del litoral de Perú y Chile, desde los 6ºS hasta los 55ºS (Larraín 1975). Su distribución batimétrica va de los 0 m a los 340 m (Larraín 1975), aunque mayoritariamente se encuentra por encima de los 30 m (Moreno et al. 2011). En el litoral de Chile central (IVª a la VIIIª región), el erizo rojo tiene una distribución restringida a zonas poco profundas, muy expuestas y con elevado hidrodinamismo (Thiel, Macaya, &

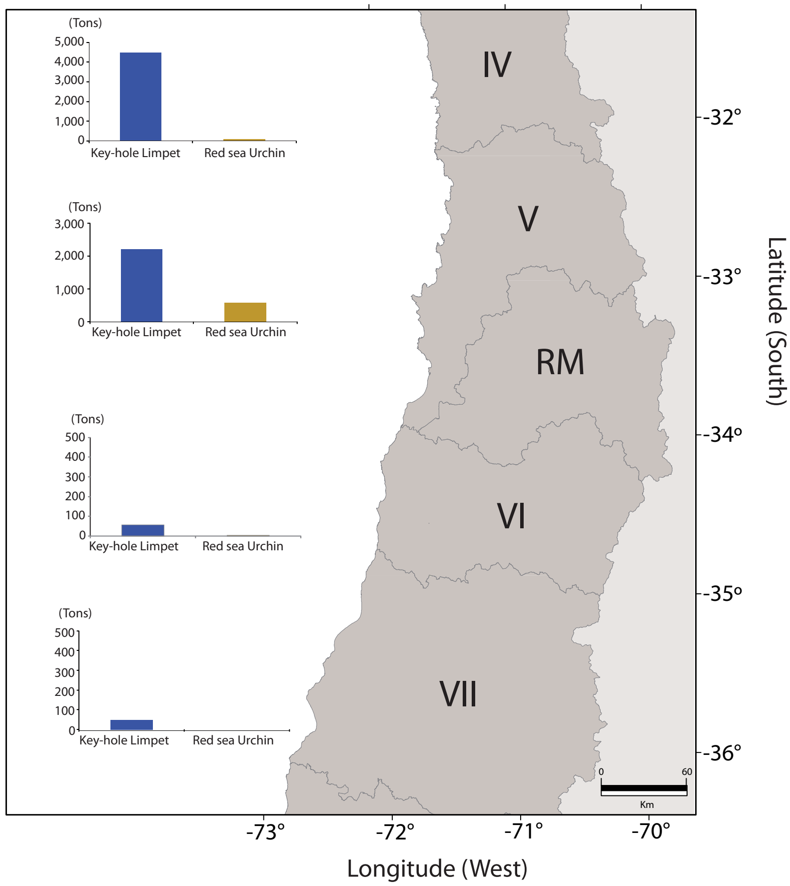


Figura 1.8. Distribución de las capturas. Desembarques acumulados de 1999 a 2013 para el erizo rojo (*Loxechinus albus*) y el complejo lapa (recurso pesquero compuesto por 10 especies diferentes) en la zona de estudio. Los datos corresponden a los registros oficiales de los desembarques anuales en toneladas (datos procedentes de áreas de manejo y áreas de libre acceso).

Acuna 2007). Es una especie que habita como epifauna en fondos duros, sobre sustrato rocoso cercano a praderas de macroalgas (Dayton 1985). Tiene un comportamiento gregario y forma grupos desde pocos individuos a millares. Se alimenta de frondas de algas flotantes (*Lessonia trabeculata*, *Lessonia nigrescens*) o ramonea sobre el sustrato (Contreras & Castilla 1987). La época de desove es variable según la latitud, en Chile central tiene lugar durante los meses de primavera (Guisado & Castilla 1987, Zamora & Stotz 1992, Guisado et al. 1998).

La lapa (*F. latimarginata*) se distribuye desde el litoral de Perú (10ºS) hasta Chile central (37ºS)(Oliva & Castilla 1992). Es un molusco herbívoro que habita en fondos duros, asociados generalmente a cinturones de algas (*Gelidium sp.*, *Lessonia trabeculata* y *Ulva sp.*), en el submareal somero (Olguín & Jerez 2003). Para *F. latimarginata* se han observado dos períodos de maduración gonadal, aunque el período en el que se observó mayor número de individuos maduros fue durante los meses de primavera (Brown et al., 1997).

Desarrollo larval, comportamiento y asentamiento

El erizo rojo (*L. albus*) es una especie dioica con fecundación externa, sus gametos son liberados a la columna de agua donde tiene lugar la fecundación. Las hembras liberan millones de ovocitos a la columna de agua, que en condiciones de laboratorio muestran un elevado porcentaje de fecundación (Arrau 1958). Los ovocitos de *L. albus* miden en promedio 120 um (observación personal). Los embriones se desarrollan en la columna de agua, pasadas 24 horas de la fecundación se inicia la fase de gastrulación. Pasados 3 días desde la fecundación, la larva equinopluteus ya está totalmente formada y empieza a alimentarse (Arrau 1958). En condiciones de laboratorio, se ha observado que a partir del tercer día la larva equinopluteus es capaz de desplazarse verticalmente (observación personal). La larva se desarrolla en el plancton alimentándose activamente, pasando por los estadios de 2, 4 y 8 brazos (Arrau 1958) (Figura 1.9A). Aunque hay pocos estudios que han evaluado la distribución vertical de las larvas de *L. albus*, un estudio desarrollado en el sur de Chile determinó un mayor número de larvas de *L. albus* en superficie durante la noche (Molinet et al., 2010), estos resultados podrían indicar que las larvas de *L. albus* tienen la capacidad de migrar verticalmente. El tiempo de desarrollo en el plancton puede variar según la temperatura a la que se desarrollan las larvas, oscilando entre 15 y más de 25 días (observación personal). Cuando la larva alcanza el estadio de larva competente, reabsorbe parte de los brazos y reduce su tamaño (Arrau 1958). La larva competente puede permanecer en el plancton durante varios días, desplazándose mediante movimiento ciliar hasta encontrar un hábitat de asentamiento adecuado (Bustos et al., 1992). En condiciones de laboratorio las larvas de *L. albus* se asientan sobre sustrato duro recubiertos de un biofilm de diatomeas bentónicas (observación personal).

La lapa *F. latimarginata* también es una especie dioica, que libera sus gametos a la columna de agua donde tiene lugar la fecundación. A diferencia de *L. albus*, *F. latimarginata* presenta ovocitos de mayor tamaño (>320 um, observación

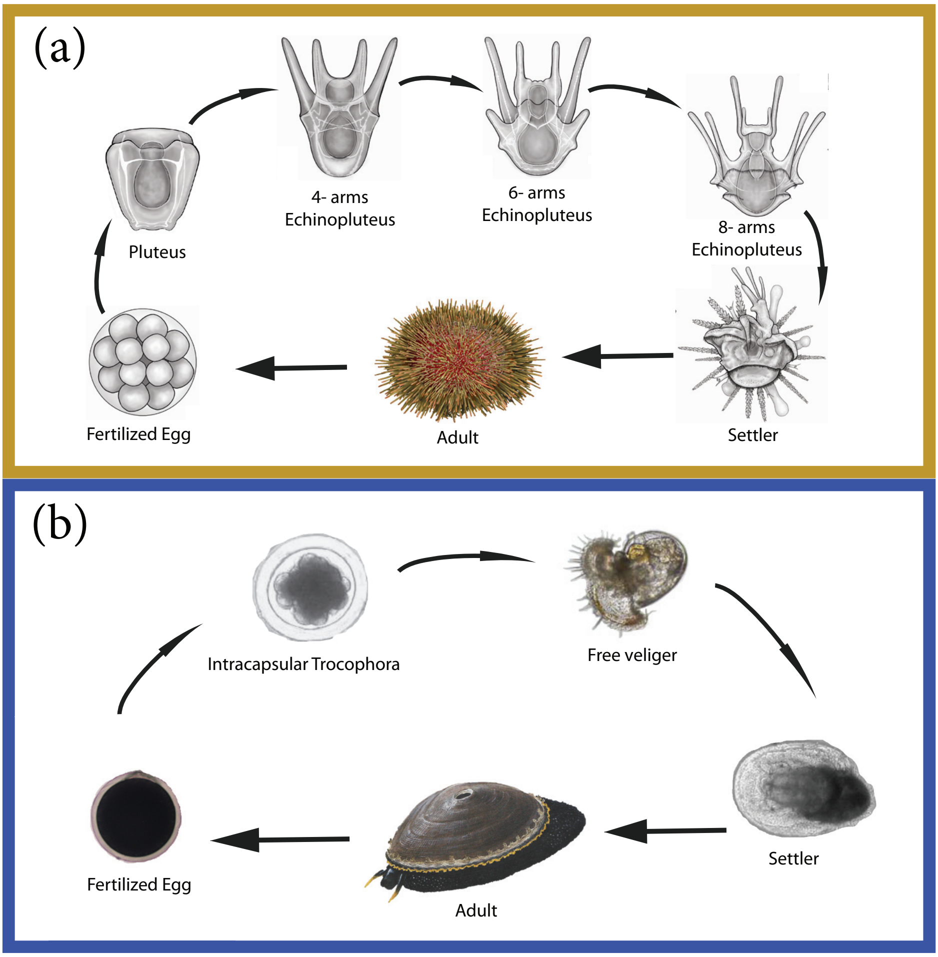


Figura 1.9. Desarrollo larval de las especies modelo de estudio, (a) el erizo rojo, *Loxechinus albus* y (b) la lapa *Fissurella latimarginata*.

personal). En condiciones de laboratorio se ha observado un elevado porcentaje de poliespermia (Chavez 2004). Hay muy pocos estudios que muestren el desarrollo larval de *F. latimarginata* (Chavez 2004), aunque si se ha reportado el desarrollo larval de otras especies del género Fissurella (Pérez et al. 2007, Reynoso-Granados et al. 2007). Las lapas del género *Fissurella* presentan larvas lecitotróficas con un desarrollo planctónico que oscila entre los 5 y los 10 días (Chavez 2004, Pérez et al. 2007, Reynoso-Granados et al. 2007) (Figura 1.9B). Los primeros estadios de desarrollo suceden dentro de la membrana del huevo (Pérez et al. 2007, Reynoso-Granados et al. 2007). Pasadas 12 horas desde la fecundación aparece una larva trocófora intracapsular que muestra movimientos rotatorios dentro del huevo. Tras 3 días de la fecundación la membrana del huevo se abre y eclosiona una larva velígera que nada activamente (Reynoso-Granados et al. 2007). En *F. latimarginata*, tras 5 días de desarrollo planctónico la larva se fija en el sustrato (Chavez 2004). En algunas especies del género Fissurella se ha observado que las larvas recién asentadas aun presentan restos del vitelo (Pérez et al. 2007).

Objetivos

Objetivos

La escala espacial en la que actúan las medidas de gestión y conservación deben estar acopladas a las características del ciclo de vida de la mayoría de las especies objetivo de una pesquería. Actualmente, en el caso de la pesquería artesanal bentónica de la costa central de Chile las estrategias de manejo y conservación de estos recursos están basadas en cuotas de extracción, aplicadas en las áreas parcialmente protegidas (TURFs) y medidas regulatorias de carácter general, aplicadas en todas las áreas, como la talla mínima legal y períodos de vedas reproductivas. Recientemente, se ha propuesto considerar en la elaboración de planes de gestión y conservación de los recursos pesqueros otros servicios ecosistémicos que provee el sistema existente de TURFs, como la conservación de la biodiversidad, y se ha sugerido que las TURFs sean consideradas como elementos clave en una futura red de reservas a lo largo de la costa de Chile, principalmente en aquellas regiones donde el establecimiento de áreas totalmente protegidas es especialmente complejo debido a la intensidad de usos costeros, como es la costa central de Chile. Sin embargo, para poder desarrollar una red exitosa es necesario identificar los procesos y factores que operan durante la fase larvaria de las especies que allí habitan, así como aquellos que condicionan la distribución y abundancia de los adultos reproductores, y las consecuencias en el aporte de estas al potencial reproductivo regional.

En la costa central de Chile existe un extenso mosaico de TURFs y áreas de libre acceso que determinan una enorme heterogeneidad espacial en el régimen de explotación pesquera, con consecuencias en la distribución y abundancia de los adultos reproductores, y por supuesto en la dinámica de las poblaciones explotadas. Además, esta región presenta una gran variabilidad temporal y espacial en la frecuencia e intensidad de los procesos oceanográficos, determinando la dinámica de retención y exportación de larvas en la costa. Esta enorme complejidad supone un reto para el manejo de los recursos explotados, y pone en relieve los vacíos de conocimiento que limitan el desarrollo de una red de reservas efectiva en la región. Estos vacíos son principalmente a) la escasez de información biológica de las especies y b) la falta de información sobre las áreas prioritarias para la conservación. Esta información es relevante para entender la conectividad entre subpoblaciones y, particularmente, su resiliencia ante los escenarios actuales de cambio global (e.g., circulación oceánica, pérdida de biodiversidad, sobrepesca) y regional (e.g., aumento en la extracción de especies proveedoras de hábitat como las macroalgas).

El objetivo general de este estudio es identificar la eficiencia de distintas secciones a lo largo de la costa de Chile central para la producción, exportación y asentamiento de larvas de organismos marinos con ciclos de vida complejo (el erizo rojo *L. albus* y la lapa *F. latimarginata*), de acuerdo a la influencia ejercida por los cambios en los patrones de abundancia y distribución de adultos reproductores sometidos a un mosaico de medidas de conservación variable; la inversión reproductiva; la historia de vida temprana; la duración de la vida larval dependiente de la temperatura y la dispersión larval mediada por las corrientes oceánicas e influenciada por los comportamientos larvales. La aplicabilidad de este estudio es aportar información relevante de la ecología de las especies objetivo para acoplar a las existentes estrategias de conservación y gestión de los recursos pesqueros bentónicos de la costa central de Chile.

Objetivos abordados en cada capítulo

Con tal fin, se han planteado una serie de objetivos específicos, que se abordan a lo largo de los tres capítulos de esta tesis doctoral.

Los objetivos del capítulo 1:

1. Determinar el efecto de la protección sobre la condición individual (medida a partir del peso seco del cuerpo) y la inversión reproductiva individual (usando como indicador el índice gonadosomático GSI) en *F. latimarginata* y *L. albus*.

2. Analizar la influencia del afloramiento costero sobre la condición e inversión reproductiva individual en las dos especies modelo de estudio.

3. Evaluar el efecto de la relación entre la protección y la localidad sobre la talla de los adultos reproductores en las dos especies modelo de estudio.

Los objetivos del capítulo 2:

1. Determinar en qué medida la protección afecta la densidad, talla y fecundidad de los individuos y la producción potencial de huevos en *F. latimarginata* y *L. albus*.

2. Desarrollar un modelo de producción potencial de huevos a lo largo de la costa central de Chile para las dos especies modelo de estudio.

3. Evaluar el efecto de la relación entre la densidad y la talla de los adultos reproductores sobre la producción potencial de huevos en las dos especies modelo de estudio.

4. Explorar cómo el efecto del escenario actual de distribución y extensión de áreas de manejo a lo largo de Chile central, influye en la producción potencial de huevos.

Los objetivos del capítulo 3:

1. Explorar y determinar el efecto de las condiciones iniciales de desove (localización geográfica, fecha y profundidad) sobre la distancia de dispersión y el éxito de reclutamiento de *F. latimarginata* y *L. albus*.

2. Determinar el efecto del comportamiento de migración vertical sobre la distancia de dispersión; el éxito en el autoreclutamiento, la retención local y el reclutamiento alóctono; y la conectividad larval de *F. latimarginata* y *L. albus*.

3. Evaluar el efecto de la relación entre la temperatura del océano y el tiempo de desarrollo de las larvas de las especies modelo de estudio sobre la distancia de dispersión, el éxito de reclutamiento y la conectividad larval.

4. Determinar si las características demográficas (variabilidad en la producción de huevos y hábitat disponible) de los sitios a lo largo de la costa, afectan el reclutamiento y la matriz de conectividad larval.

Estructura de la tesis

Este trabajo de tesis doctoral se estructura en tres partes. En la primera parte, se presenta una introducción general donde se exponen las principales fases del ciclo de vida de los invertebrados bentónicos, se definen términos claves en la tesis, como conectividad, transporte y dispersión larval y se presentan los principios en los que se basan los modelos basados en individuos (IBMs) utilizados en este trabajo. Además, se explica la historia de la pesca artesanal en Chile y los principales retos que enfrenta el actual sistema de gestión, y se presenta la costa central de Chile como modelo de estudio, definiendo sus principales características oceanográficas y socioeconómicas. A continuación, se explican los rasgos biológicos (hábitat, desarrollo larval y distribución de las capturas) de las dos especies de invertebrados bentónicos modelo de estudio, la lapa (*F. latimarginata*) y el erizo rojo (*L. albus*). Se finaliza esta primera parte definiendo el objetivo general de este estudio y los objetivos específicos abordados en cada capítulo.

En la segunda parte, se presentan los artículos de investigación publicados y sometidos a publicación. Esta parte cuenta con tres capítulos. En el primer capítulo (Artículo 1) se exploran los efectos de la protección y el afloramiento costero sobre la inversión reproductiva individual de los adultos reproductores de ambas especies modelo de estudio, la lapa (*F. latimarginata*) y el erizo rojo (*L. albus*). Se explican los resultados de un estudio de campo realizado en cinco localidades de la costa central de Chile, en el cual se escogieron localidades con niveles contrastantes de influencia del afloramiento costero y distinto nivel de protección (TURFs, AMP no-take y ALAs). Finalmente se discuten los resultados de este trabajo contextualizando sus implicaciones para la selección de sitios prioritarios para la conservación.

El segundo capítulo (Articulo 2) se centra en la fase adulta de las dos especies modelo de estudio (*F. latimarginata* y *L. albus*), aplicando una metodología para estimar la producción potencial de huevos a lo largo de la costa central de Chile. El modelo de predicción espacial desarrollado está basado en el análisis comparativo de los datos de densidad, talla y fecundidad obtenidos en áreas con distinto régimen de explotación pesquera (solo se analizan TURFs y ALAs en este caso). Las predicciones del modelo se sustentan en los datos obtenidos en un estudio de campo realizado en ocho áreas dentro de la región de estudio y en el análisis de la distribución de hábitats adecuados para la reproducción de ambas especies y el nivel de protección. A partir de estos datos se genera una predicción de los patrones espaciales de producción potencial de huevos, con la finalidad de identificar las latitudes más relevantes para la reproducción de ambas especies. Se discute como las áreas parcialmente protegidas, como las TURFs, pueden aumentar la producción de propágulos de especies explotadas para así repoblar las áreas de libre acceso (ALA).

En el tercer capítulo (Artículo 3) se da más énfasis a las fases tempranas de la vida de estas especies con ciclos complejos, evaluando los efectos del comportamiento de migración vertical y el tiempo de desarrollo dependiente de la temperatura de las larvas mientras son transportadas por las corrientes oceánicas sobre la distancia de dispersión, el éxito de reclutamiento y la conectividad larval de *F. latimarginata* y *L. albus* en la costa central de Chile. Se obtiene una ecuación que describe el tiempo de desarrollo termo-dependiente para ambas especies en base a experimentos de laboratorio. Se programa un modelo simple de migración vertical basado en la salida y puesta del sol. La ecuación que describe el tiempo de desarrollo termo-dependiente y el modelo de migración vertical se acoplan como submodelos en un SEIBM. Se discute como las condiciones iniciales de desove (localización geográfica, fecha y profundidad) y los rasgos larvales estudiados, modifican los procesos de dispersión, retención y su influencia en los niveles y localización del reclutamiento. En base a la integración de los resultados obtenidos en el segundo capítulo (Artículo 2) se evalúa la conectividad realizada en la región y se identifican áreas relevantes para la llegada y salida de larvas. A partir de los resultados obtenidos en este capítulo se proponen áreas prioritarias para la conservación de la lapa y el erizo rojo.

La tercera parte, es una síntesis de los artículos sometidos a publicación (capítulos 1, 2 y 3) e incluye una discusión general de los resultados obtenidos, además se describen las principales implicaciones para el manejo de los recursos bentónicos en Chile central que se pueden extraer de estos estudios. También se comentan las principales limitaciones de la presente disertación de tesis y las recomendaciones para futuras investigaciones. Finalmente se señalan de forma esquemática las principales conclusiones obtenidas durante la realización de esta tesis doctoral.

En los anexos se presentan los resúmenes en castellano de los artículos 1, 2 y 3, escritos en inglés, así como los artículos publicados correspondientes a los capítulos 1 y 2 en su formato original y las figuras anexas del capítulo 3.

Informe de los directores

Informe de los directores

La doctoranda Marta Blanco Sánchez presenta la tesis doctoral titulada "Historia de vida temprana e inversión reproductiva de invertebrados bentónicos: integración al manejo y conservación a través de modelos de dispersión/ Early life history and reproductive investment of benthic invertebrates: integration to management and conservation through dispersal models".

La directora Miriam Fernández Bergia y el co-director Andrés Ospina Álvarez informan que la tesis está compuesta de tres trabajos en formato artículo. Dos de los trabajos (artículo 1 y 2) ya han sido publicados en revistas científicas internacionales incluidas en el Science Citation Index (SCI), el tercero ha sido aceptado con comentarios menores. A continuación se detalla la contribución que ha realizado la doctoranda en cada uno de los artículos, así como el factor de impacto (según Thomas Institute for Scientific Information) de las revistas.

Artículo 1

FERNANDEZ, M., BLANCO, M., RUANO-CHAMORRO, C., SUBIDA, M.D., 2017. REPRODUCTIVE OUTPUT OF TWO BENTHIC RESOURCES (*FISSURELLA LATIMARGINATA* AND *LOXECHINUS ALBUS*) UNDER DIFFERENT MANAGEMENT REGIMES ALONG THE COAST OF CENTRAL CHILE. LATIN AMERICAN JOURNAL OF AQUATIC RESEARCH, 45(2), 391-402.

Autores: Fernandez, M., Blanco, M., Ruano-Chamorro, C., Subida, M.D.

Revista: Latin American Journal of Aquatic Research (LAJAR). 2017

Factor de Impacto: 0.59

La doctoranda ha contribuido en el muestreo de campo, el procesado de las muestras en el laboratorio, el análisis de los datos y redacción del apartado de métodos del manuscrito final.

Artículo 2

BLANCO, M., OSPINA-ALVAREZ, A., GONZÁLEZ, C., FERNANDEZ, M., 2017. EGG PRODUCTION PATTERNS OF TWO INVERTEBRATE SPECIES IN ROCKY SUBTIDAL AREAS UNDER DIFFERENT FISHING REGIMES ALONG THE COAST OF CENTRAL CHILE. PLOS ONE, 12 (5), e0176758.

Autores: Blanco, M., Ospina-Álvarez, A., González, C., & Fernández, M.

Revista: PloS one

Factor de Impacto: 3.54

La doctoranda ha contribuido realizando todo el muestreo de campo y el procesado de las muestras en el laboratorio. Contribuyó además en el trabajo de modelación, análisis y tratamiento de los datos. Fue la principal contribuyente en la redacción del manuscrito.

Artículo 3

BLANCO, M., OSPINA-ALVAREZ, A., AIKEN, C.M., NAVARRETE, S.A., FERNANDEZ, M. (SUBMITTED). INFLUENCE OF LARVAL TRAITS ON DISPERSAL AND CONNECTIVITY PATTERNS OF TWO EXPLOITED MARINE INVERTEBRATES IN CENTRAL CHILE.

Autores: Blanco, M., Ospina-Álvarez, A., Aiken, C.M., Navarrete, S.A., Fernández, M.

Revista: Marine Ecology Progress Series (MEPS)

Factor de Impacto: 2.29

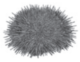
La doctoranda ha jugado un rol fundamental en la modelación y diseño experimental, siendo responsable del montaje y seguimiento de los experimentos de laboratorio, análisis y tratamiento de los datos y redacción del manuscrito.

Los coautores principales de los artículos que componen esta tesis no han utilizado implícitamente o explícitamente ninguno de estos trabajos para la elaboración de otras tesis doctorales.

Firmado:

Dra. Miriam Fernández Bergia
Directora de la Tesis

Dr. Andrés Ospina Álvarez
Co-Director de la Tesis



Part II
Chapters and Publications

Chapter 1

Reproductive output of two benthic resources (*Fissurella latimarginata* and *Loxechinus albus*) under different management regimes along the coast of central Chile

Chapter 1

Lat. Am. J. Aquat. Res., 45(2): 391-402, 2017
DOI: 10.3856/vol45-issue2-fulltext-14

Research Article

Reproductive output of two benthic resources (*Fissurella latimarginata* and *Loxechinus albus*) under different management regimes along the coast of central Chile

Miriam Fernández[1], Marta Blanco[1], Cristina Ruano-Chamorro[1] & Maria Dulce Subida[1]
[1]Núcleo Milenio Centro de Conservación Marina, Estación Costera de Investigaciones Marinas
Departamento de Ecología, Facultad de Ciencias Biológicas
Pontificia Universidad Católica de Chile, Santiago, Chile
Corresponding author: Miriam Fernandez (mfernandez@bio.puc.cl)

ABSTRACT. The biological and ecological benefits of fully and partially marine protected areas are well documented. However, the benefits reaching areas beyond the limits of the reserves are still emerging in spite the fact that they are essential for fishing grounds recovery and to gain support for the protection of the ocean among stakeholders. We analyzed the influence of protection on gonadosomatic index, and also body dry weight, of two economically and ecologically important species: the keyhole limpet, *Fissurella latimarginata* and the red sea urchin, *Loxechinus albus*, in order to determine the value of protected areas in directly enhancing reproduction, and therefore potential seeding on exploited areas. We compared two levels of protection in central Chile, determined by fisheries management regimes (in turn associated to fishing pressure): a) areas with fishing restrictions (low or none fishing effort; territorial use rights for fisheries and no-take areas) and b) open access areas (high exploitation rates). We also evaluated the independent influence of upwelling on both variables. Our results show for both species that a) body dry weight is not affected by management regime, b) management regime did not show a consistent impact on gonadosomatic index and c) upwelling did not affect the response variables. Our findings help disentangling the main factors determining reproductive patterns under contrasting human impact scenarios, suggesting that the selection of sites for establishing marine protected areas seems to be less relevant than efficient control of fishing effort and minimum legal size to assure natural seeding.

Keywords: *Fissurella latimarginata*, *Loxechinus albus***,** seeding, reproduction, marine protected areas, TURF, conservation, management, upwelling.

Abstract

The biological and ecological benefits of fully and partially marine protected areas are well documented. However, the benefits reaching areas beyond the limits of the reserves are still emerging in spite the fact that they are essential for fishing grounds recovery and to gain support for the protection of the ocean among stakeholders. We analyzed the influence of protection on gonadosomatic index, and also body dry weight, of two economically and ecologically important species: the keyhole limpet, *Fissurella latimarginata* and the red sea urchin, *Loxechinus albus*, in order to determine the value of protected areas in directly enhancing reproduction, and therefore potential seeding on exploited areas. We compared two levels of protection in central Chile, determined by fisheries management regimes (in turn associated to fishing pressure): (a) areas with fishing restrictions (low or none fishing effort; territorial use rights for fisheries and no-take areas) and (b) open access areas (high exploitation rates). We also evaluated the independent influence of upwelling on both variables. Our results show for both species that (a) body dry weight is not affected by management regime, (b) management regime did not show a consistent impact on gonadosomatic index, and (c) upwelling did not affect the response variables. Our findings help disentangling the main factors determining reproductive patterns under contrasting human impact scenarios, suggesting that the selection of sites for establishing marine protected areas seems to be less relevant than efficient control of fishing effort and minimum legal size to assure natural seeding.

Keywords

Seeding, reproduction, marine protected areas, TURFs, conservation, management, upwelling.

Introduction

Marine protected areas (MPA) have increased worldwide in response to increasing human impacts on the ocean (Halpern et al. 2008). The benefits of MPA, particularly for fished areas, have been widely reported (Roberts et al. 2001, Halpern 2003, Lester et al. 2009). Most of the evidence focused on the benefits of protection inside the boundaries of protected areas, measured on a set of biological variables such as species richness as well as abundance, biomass, and/or adult size of exploited species (Jennings et al. 1996, Roberts et al. 2001, Halpern 2003, Shears et al. 2006, Lester et al. 2009). It is clear that fully protected areas confer more benefits than partially protected areas on most of these biological variables (Lester & Halpern 2008, Gelcich et al. 2012). However, it is also evident that establishing fully protected areas generates social resistance (West et al. 2006). Thus, there is a compromise between reaching higher benefits fully protecting smaller fractions of the ocean and achieving lower enhancement but partially protecting larger proportions of the world ocean. Territorial Use Rights for Fisheries (TURF), implemented for management purposes, can also provide ancillary benefits for marine conservation as partially protected areas, over large fractions of the ocean (Gelcich et al. 2012).

The performance of fully and partially MPAs beyond the limits of the reserve is essential for fishing grounds recovery and to gain support among stakeholders (Roberts et al. 2001, Gell & Roberts 2002, Halpern & Warner 2003, Russ et al. 2004, Sale et al. 2005). Spillover of exploitable adult biomass from no-take reserves clearly benefits local fisheries outside the boundaries of protected areas (Roberts et al. 2001, Goñi et al. 2006). The benefits may reach even larger distances through the export of dispersive propagules, which seem to be enhanced inside protected areas. The enhancement in egg and larval production has been associated to higher reproductive potential inside both fully protected areas due to the combined effect of increased adult size and higher density of exploited species (Rogers-Bennett et al. 2002, Gell & Roberts 2003, Willis et al. 2003, Pelc et al. 2009). Empirical evidence shows increases in reproductive potential (egg or gonad production) ranging between 2 and 18 fold in protected areas with respect to fished areas (Rogers-Bennett et al. 2002, Willis et al. 2003, Pelc et al. 2009). The benefits of partially protected areas could be lower than fully protected areas, as the increase in size and density, two critical variables affecting egg production, is higher in no-take areas than in partially protected areas (Lester et al. 2009, Gelcich et al. 2012). All the analyses, however, have focused on the indirect consequences of enhanced size and density, while the direct influence of protection on reproductive investment has rarely been assessed (Kaiser et al. 2007).

Direct influence of protection on seeding is expected to be positive if sites selected for conservation or TURFs are particularly productive (an attribute often dominant in the selection of areas for TURFs). In fact, the 20 to 25% increases in gonad weight observed in the scallop Pecten maximus between protected and open access areas suggest that protection can directly affect reproductive investment (Kaiser et al. 2007). However, negative effects can also be expected under density-dependent feeding, or parasitism scenarios (Loot et al. 2005, Wood et al. 2013). For instance, infection rates of several invertebrate species, including the keyhole limpet Fissurella crassa, are significantly higher in marine protected areas (Loot et al. 2005, Wood et al. 2013). However, the higher abundance of parasites infecting the gonads of Fissurella spp. in partially protected areas (TURFs) seem to enhance the gonadosomatic index in TURFs, suggesting a potential positive direct effect of fishing restriction on the reproductive success of keyhole limpets (Aldana et al. 2014). Further evidence on the direct influence of protection on reproductive output are needed to better understand the role of fully and partially protected areas on seeding beyond the boundaries of protection, the influence of site selection for conservation and management, and the relevance of individual reproductive potential for conservation planning and management.

The coast of central Chile provides a good model to analyze the direct effect of protection on reproduction (e.g. gonad investment). First, this section of the coast is heavily impacted by artisanal fisheries (Fernández & Castilla 2005). Second, there is a mosaic of human impact that includes fully and partially (TURFs; Gelcich et al. 2012) protected areas interspaced with open access fishing zones (Fernández & Castilla 2005). Thus, levels of protection of the coastal ecosystem can be associated to fisheries management regimes. Third, the spatial variation in upwelling influence on coastal areas also allows assessing the effect of this environmental driver on reproduction. Finally, there is a need to advance in management and conservation plans of coastal areas, identifying the most relevant zones for propagules production (Tognelli et al. 2009). We compared two levels of protection, determined by fisheries management regimes (in turn associated to fishing pressure) on reproductive investment (gonadosomatic index) and body dry weight of two economically and ecologically important rocky reef species in central Chile: the keyhole limpet, *Fissurella latimarginata* and the red sea-urchin, *Loxechinus albus*. Both variables, body dry weight and gonadosomatic index, provide indication of the general physiological condition (i.e. energy assigned to reserves) of the organisms. Additionally, we also evaluated the independent influence of upwelling on body dry weight and gonadosomatic index, in order to help interpreting the potential influence of environmental conditions on reproductive investment. Thus, our results have local and global relevance, as they allow defining specific management and conservation strategies for the study area but also they can help informing on the direct influence of protection on reproduction (and therefore on seeding) besides the indirect effect expected through enhanced size and density of reproductive individuals.

Material and Methods

The study system

Both model species are targeted by the artisanal fishery that operates along the coast of central Chile. This geographic area (from 30ºS to 36ºS) is characterized by high human impact (particularly fishing), low number of fully marine protected areas (<0.001%), and large fractions of the coast under a co-management system based Territorial Use Rights for Fisheries, covering 30% of the coastal area (Fernández & Castilla 2005). Therefore, the TURF system confers most of the protection to coastal marine ecosystems, contributing to sustainable exploitation and conservation goals (Gelcich et al. 2012). Since levels of protection are associated to fisheries management regimes (no-take, TURF and open access), the effect we actually evaluated, we used both terms indistinctly throughout the manuscript. The coastal landscape of the study area is also characterized by strong heterogeneity driven by spatially persistent differences in oceanographic conditions that affect temperature and determine the local supply of nutrients and hence, primary production (upwelling, Wieters et al. 2003, Navarrete et al. 2005, Wieters 2005, Tapia et al. 2009, 2014). Temperature and food supply can affect energy budget of organisms, determining the energy assigned to body mass and gonads (Clarke 1987, Leslie et al. 2005, Monaco et al. 2014). For this reason, the role of upwelling intensity in modifying reproductive investment needs to be considered in our assessment, despite the fact that we cannot simultaneously evaluate both factors (management regime and upwelling) at a given site (a site corresponds to one or the other: low or high upwelling influence).

Specifically, our study area was located on a small fraction of the coast of central Chile, between 32.6ºS and 33.5ºS. Within this ecoregion (Camus 2001), we selected five sites (Maitencillo, Laguna Verde, Quintay, El Quisco and Las Cruces; Fig. 1). Laguna Verde and Quintay were classified as sites more strongly influenced by upwelling (see Wieters 2005, Tapia et al. 2009, 2014) than the remaining three sites (low upwelling). The influence of protection was associated to the management regimes operating in this region, we sampled (a) areas with restricted access for fishing (RAA), and (b) open access areas (OAAs). In each site we sampled an OAA adjacent to a RAA (named here area or sampling area). Among the latter,

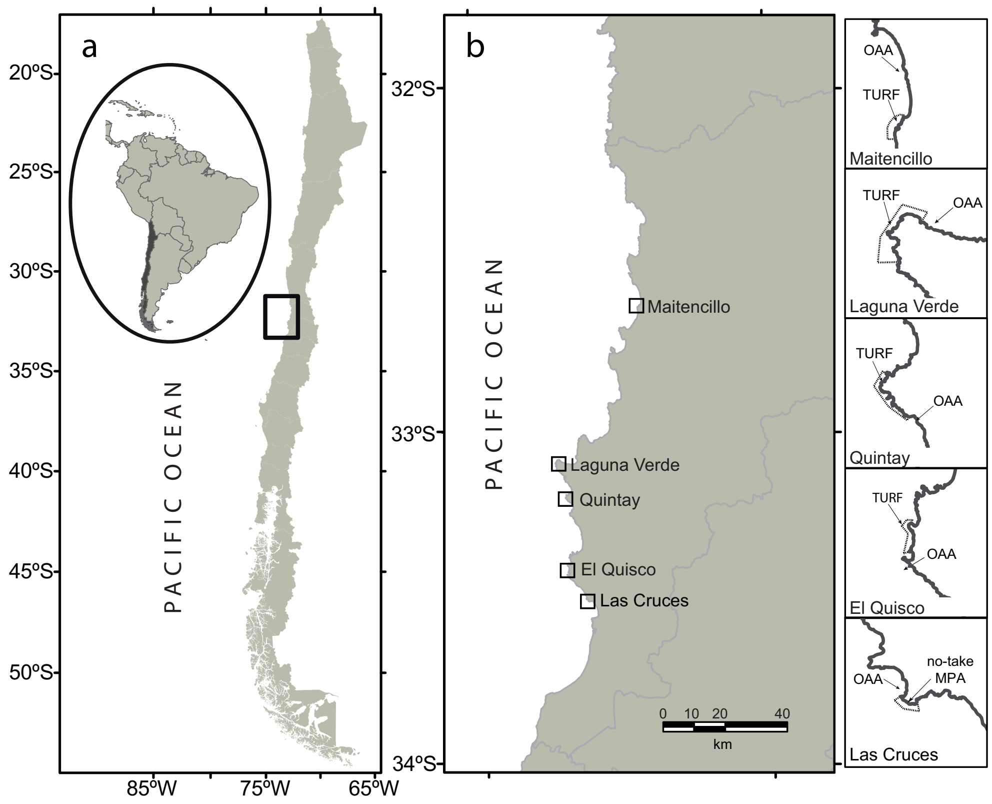


Fig. 1. Maps of the general location of the study region showing (a) sites and (b) specific areas where samples were collected in Fishing Restricted Access Areas (either no-take area or TURF) and adjacent Open Access Areas (OA).

we sampled one no-take area (Las Cruces) and four TURFs. Thus, altogether we sampled ten areas (Figure 1). We pooled no-take and TURFs in the analysis, as in the sampling region there is only one no-take area. Otherwise we would not have been able to determine if potential differences were exclusively due to human impact or environmental variability. Previous evidence suggests that the no-take area of Las Cruces exhibits a similar response of traditional biological variables (size, density) than some TURFs for benthic resources (Gelcich et al. 2012).

Sampling and data analysis

At each sampling area between 13 and 46 reproductive individuals of the keyhole limpet *Fissurella latimarginata* and the red sea-urchin *Loxechinus albus* were collected during the reproductive peak reported for both species (Table 1; Guisado & Castilla 1987, Brown et al. 1997). Individuals, larger than minimum size of reproduction (6 cm for limpets and 7 cm for urchins) were collected by professional divers in each site. The sampling was repeated in 2012 and 2014. Since the same patterns in the response variables were observed between years, we pooled all the samples in order to increase sample size. In total, we sampled 295 *F. latimarginata* and 273 *L. albus* following all bioethics protocols approved for this study (CBB-233/2012).

At the laboratory, body size of all specimens was measured using a caliper (± 0.1 mm), considering peristomial length for limpets and diameter without spines for sea-urchins. After obtaining the wet weight of each individual (mg), animals were dissected and the gonads were extracted. The soft and hard (calcareous) body parts, in addition to the gonads, were placed first on towel paper for 10 minutes to eliminate the excess of water, and then separated on labeled containers. Subsequently, all parts were dried in a standard oven at 60ºC for 48 h. Finally, dry weights were obtained with a Sartorius BP211D digital balance to the nearest 0.01 mg. Body dry weight was considered as a proxy of body condition.

In order to compare reproductive output between fisheries management regimes, the proportion between gonad dry weight and soft body dry weight was obtained (Gonadosomatic Index; GSI). We also compared individual body dry weights between fisheries management regimes to further evaluate effect of protection levels (associated here to management regimes) on energy reserves that can be assigned either to body mass or gonads. Since body mass and gonadosomatic

Table 1. Sample size and body size ranges of reproductive individuals collected to estimate dry weight and gonadosomatic index for each species and fisheries management regime.

Species	Site	Fishing Condition	Sample size	Body size range (cm)
F. latimarginata	Maitencillo	Restricted access	38	(6.42 - 10.77)
		Open access	46	(6.05 - 10.20)
	Laguna Verde	Restricted access	20	(8.03 - 9.48)
		Open access	37	(6.39 – 8.11)
	Quintay	Restricted access	37	(7.59 – 9.87)
		Open access	34	(7.17 – 9.86)
	El Quisco	Restricted access	15	(7.24 – 9.79)
		Open access	20	(7.07 – 9.61)
	Las Cruces	Restricted access	32	(6.60 – 11.41)
		Open access	16	(7.20 – 10.26)
L. albus	Maitencillo	Restricted access	38	(7.31 – 11.47)
		Open access	35	(7.03 – 10.90)
	Laguna Verde	Restricted access	40	(7.94 – 10.50)
		Open access	17	(7.02 – 9.34)
	Quintay	Restricted access	39	(8.60 – 10.80)
		Open access	38	(8.57 – 12.83)
	El Quisco	Restricted access	20	(7.65 – 11.32)
		Open access	10	(8.23 – 11.58)
	Las Cruces	Restricted access	23	(8.83 – 11.42)
		Open access	13	(7.21 – 9.84)

index are influenced by size, and size is affected by levels of protection, the first step was to assess the effect of fisheries management regime on mean individual size. A two-way analysis of variance (ANOVA) with a complete non-balanced block design without replication was used to assess the effect of fisheries management regime (two levels, fixed factor) blocked by site (five levels, random factor) on mean individual size. We used a complete block design in order to account for the spatial auto-correlation of the observations. Spatial autocorrelation might occur because observations from neighbor areas with different management regimes (within site observations) might be more similar to each other than to observations from other sites since environmental conditions might differ among sites not related to management regimes. Data are slightly unbalanced due to the slightly different number of individuals measured in each area (Table 1). Fligner-Killeen test was used to assess the homogeneity of variances and Shapiro-Wilk test was used to assess the normality of the error distributions. The ANOVA assumptions were met for *F. latimarginata* but not for *L. albus*. Thus, in this case a Generalized Linear Model (GLM) using "quasi-poisson" family error distribution was performed. The model fit was checked with chi-square test for deviance vs. the degrees of freedom.

Since individual body dry weight (IDW) and in the gonadosomatic index (GSI) were highly correlated with body size ($r > 0.45$ in all cases), we used body size as a covariate in our analyses to assess the effects of fisheries management regime and upwelling. Following the method of residuals analysis proposed by Ouréns et al. (2012), we first computed the individual linear regression model between each log-transformed response variable (IDW and GSI) and mean individual body size for each combination of levels of both factors. Then, for each significant linear model we removed the effect of the covariable (body size) on the response variable (IDW and GSI) extracting the residuals for each linear regression, and used the residuals as the new response variable in subsequent analyses. When no significant relationship was found between the log-transformed response variables and the log-transformed body size (only three models, all for *L. albus*), the new response variable were obtained by subtracting each observation from the mean. We assessed the effect of fisheries management regime on each new variable by using a 2-way ANOVA with the same non-balanced complete block design (by site) described above. Contrastingly, in order to test for the effect of upwelling (fixed factor) we used a 2-way ANOVA with a nested design (site nested within upwelling) due to environmentally driven site differences within levels of factor upwelling. Whenever ANOVA assumptions were not met, GLMs (family structure "quasi-poisson") were used instead; again, the GLM model fit was checked with a chi-square test for deviance vs. the degrees of freedom. Laguna Verde was excluded from the analysis of *F. latimarginata* because there was no overlap in size between the two management regimes of this site. Similarly, Laguna Verde and Las Cruces were also excluded for *L. albus*.

All the statistical analyses were carried out using the free software R version 3.1.3 (R 2013).

Results

Body size

We found a significant effect of fisheries management regime (F 1,289 = 56.22, P < 0.0001) and site (F 4,289 = 12.32, P < 0.0001) on body size of keyhole limpets. However, management regime did not have the same effect in all sites (Fig. 2A) in spite of a general trend towards larger body sizes in RAA. Laguna Verde and El Quisco showed the greater differences between RAA and OAA (largest individuals in RAA). Differences in body size between pairs of sites were not related to the distance (km) between them (Fig. 2A). Thus, differences in mean size of keyhole limpets were observed between El Quisco and Quintay (which are close together), but also between El Quisco and Maintencillo, or between Quintay and Maintencillo, which are further away (Fig. 1).

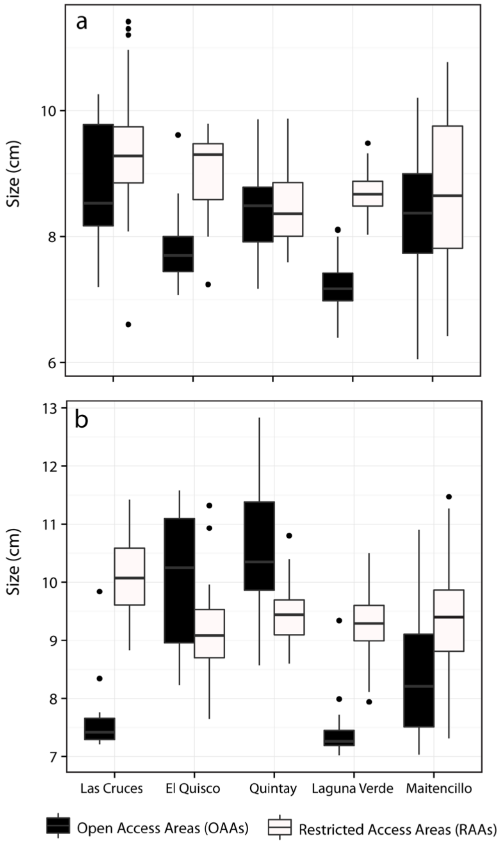


Fig. 2. Boxplots showing individual body size for each sampling site in areas under different fishing management regimes. White bars represent areas with entry restriction to fishing named here Restricted Access Areas (RAAs, include one no-take area and four Territorial Use Rights for Fisheries; TURF). Black bars indicate areas with no access restrictions, called here Open Access Areas (OAAs). (a) *Fissurella latimarginata* and (b) *Loxechinus albus*.

We also found a significant effect of fisheries management regime (F 1,271 = 41.87, P < 0.001) and site (F 4,267 = 33.99, P < 0.001) on the body size of sea-urchins (Figure 2B). Larger sea-urchins in RAA were observed in Las Cruces, Laguna Verde and Maitencillo, and the opposite trend in El Quisco and Quintay (Fig. 2B). As observed for keyhole limpets, mean differences in body size between pairs of sites was not related to the distance between sites: differences were observed between both the closest sites (Laguna Verde and El Quisco) and the two farthest ones (Las Cruces and Maitencillo).

Since body size showed significant differences between fisheries management regimes and sites, it was treated as a covariable in the remaining analysis conducted to test for the influence of fisheries management regime and upwelling.

Body weight

Body dry weight was significantly correlated with body size in both species, regardless of the fisheries management regime or site (Table 2; Fig. 3). After removing the influence of size on body weight (residual analysis), no influence of fisheries management regime on body dry weight of keyhole limpets (F 1,233 = 0.99, P = 0.32) and red sea-urchin (F 1,176 = 1.25, P = 0.26) were detected.

Body dry weight also increased significantly with body size when sites were analyzed considering the influence of upwelling, by pooling data from both management regimes for each site (Table 3; Fig. 4). The nested ANOVA performed on the residuals of the relationship between body dry weight and body size did not detect any influence of upwelling condition. The results were consistent between species (keyhole limpet: F 4,290 = 0.11, P = 0.97; red sea-urchin: F 4,268 = 0.13, P = 0.97).

Reproductive output

Gonadosomatic index was also significantly correlated with body size in both species for most sites and both fisheries management regimes, with some exceptions (see Table 4; Fig. 5). The residual analyses showed no effect of fisheries management regime (F 1,233 = 1.39, P = 0.24) or site (F 3,233 = 0.13, P = 0.94) on gonadosomatic index of the keyhole limpet after removing the effect of size (residuals). Although data from the site that was excluded from the analysis

Table 2. Results of the relationship between body dry weight (log transformation) and size (log transformation) of the keyhole limpet *Fissurella latimarginata* and the red sea-urchin *Loxechinus albus* for the different sites and fisheries management regimes. RAA indicates Restricted Access Areas for fishing (which can be either no-take areas or territorial use rights for fisheries; TURF). OAA indicates Open Access Areas.

Site	Fishing regime	*Fissurella latimarginata*			*Loxechinus albus*		
		Intercept	Slope	P-value	Intercept	Slope	P-value
Las Cruces	OAA	-5.68	3.71	<0.001	-1.63	2.73	<0.001
	RAA (no take)	-3.00	2.55	<0.001	-1.09	2.55	<0.001
Quisco	OAA	-5.02	3.29	<0.001	-1.58	2.74	<0.001
	RAA (TURF)	-5.99	3.97	<0.001	-2.29	3.05	<0.001
Quintay	OAA	-6.86	4.19	<0.001	0.15	1.99	<0.001
	RAA (TURF)	-3.28	2.49	<0.001	-1.76	2.79	<0.001
Laguna Verde	OAA	-1.03	1.44	0.02	-0.26	2.04	<0.001
	RAA (TURF)	-4.16	3.06	0.009	-1.95	2.88	<0.001
Maintencillo	OAA	-2.85	2.45	<0.001	-2.73	3.24	<0.001
	RAA (TURF)	-5.03	3.41	<0.001	-1.41	2.63	<0.001

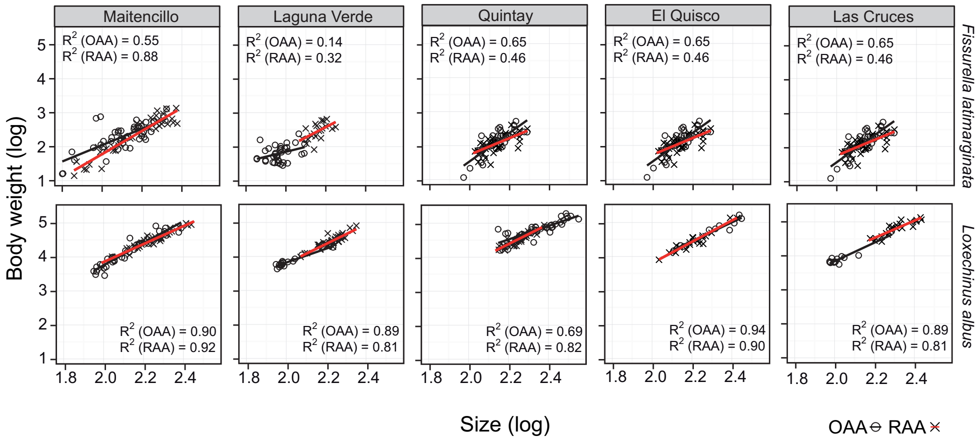


Fig. 3. Relationship between body dry weight (log) and size (log; length [mm] in the keyhole limpet *F. latimarginata* and diameter [mm] in the sea-urchin *Loxechinus albus*) in the five study sites, considering one open access area (OA; identified by circles and black line) and one Restricted Access Area (RAA; identified by crosses and red line) per site. The regression coefficients (R2) for each fishing regime and site are also shown. Table 2 includes the parameters of the regressions.

(Laguna Verde) cannot be statistically compared because of lack of overlap in size, the slopes between both fishing regimes showed similar trends (Fig. 5). In the case of the red sea-urchin, no differences in gonadosomatic index after removing the effect of size were found among sites (P > 0.9 in all cases). Although fisheries management regime showed significant effects on the residuals of the regressions between gonadosomatic index and size, no consistent pattern was detected across sites.

The gonadosomatic index significantly increased with size in both species only at the sites characterized by low upwelling influence (Table 5; Fig. 6). Nevertheless, the residual analysis of the relationships between gonadosomatic index and size did not show significant differences between upwelling conditions neither for the keyhole limpet (F 4, 290 = 0.03, P = 0.99) nor for the red sea-urchin (F 4, 268 = 0.4, P = 0.81).

Table 3. Results of the relationship between body dry weight (log transformation) and size (log transformation) for the keyhole limpet *Fissurella latimarginata* and the red sea-urchin *Loxechinus albus* for the different sites and upwelling conditions.

Site	Environmental condition	*Fissurella latimarginata*			*Loxechinus albus*		
		Intercept	Slope	P-value	Intercept	Slope	P-value
Las Cruces	Low upwelling	-4.31	3.12	<0.001	-2.19	3.02	<0.001
Quisco	Low upwelling	-8.58	5.08	<0.001	-2.04	2.90	<0.001
Quintay	High upwelling	-5.00	3.31	<0.001	-0.87	2.41	<0.001
Maintencillo	Low upwelling	-3.82	2.88	<0.001	-2.14	2.96	<0.001
Laguna Verde	High upwelling	-3.99	2.96	<0.001	-1.61	2.72	<0.001

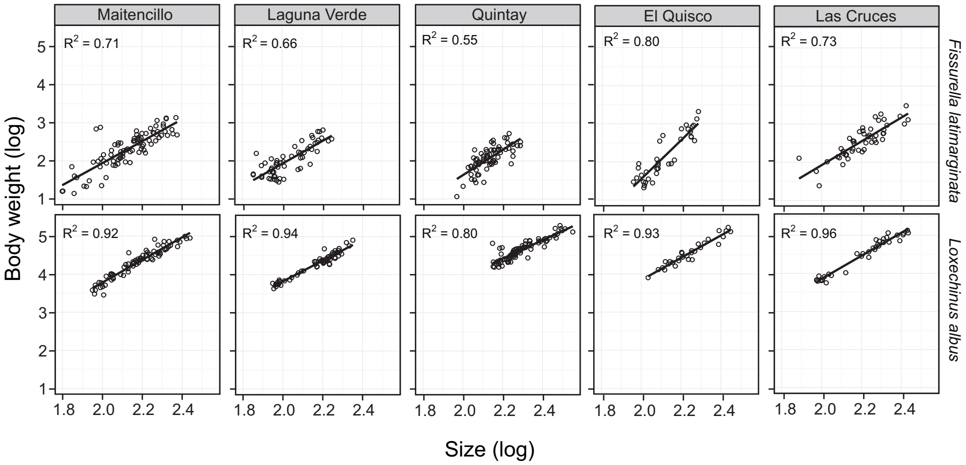


Fig. 4. Relationship between body dry weight (log) and size (log; length in the keyhole limpet *F. latimarginata* [mm] and diameter [mm] in the red sea-urchin *Loxechinus albus*) in the five study sites. Two sites were labeled as high upwelling (Quintay and Laguna Verde) and the remaining as low upwelling. The regression coefficients (R2) for each site are shown. Table 3 includes the parameters of the regressions.

Discussion

The main conclusions of our study are the consistent patterns evidenced by (a) the lack of effect of fisheries management regime (related to protection level) on the individual body dry weight in both species, (b) the poor influence of fisheries management regime on reproductive investment (i.e. gonadosomatic index), suggesting that the selection of sites for sitting of marine protected areas or TURFs seems to be less relevant for seeding than efficient control of fishing effort and minimum legal size, as these two variables are major indirect determinants of egg production (Rogers-Bennett et al. 2002, Willis et al. 2003, Pelc et al. 2009), and (c) the lack of effect of upwelling on body condition (body dry weight) and reproductive investment (gonadosomatic index). Although in general we found no effects of the study variables, the results are of local and global interest. First, because we clearly show that at the spatial scale of our analysis, the main driver of coastal dynamics in the study area (upwelling; see Wieters et al. 2003, Navarrete et al. 2005, Wieters 2005, Tapia et al. 2009, 2014) does not influence critical indicators of general physiological conditions and reproductive investment in two herbivore species. And second, because our results help disentangling the main determinants of reproductive patterns observed in protected areas, which is critical for decision making (e.g., site selection for conservation and management, spatial planning).

Table 4. Results of the relationship between gonadosomatic index (log transformation) and size (log transformation) of the keyhole limpet *Fissurella latimarginata* and the red sea-urchin *Loxechinus albus* for the different sites and fisheries management regimes. RAA indicates Restricted Access Areas for fishing (which can be either no-take areas or territorial use rights for fisheries; TURF). OAA indicates Open Access Areas.

Site	Fishing regime	*Fissurella latimarginata*			*Loxechinus albus*		
		Intercept	Slope	P-value	Intercept	Slope	P-value
Las Cruces	OAA	-12.81	5.17	0.011	-2.33	-0.10	0.922
	RAA (no take)	-4.34	1.31	0.11	-5.01	1.25	0.021
Quisco	OAA	-11.54	4.50	0.018	-2.69	0.21	0.766
	RAA (TURF)	-7.79	2.95	0.012	-9.88	3.21	0.003
Quintay	OAA	-7.72	2.71	0.034	-3.94	0.61	0.309
	RAA (TURF)	2.97	-2.37	0.11	-1.28	-0.61	0.495
Laguna Verde	OAA	-7.23	2.65	<0.001	-4.92	1.11	0.045
	RAA (TURF)	-8.51	3.08	<0.001	-5.99	1.52	0.009
Maintencillo	OAA	0.18	-0.99	0.60	-1.96	-0.34	0.773
	RAA (TURF)	-2.85	0.65	0.58	-11.39	3.91	0.001

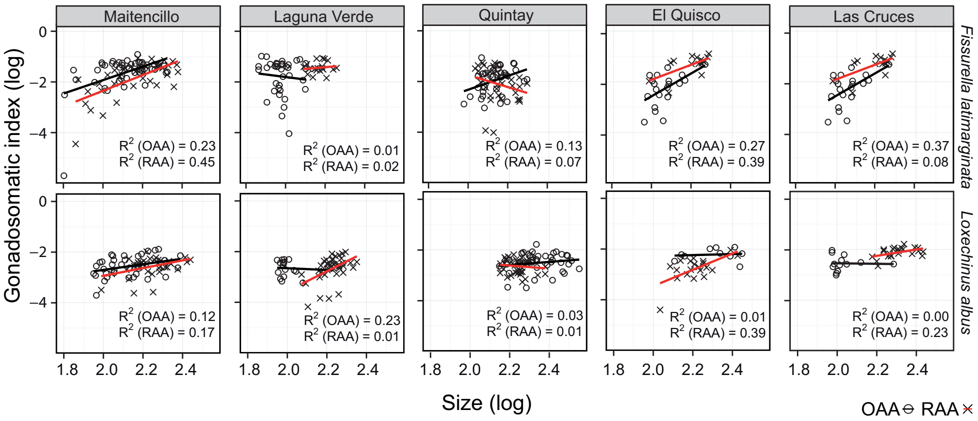


Fig. 5. Relationship between gonadosomatic index (log) and size (log; length [mm] in the keyhole limpet *F. latimarginata* and diameter [mm] in the case of the red sea-urchin *Loxechinus albus*) in the five study sites, considering one open access area (OA; identified by circles and black line) and one Restricted Access Area (RAA; identified by crosses and red line) per site. The regression coefficients (R2) for each fishing regime and site are shown. Table 4 includes the parameters of the regressions.

In line with existing evidence, our results show the benefits of protection for enhancing size of exploited species inside the boundaries of protected areas (Lester et al. 2009, Gelcich et al. 2012). However, (a) in some sites significant larger sizes in the RAA with respect to OAA were not found, in spite the suggestive general trend towards size enhancement, and (b) in El Quisco and Quintay mean size of the red sea-urchin exhibited the opposite pattern (larger sizes in open access areas). A plausible explanation is that most of our RAA are only partially protected from fishing. Across all sites we observed, on average, 17% and 28% increase in body size with protection in the keyhole limpet and in the red sea-urchin, respectively. A larger average increase in size (30%) has been reported in global analyses comparing individual size between no-take and open access areas (Lester et al. 2009). However, smaller changes, comparable with our results (~17%), have been observed in global comparisons between partially protected and open access areas, including an broad range of species (Lester & Halpern 2008), suggesting the higher benefits of full protection within the limits of the reserves. Nevertheless, our findings reinforce and highlight the benefits of partially protected areas, particularly in regions where excluding human activities does not seem a viable option (Tognelli et al. 2009). Our results suggest the need of further exploration of the influence of fishing effort on mean size of exploited species (e.g. comparing TURFs across a gradient of fishing level) since exploitation seems to be the major determinant of differences in body size. Another suggestion that fishing, rather than environmental factors, determines local mean body size, is that variability in mean body size across sites was not consistent between the two grazer species, and did not show a regional effect, as differences occurred among the closest or the farthest sites. Therefore, it seems relevant to determine the level of human impact that affects body size, and as a consequence influences the variables related to reproductive investment, critical for management and conservation, such as egg production.

Table 5. Results of the relationship between gonadosomatic index (log transformation) and size (log transformation) of the keyhole limpet *Fissurella latimarginata* and the red sea-urchin *Loxechinus albus* for the different sites and upwelling conditions.

Site	Environmental condition	*Fissurella latimarginata*			*Loxechinus albus*		
		Intercept	Slope	P-value	Intercept	Slope	P-value
Las Cruces	Low upwelling	-7.43	2.69	0.001	-5.24	1.35	<0.001
Quisco	Low upwelling	-12.68	5.11	<0.001	-8.11	2.46	0.001
Quintay	High upwelling	-2.18	0.07	0.941	-4.02	0.63	0.113
Maintencillo	Low upwelling	-7.47	2.69	<0.001	-4.72	0.99	0.004
Laguna Verde	High upwelling	-4.01	1.15	0.130	-3.97	0.60	0.224

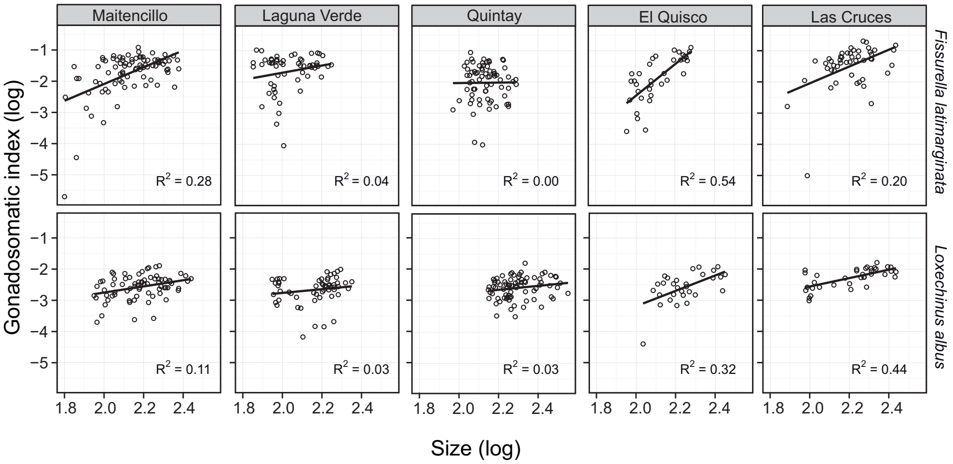


Fig. 6. Relationship between gonadosomatic index (log) and size (log; length [mm] in the keyhole limpet *F. latimarginata* and diameter [mm] in the case of the red sea-urchin *Loxechinus albus*) in the five study sites. Two sites are classified as high upwelling (Quintay and Laguna Verde) and the remaining as low upwelling intensity. The regression coefficients (R2) per site are shown. Table 5 includes the parameters of the regressions.

Enhanced size in protected areas can amplify the benefits of protection outside the boundaries of protected zones by increasing individual production of dispersive propagules (Gell & Roberts 2003). Empirical evidence predicts between 2 to 5 times increase in abalone egg production in protected areas with respect to fished areas, associated to 30% increase of size of adults (Rogers-Bennett et al. 2002). The contribution of partially protected areas to potential egg production may be less significant than no-take areas since smaller changes in size, as those observed in this study, can have tremendous impact on potential fecundity (Espinosa et al. 2006). However, not only size, but also density is enhanced in partially and fully protected areas (Lester & Halpern 2008). The relative importance of increased size and abundance in protected areas on reproductive potential is yet poorly understood. Most studies report increases in egg production within protected areas due to the combined influence of size and density (Rogers-Bennett et al. 2002, Willis et al. 2003, Pelc et al. 2009). Another element contributing to local reproductive potential is the direct influence of fishing regime on reproductive investment; however this is even less understood (Kaiser et al. 2007) and our results help filling this important gap. Density-dependent reproduction or parasite load can be potential mechanisms behind direct effect of protection on reproductive investment.

Our evaluation on the direct influence of protection on both reproductive investment and general condition of keyhole limpets and red sea-urchins showed a consistent lack of effect of protection on body dry weight and gonadosomatic index. This finding contrast with the results of similar comparison in the scallops Pecten maximum, showing that gonad weight per unit of body size increased between 19% and 24% in the areas protected from fishing, associated to a 8-fold increase in density (Kaiser et al. 2007). Our results showing persistent patterns in the comparison of fishing management regimes are solid as they are based on comparisons among five sites and two species. Moreover, fishing management regime consistently showed no effect regardless of upwelling condition. Contrasting results on the direct influence of protection on reproductive investment (e.g., Kaiser et al. 2007, this study) suggest the need to advance our understanding of the mechanisms behind. Clearly, density-dependent effects (e.g. feeding, parasitism, behavior such as territorialism) might influence individual energy budgets and determine differential investment in gonads in protected areas (Kaiser et al. 2007, Aldana et al. 2014). However, the potential factors appear to be complex.

For instance, parasitic biomass in gonads seems to generate contrasting patterns on gonad investment (Loot et al. 2005, Aldana et al. 2014). External factors may also play a role. In our particular case, we expected that partially protected areas (TURFs) would exhibit larger effects on both response variables than no-take or open access areas, as fishers might select the most productive areas for TURFs. However, we cannot conclude that fishers' selection for productive sites, or density dependent factors determine the patterns found in this study. The lack of direct effect of protection on reproductive investment drives our main conclusion that the selection of particular areas for sitting marine protected areas seems to be less relevant than effective enforcement, which promotes enhancement of size and density (Halpern 2003, Lester & Halpern 2008, Lester et al. 2009).

It is also remarkable that the upwelling gradient analyzed here, including the influence of a major upwelling center (Curaumilla), did not influence reproductive output or body size condition. A five-fold increase in planktonic chlorophyll-a produces a 3-fold increase in larval production of the filter feeding barnacle Balanus glandula (Leslie et al. 2005). Despite macroalgal growth seems to be higher in areas under high upwelling influence (Wieters 2005), this effect does not seem to be transmitted to herbivores in the form of body dry weight or gonadosomatic index (but see Pulgar et al. 2013). Our results again highlight that this environmental factor, at least at the scale of variability of our study sites, does not seem to be a major determinant for body condition of the main herbivores exploited in central Chile.

Our results strongly suggest that at the local level (Chile), major fishing regulations such as minimum legal size and quotas, need to be enforced, in order to control size and density of reproductive individuals. Recent studies have shown that illegal fishing of benthic resources can generate catch levels similar to the legally reported landing (González et al. 2006), clearly suggest poor enforcement. Our results show that maintaining larger individuals in protected areas is critical for seeding. Therefore, special incentives should be created to maintain the Chilean TURF system, because of its contribution to egg production by enhancing size and density of exploited benthic species. Our analysis also allowed to extrapolate the value of fully and partially protected areas (including TURFs) on less studied variables, such as reproductive output and egg production.

Acknowledgments

This work was funded by Iniciativa Científica Milenio (Project CCM RC 1300004) from Ministerio de Economía, Fomento y Turismo de Chile, and Fondecyt (Projects: 1130976 to MFB, and 11130580 to MDS). The authors thank B. Bularz, S. López, R. Calderón, M. Figueroa, M. Saldías and M. Andreu for their help in data collection and processing samples in the laboratory. We are also very grateful to fishermen of Maitencillo, Laguna Verde, Quintay, and El Quisco. We appreciate the comments of two anonymous reviewers to help improving the manuscript.

References

Aldana M, Pulgar JM, Orellana N, Patricio Ojeda F, García-Huidobro MR (2014) Increased parasitism of limpets by a trematode metacercaria in fisheries management areas of central Chile: Effects on host growth and reproduction: Management areas and parasitism. Ecohealth 11:215–226

Brown G. DI, Gonzalez M, Lopez D, Duran L, Rivero R, Collado G, Betancourt C (1997) Informe Final Proyecto FIP-IT/94-33. Estudio de los ciclos vitales de las especies comerciales de lapas del genero *Fissurella* sp, en las regiones I a X. :196

Camus PA (2001) Biogeografía marina de Chile continental. Rev Chil Hist Nat 74:587–617

Clarke A (1987) Temperature, latitude and reproductive effort. Mar Ecol Prog Ser 38:89–99

Espinosa F, Guerra-García JM, Fa D, García-Gómez JC (2006) Aspects of reproduction and their implications for the conservation of the endangered limpet, *Patella ferruginea*. Invertebr Reprod Dev 49:85–92

Fernández M, Castilla JC (2005) Marine conservation in Chile: Historical perspective, lessons, and challenges. Conserv Biol 19:1752–1762

Gelcich S, Fernández M, Godoy N, Canepa A, Prado L, Castilla JC (2012) Territorial user rights for fisheries as ancillary instruments for marine coastal conservation in Chile. Conserv Biol 26:1005–15

Gell FR, Roberts CM (2002) The fishery effects of marine reserves and fishery closures. WWF-US, 1250 24th Street, NW, Washington, DC 20037, USA.

Gell FR, Roberts CM (2003) Benefits beyond boundaries: the fishery effects of marine reserves. Trends Ecol Evol 18:448–455

González J, Stotz W, Garrido J, Orensanz JM, Parma AM, Tapia C, Zuleta A (2006) The Chilean turf system: How is it performing in the case of the loco fishery? Bull Mar Sci 78:499–527

Goñi R, Quetglas A, Reñones O (2006) Spillover of spiny lobsters *Palinurus elephas* from a marine reserve to an adjoining fishery. Mar Ecol Prog Ser 308:207–219

Guisado C, Castilla J (1987) Historia de vida, reproducción y avances en el cultivo del erizo comestible chileno *Loxechinus albus* (Molina, 1782) (Echinoidea, Echinidae). In: Arana P (ed) Manejo y desarrollo pesquero. Escuela de Ciencias del Mar. Universidad Católica de Valparaiso, p 59–68

Halpern BS (2003) The impact of marine reserves: Do reserves work and does reserve size matter? Ecol Appl 13:S117–S137

Halpern BS, Walbridge S, Selkoe KA, Kappel C, Micheli F, D'Agrosa C, Casey K, Ebert C, Fox H., Fujita R, Heinemann D, Lenihan H., P.Madin E., Perry M., Selig E., Spaldin M, Steneck R, Watson R (2008) A Global Map of Human Impact on Marine Ecosystems. Science (80-) 319:948–952

Halpern BS, Warner RR (2003) Matching marine reserve design to reserve objectives. Proc R Soc Lond B 270:1871–8

Jennings S, Marshall SS, C. Polunin NV (1996) Seychelles marine protected areas: comparative structure and status of reef fish communities. Biol Conserv 75:201–209

Kaiser MJ, Blyth-Skyrme RE, Hart PJB, Edwards-Jones G, Palmer D (2007) Evidence for greater reproductive output per unit area in areas protected from fishing. Can. J. Fish. aquat. Sci. 64: 1284-1289

Leslie HM, Breck EN, Chan F, Lubchenco J, Menge BA (2005) Barnacle reproductive hotspots linked to nearshore ocean conditions. Proc Natl Acad Sci U S A 102:10534–10539

Lester SE, Halpern BS (2008) Biological responses in marine no-take reserves versus partially protected areas. Mar Ecol Prog Ser 367:49–56

Lester SE, Halpern B., Grorud-Colvert K, Lubchenco J, Ruttenberg BI, Gaines SD, Airamé S, Warner RR (2009) Biological effects within no-take marine reserves: a global synthesis. Mar Ecol Prog Ser 384:33–46

Loot R, Aldana M, Navarrete SA (2005) Effects of Human Exclusion on Parasitism in Intertidal Food Webs of Central Chile. 19:203–212

Monaco CJ, Wethey DS, Helmuth B (2014) A Dynamic Energy Budget (DEB) model for the keystone predator *Pisaster ochraceus*. PLoS One 9

Navarrete SA, Wieters EA, Broitman BR, Castilla JC (2005) Scales of benthic-pelagic coupling and the intensity of species interactions: from recruitment limitation to top-down control. Proc Natl Acad Sci U S A 102:18046–18051

Ouréns R, Freire J, Fernández L (2012) Definition of a new unbiased gonad index for aquatic invertebrates and fish: Its application to the sea urchin *Paracentrotus lividus*. Aquat Biol 17:145–152

Pelc R, Baskett M, Tanci T, Gaines S, Warner R (2009) Quantifying larval export from South African marine reserves. Mar Ecol Prog Ser 394:65–78

Pulgar J, Aldana M, Alvarez M, Garcia-Huidobro R, Molina P, Morales JP, Pulgar VM (2013) Upwelling affects food availability, impacting the morphological and molecular conditions of the herviborous limpet *Fissurella crassa* (Mollusca: Archeogastropoda). J Mar Biol Assoc United Kingdom 93:1–6

R DCT (2013) R: A Language and Environment for Statistical Computing.

Roberts CM, Bohnsack JA, Gell F, Hawkins JP, Goodridge R (2001) Effects of marine reserves on adjacent fisheries. Science (80-) 294:1920–1923

Rogers-Bennett L, Haaker PL, Karpov KA, Kushner DJ (2002) Using Spatially Areas Explicit for Data to Marine Protected Abalone in California. Conserv Biol 16:1308–1317

Russ GR, Alcala AC, Maypa AP, Calumpong HP, White AT (2004) Marine reserve benefits local fisheries. Ecol Appl 14:597–606

Sale PF, Cowen RK, Danilowicz B., Jones GP, Kritzer JP, Lindeman KC, Planes S, Polunin NVC, Russ GR, Sadovy YJ, Steneck RS (2005) Critical science gaps impede use of no-take fishery reserves. Trends Ecol Evol 20:74–80

Shears NT, Grace RV, Usmar NR, Kerr V, Babcock RC (2006) Long-term trends in lobster populations in a partially protected vs. no-take Marine Park. Biol Conserv 132:222–231

Tapia FJ, Largier JL, Castillo M, Wieters E a, Navarrete S a (2014) Latitudinal discontinuity in thermal conditions along the nearshore of central-northern Chile. PLoS One 9:e110841

Tapia FJ, Navarrete SA., Castillo M, Menge BA., Castilla JC, Largier J, Wieters EA., Broitman BL, Barth J a. (2009) Thermal indices of upwelling effects on inner-shelf habitats. Prog Oceanogr 83:278–287

Tognelli MF, Fernández M, Marquet PA (2009) Assessing the performance of the existing and proposed network of marine protected areas to conserve marine biodiversity in Chile. Biol Conserv 142:3147–3153

West P, Igoe J, Brockington D (2006) Parks and Peoples: The Social Impact of Protected Areas. Annu Rev Anthropol 35:251–277

Wieters E (2005) Upwelling control of positive interactions over mesoscales: a new link between bottom-up and top-down processes on rocky shores. Mar Ecol Prog Ser 301:43–54

Wieters E, Kaplan D, Navarrete S, Sotomayor A, Largier J, Nielsen K, Véliz F (2003) Alongshore and temporal variability in chlorophyll a concentration in Chilean nearshore waters. Mar Ecol Prog Ser 249:93–105

Willis TJ, Millar RB, Babcock RC (2003) Protection of exploited fish in temperate regions: high density and biomass of snapper. J Appl Ecol 40:214–227

Wood CL, Micheli F, Fernández M, Gelcich S, Castilla JC, Carvajal J (2013) Marine protected areas facilitate parasite populations among four fished host species of central Chile. J Anim Ecol 82:1276–87

Chapter 2

Egg production patterns of two invertebrate species in rocky subtidal areas under different fishing regimes along the coast of central Chile

Chapter 2

PLOS | ONE

RESEARCH ARTICLE

Egg production patterns of two invertebrate species in rocky subtidal areas under different fishing regimes along the coast of central Chile

Marta Blanco*, **Andres Ospina-Álvarez, Catherine González, Miriam Fernández**¤

Núcleo Milenio - Centro de Conservación Marina CCM, Estación Costera de Investigaciones Marinas ECIM, Departamento de Ecología, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Santiago, Chile

¤ Current address: Departamento de Ecología, Pontificia Universidad Católica de Chile, Santiago, Chile
* marblasa@gmail.com

Abstract

Fishing is a major source of human impact, reducing density and size of a wide range of exploited species in comparison to areas exhibiting strong regulations (no-take and partially protected areas, including Territorial Use Rights for Fisheries, TURFs). Since size and density might have important consequences on reproduction, and therefore natural re-seeding, we monitored adult size, density and potential fecundity of the keyhole limpet (*Fissurella latimarginata*) and the red sea urchin (*Loxechinus albus*) in areas under two fishing regimes (TURFs and Open Access Areas, OAAs). Analyzing the distribution of suitable habitats, we predict spatial patterns of potential egg production, to identify reproductive hotspots along the central coast of Chile. The current system of TURFs in central Chile showed higher potential egg production of *F. latimarginata* and of *L. albus* than expected under a complete OAAs scenario (67 and 52% respectively). Potential egg production showed more than a twofold reduction when the complete TURFs scenario was compared against complete OAAs condition in both species. Individual size and density explained between 60% and 100% of the variability in potential egg production, suggesting the importance of the enhancement of both biological variables in TURFs in Chile. Potential egg production for both species in the northern part of the studied domain was higher due to the combined effect of (a) suitable habitat and (b) concentration of TURFs. Our results suggest that partially protected areas, such as TURFs can significantly enhance the production of propagules that could seed exploited areas.

Citation: Blanco M, Ospina-Álvarez A, González C, Fernández M (2017) Egg production patterns of two invertebrate species in rocky subtidal areas under different fishing regimes along the coast of central Chile. PLoS ONE 12(5): e0176758. https://doi.org/10.1371/journal.pone.0176758

Editor: James P. Meador, Northwest Fisheries Science Center, UNITED STATES

Received: March 15, 2016

Accepted: April 14, 2017

Published: May 8, 2017

Data Availability Statement: All relevant data are within the paper and its Supporting Information files.

Abstract

Fishing is a major source of human impact, reducing density and size of a wide range of exploited species in comparison to areas exhibiting strong regulations (no-take and partially protected areas, including Territorial Use Rights for Fisheries, TURFs). Since size and density might have important consequences on reproduction, and therefore natural re-seeding, we monitored adult size, density and potential fecundity of the keyhole limpet (*Fissurella latimarginata*) and the red sea urchin (*Loxechinus albus*) in areas under two fishing regimes (TURFs and Open Access Areas, OAAs). Analyzing the distribution of suitable habitats, we predict spatial patterns of potential egg production, to identify reproductive hotspots along the central coast of Chile. The current system of TURFs in central Chile showed higher potential egg production of *F. latimarginata* and of *L. albus* than expected under a complete OAAs scenario (67 and 52% respectively). Potential egg production showed more than a twofold reduction when the complete TURFs scenario was compared against complete OAAs condition in both species. Individual size and density explained between 60% and 100% of the variability in potential egg production, suggesting the importance of the enhancement of both biological variables in TURFs in Chile. Potential egg production for both species in the northern part of the studied domain was higher due to the combined effect of (a) suitable habitat and (b) concentration of TURFs. Our results suggest that partially protected areas, such as TURFs can significantly enhance the production of propagules that could seed exploited areas.

Keywords

Fecundity, egg production, conservation planning, TURFs, Marine Protected Areas, reserve networks, artisanal fisheries

Introduction

Coastal zones are among the most impacted ecosystems of the world (Halpern et al. 2008). Overfishing in particular is one of the most pervasive sources of human impact, that can reduce abundance of target species and propagate effects to the whole community (Pauly et al. 1998, Castilla 1999, Myers & Worm 2003). In fact, 63% of assessed stocks and 82% of unassessed stocks currently require rebuilding (Worm et al. 2009, Costello et al. 2013). This situation is of major concern in fisheries that are critically important for diversity and food security, such as artisanal fisheries, which currently concentrate approximately 50% of the world catch and 90% of the fishers worldwide (FAO 2014). Therefore, there is an urgent need to improve fisheries management in general and artisanal coastal fisheries in particular. The tools to advance in management of artisanal fisheries range from new ecosystem approaches, total allowable catches as well as spatial management including limited-entry areas (e.g., Territorial Use Rights for Fisheries; TURFs) and permanent fishing bans (e.g., Marine Reserves) (Freire & García-Allut 2000, Levin et al. 2009, Afflerbach et al. 2014).

The benefits of the permanent fishing bans established in no-take areas have been widely reported, showing higher abundance (Denny et al. 2004, Shears et al. 2006, Aburto-Oropeza et al. 2011), larger adult size of exploited species (Castilla & Durán 1985, Edgar & Barrett 1999); and also higher species richness (Jennings et al. 1996) in comparison with background areas (Roberts et al. 2001, Halpern 2003, Lester et al. 2009). Partially marine protected areas, including limited-entry TURFs, show in many cases similar patterns than no-take areas in these relevant biological variables (species richness, abundance and adult size of target species) (Lester & Halpern 2008, Gelcich et al. 2012), conferring clear benefits over open access or background areas. These results are critically important because very often the implementation of no-take areas generates social resistance (Murray et al. 1999, Lester & Halpern 2008). Thus, although no-take areas cannot be completely replaced by partially marine protected areas (Lester & Halpern 2008), the latter can offer the opportunity of protection enhancing stakeholders' compromise and secondarily improving our understanding on ecosystems functioning (Castilla 2000, Walters et al. 2007, Wood et al. 2013).

Understanding the performance of fully or partially protected marine areas (no-take areas, TURFs) beyond the limits of the reserve is essential to really show the benefits for fishing grounds recovery and sustainable use of marine resources (Roberts et al. 2001, Gell & Roberts 2003, Halpern & Warner 2003, Sale et al. 2005). Spill over of exploitable biomass from no-take reserves clearly benefits fisheries (Goñi et al. 2006), and may help gain support for protected areas among stakeholders (Russ et al. 2004). Additionally, larger sizes and increased abundances of exploited species inside both fully (Gell & Roberts 2003, Lester et al. 2009) and partially (Gelcich et al. 2012) protected areas suggest that either process can enhance reproductive potential in protected areas in general. In fact, empirical evidence predicts between 2 to 5 times higher egg production in protected areas with respect to fished areas, based on a 30% larger commercial size abalone (Rogers-Bennett et al. 2002). For snapper (Pagrus auratus) relative egg production was estimated to be 18 times higher in no-take reserves than in adjacent fished areas (Willis et al. 2003). A 3-times greater gonad production per unit of area was also estimated in mussels inside marine reserves in South Africa, based on the combined effects of increased density and larger size individuals (Pelc et al. 2009). However, in sites exhibiting larger size individuals inside protected areas, but where density was not amplified, gonad production per unit of area was not higher, suggesting the importance of enhanced density on egg production. Egg production is also expected to change depending on the time elapsed since protection was established, allowing increase in size and abundance of exploited species. In fact, empirical evidence show an annual increase in egg production of lobster (Jasus edwarsii) after protection ranging between 4.8% and 9.1% in no-take reserves in New Zealand (Kelly et al. 2000). However, all these evidences do not account for the direct influence of protection on reproductive investment, as the analyses do not separate the relative importance of the indirect effect of enhancement of size and abundance of adult individuals on reproduction, from the direct influence of protection on gonad investment (Manríquez & Castilla 2001). Direct estimates of gonad weight in scallops (Pecten maximus) suggest that there can be an additional benefit of protection, directly on gonad investment, with gonad weight ranging between 20% and 25% higher in protected areas (Kaiser et al. 2007). Therefore, it is important to assess the relative importance of protection on adult size, density and gonad investment in enhancing reproductive potential of protected areas, since it is essential to understand (a) the influence of fishing effort on reproduction of exploited species, and (b) prospective spillover effects on background areas and networks of marine protected areas. It is also relevant to advance our understanding of the contribution of partially protected areas, such as TURFs that are growing globally, on biological variables beyond diversity, size or abundance.

The coast of central Chile is a good model to examine the influence of relevant, but poorly addressed biological variables, such as egg production, and also the most important variables influenced by human impact (size and density) in determining egg production. First, because the coast of Chile is one of the most productive coastal ecosystems of the world, yet, it is heavily impacted by artisanal fisheries, targeting a large number of fish, invertebrates and algae in rocky shores (Fernández & Castilla 2005). Second, because there is a mosaic of human impact, or fishing regimes, that includes few fully protected areas and a system of partially protected areas by fishers (TURFs), interspaced with unregulated fishing zones. Finally, because there is a need to advance in management and conservation plans for coastal areas, identifying the most relevant zones for propagules production (Tognelli et al. 2009), and the main determinants. Therefore, the main goal of this study was to develop a spatial model to predict potential egg production along the coast of central Chile, to analyze (a) the influence of human impacts on propagules production; and also (b) the most critical determinant of potential egg production. We chose two economically and ecologically valuable rocky reef species as a model, the keyhole limpet, *Fissurella latimarginata*, and the red sea urchin, *Loxechinus albus* both targeted by artisanal fishers. Thus, our results can have local relevance, but globally can also inform about the most important variables explaining egg production, and the potential losses in reseeding as a consequence of fishing.

Material and Methods

The Study System

The artisanal benthic fishery operating in Chile is characterized by a TURF system that was experimentally established in the early 90s, and formally implemented in the late 90s (Fernández & Castilla 2005). Under this TURF system, the fishers are organized within unions that administer a TURF and are obligated to conduct regular stock assessments. Fishers administering a TURF maintain a surveillance system and have exclusive fishing access to that TURF. Each year the fisher unions independently decide on the best local strategy to harvest their assigned quotas, following other nationwide regulations (such as minimum legal size, reproductive bans). However, the majority of the traditional fishing grounds is not under a TURF system and operates as traditional open access areas (Gelcich et al. 2012). In open access areas (OAAs), fishers holding a fishing license can extract benthic resources following national regulations (e.g., minimum legal size, reproductive bans). The fishing licenses restrict fishing activities to regional levels (at the scale of hundreds of kilometers). Minimum legal size and reproductive bans also regulate exploitation of benthic resources in OAAs, but enforcement is poor. Several species are targeted by the artisanal benthic fisheries in central Chile. However, the primary target resources include locos (Concholepas concholepas), keyhole limpets (a set of Fissurella species) and sea urchins (*Loxechinus albus*) (Fernández & Castilla 2005).

In spite of the increase in the fraction of the ocean protected in Chile, the coast of central Chile is exhibiting high influence of human impact, and low number (and surface area) of protected areas (Fernández & Castilla 2005). For this reason, the co-management system based on Territorial Use Rights for Fisheries (TURF) is seen as critical for management and conservation (Gelcich et al. 2010). First, abundance of benthic resources is higher inside TURFs than in background exploited areas (Gelcich et al. 2012). There is also evidence of larger sized individuals of exploited species inside TURFs (Brown et al. 1997, Anger & Moreira 1998, Castilla & Fernandez 1998, Gelcich et al. 2012). Moreover, TURFs in central Chile show similar patterns of abundance and adult size of exploited species than no-take areas (Gelcich et al. 2012). Second, social resistance to TURFs is not comparable with no-take areas. In fact, there are only 4 marine protected areas along more than 1000 km of coastline in the most populated region of Chile (from 30ºS to 36ºS); less than 0.001% protection of the coastal area. In contrast, in the same region there are 97 operative TURFs, covering 30% of the coastal area. Therefore, the TURF's system confers the opportunity to generate a network of partially protected areas that can serve both, together with other fully protected areas, to sustainable exploitation and to meet conservation goals (Gelcich et al. 2012). For this reason, it becomes important to assess the value of TURFs beyond their limits (e.g., potential egg production) and also, to evaluate what variable enhanced in protected areas (size, abundance, gonad investment) is the most critical determinants of potential egg production.

The predictions of our study cover the coast of central Chile, specifically between 31.57ºS and 36.00ºS (Fig 1A). In this region there are 75 operative TURFs, covering 31% of coastal area. Along this 795 km of coastline, we selected four sites concentrated between 32.61ºS and 33.50ºS, were samples were conducted to assess adult size, density and gonad investment. At each site, we selected areas with different fishing regimes: areas limiting fishing access and catches (TURFs) and areas where fishers are not restricted to enter and fish (OAAs). We sampled eight sites, four TURFs and four adjacent OAAs (Fig 1B). At each site, we measured size and density (individuals/m2) of both species by direct sampling, during 2012, and estimated potential fecundity (oocytes/female). Using this information, we estimated potential egg production, based on potential fecundity per unit of area per fishing regime.

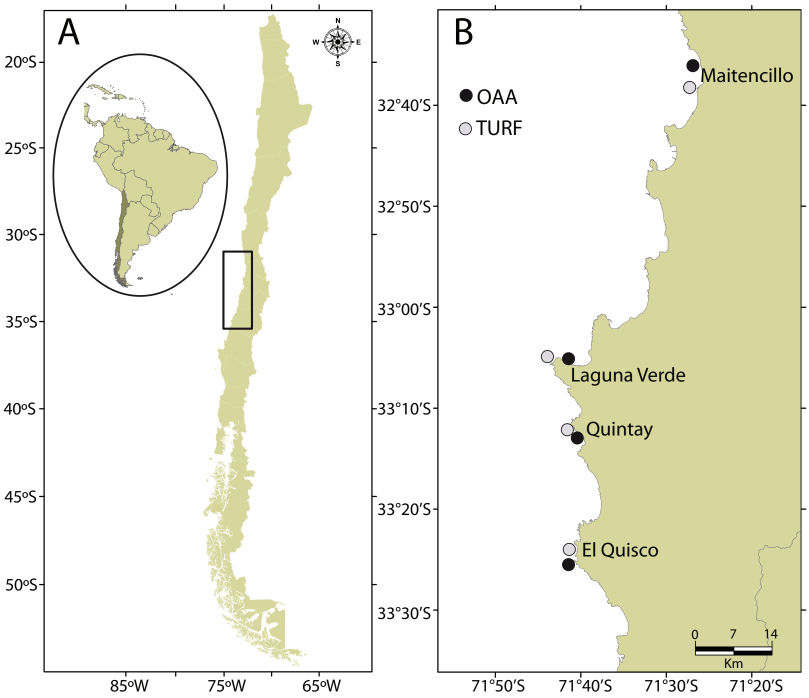


Fig. 1. Map of the study area. Maps of Chilean coast showing (A) the study region and (B) the sampling sites where direct collection of organisms was conducted. Fishing regimes are indicated in black circles (Open Access Areas; OAAs) and gray circles (Territorial Use Rights for Fisheries; TURFs).

Ethics Statement

The Chilean Navy and the Undersecretary of Fishing granted all necessary permission and permits to conduct the described fieldwork. Non-destructive manipulation of endangered or protected species was required.

Estimates of Potential Fecundity

Potential fecundity, defined as the number of oocytes in the ovary (per female) (Anger & Moreira 1998), was estimated. Individuals were collected at the beginning of the reproductive seasons (August - September) reported for *F. latimarginata* (Brown G. et al. 1997) and for *L. albus* (González et al. 1987). A total of 88 females of keyhole limpets and 75 females of sea urchins, larger than minimum size of reproduction (6 cm and 7 cm, respectively), were collected by professional divers. Specimens were frozen immediately and, later, length and wet gonad weight were recorded for each female. A small weighed fragment (0.2 ± 0.09 mg; mean= 0.119 mg) of the gonad was taken from the ovaries of each female, and preserved in 70% alcohol. Oocytes from each fragment were separated from the ovarian membrane through a washing process (Lowerre-Barbieri & Barbieri 1993). We used a 55 um mesh sieve to collect oocytes, which were then transferred to 100 ml vessel. A minimum of 3 aliquots of 3 ml were used to count the oocytes under the microscope. The number of oocytes was then expressed as the number of oocytes per mg of ovary. Oocytes per female were then calculated extrapolating the count to the total ovary weight. Thus, we were able to estimate potential fecundity, associated to the size distribution of each fishing regime, using the extracted model coefficients (α, intercept) and (β, slope) for the potential fecundity-size relationship described by the following regression model (Eq.1).

$$F=\alpha * e\hat{}(L * \beta) \qquad \text{Equation 1}$$

Where F is the potential fecundity (oocytes/female) and L is the size of each individual. Size was measured as peristomial length for keyhole limpets and diameter without spines for sea urchins. Mean potential fecundity per fishing regime was estimated as the average potential fecundity from all individuals of the sample characterizing each fishing regime, for each site.

To estimate potential egg production between fishing regimes, defined as the potential of a given site to produce eggs (oocytes) taking into account density and individual potential fecundity, densities of keyhole limpets and sea urchins were estimated using a visual census. We sampled four 50 m transects per site, positioned perpendicular to the coastline from 3 to 15 m depth, separated 30 m apart from each other. All individuals of both species were counted on a 2 m width strip along transect. We used existing data to determine the fraction of *F. latimarginata* from the remaining Fissurella species in the sample (see below). To estimate densities per square meter, counts per transect was summed across all stations. Finally, density per square meter was estimated.

In order to characterize size in each fishing regime professional divers took a sample ranging from 29 to 39 keyhole limpets per site (252 keyhole limpets total for fishing regime), and between 17 and 20 sea urchins per site (144 sea urchins total for fishing regime). An exception was El Quisco OAA were only 10 urchins were collected. Total length was measured. Using this sampling we estimated the proportion of females (R) sexing individuals at the laboratory by a dissecting procedure (N= 196 keyhole limpets and N=144 urchins). We relied on a large sampling conducted in 11 sites in our study region, between 1999 and 2009, to estimate (a) the proportion of *F. latimarginata* (K) and (b) the proportion of mature individuals (S). We considered mature individuals those that have reached the minimum size of reproduction (6 cm for *F. latimarginata* and 7 cm for *L. albus*). Based on size frequency distribution obtained from 9,245 individuals of *F. latimarginata* and 9,643 individuals of *L. albus*, we obtained the fraction of mature individuals. Based on a sample of 22,456 individuals, we estimated the fraction of *F. latimarginata*.

Using Eq. 1, we obtained the mean potential fecundity in each site. Density, size, potential fecundity and mean potential egg production were compared between fishing regimes. We considered fishing regime as a fixed factor with two levels TURFs and OAAs. These comparisons were conducted using a Generalized Linear Model (GLM) analysis. For the variable density, we used quasipoisson family error distribution. For the variable potential fecundity and potential egg production we used inverse gaussian and for size we used gaussian family error distribution. The choice of the most appropriate link function and error distribution was made based on residual analyses. We tested the goodness of fitted model with a Chi-

Squared test based on residual deviance and degrees of freedom (significance level 0.05). All the statistical analysis were done using R software, version (3.1.3) (R 2013).

Potential Egg Production

To determine the spatial variability in potential egg production in relation to fishing regimes, we used the following equations:

$$P_{(F.latimarginata)}=F*D*R*S*K \qquad \text{Equation 2}$$

$$P_{(L.albus)}=F*D*R*S \qquad \text{Equation 3}$$

Where P is the potential egg production (oocytes/m2), F is the potential fecundity (oocytes/female) from Eq. 1, D is the density (individuals/m2), R is the proportion of females, S is the proportion of mature individuals and K (parameter used for *F. latimarginata* in Eq. 2), is the proportion of *F. latimarginata* in the sample of keyhole limpets. Parameters R, S and K were assumed fixed while potential fecundity (F) and density (D) varied spatially depending on available rocky shore habitat and fishing regime. Spatial variability in F and D of Eqs. 2 and 3, derive from Eqs. 4 to 6.

Spatial Data

In order to account for spatial variability of rocky habitat and fishing regimes (TURFs and OAAs) along the coast of central Chile, we developed an indicator of the condition of small fractions of the coast (grids of 2 latitudinal kilometers). Condition was determined based on availability of suitable habitat and fishing regime. First, the coastline was obtained from digitalized Chilean Military Geographic Institute (IGM) charts 1:250,000. Then, we characterized the habitat type using high-resolution satellite photography. Second, we characterized the fishing regime (TURFs and OAAs) based on the presence or absence of TURFs in each coast fragment, using data available from SUBPESCA. All digitalization was conducted with the software ArcGis 9.3. The results were expressed as a percentage of total coast length containing suitable habitat and TURFs in a grid of two latitudinal kilometers. Third, a scaling factor between fishing regime (Ratio TURF/OAA) was estimated to account for differences in density (D) and potential fecundity (F) between fishing regimes (TURFs and OAAs). The factor was calculated for each parameter (D and F) for each species. Finally, we created an indicator to associate the scale of increase in density or potential fecundity (Ratio TURF/OAA) to the percentage of suitable habitat (rocky shores) associated to restricted areas (pTURF). This indicator of spatial variability (Spatial Var) was calculated considering the Ratio TURF/OAA for density (D) and potential fecundity (F), for 134 coastal units (2 latitudinal km grid) along the study area (Eq. 4).

$$\text{Spatial Var}=(\text{pTURF}*\text{Ratio (TURF/OAA)})+(\text{pR}-\text{pTURF}) \qquad \text{Equation 4}$$

Where pR is the percentage of coastline with rocky shore habitat. In order to obtain the indicator of spatial variability (Spatial Var) for each coastal unit, a linear regression between the indicator (Spatial Var) and the variables of interest (potential fecundity and density) was estimated for the 8 grids containing the areas sampled in our study. Then, we used these relationships to predict potential fecundity (F) and density (D) for the 134 units of our regional domain.

$$D=\text{Spatial Var}*\beta_D \qquad \text{Equation 5}$$

$$F=\text{Spatial Var}*\beta_F \qquad \text{Equation 6}$$

Where Spatial Var is the value obtained by Eq. 4, βD is the slope of the regression between density (D) and Spatial Var, and βF is the slope of the regression between potential fecundity (F) and Spatial Var. When Spatial Var is 0, the value of density, and therefore potential fecundity, is always 0 (not suitable rocky habitat). Using all these estimates, we were able to calculate potential egg production (P) for the study area:

$$P_{(F.latimarginata)}=(\text{Spatial Var}*\beta_F)*(\text{Spatial Var}*\beta_D)*R*S*K \qquad \text{Equation 7}$$

$$P_{(L.albus)}=(\text{Spatial Var}*\beta_F)*(\text{Spatial Var}*\beta_D)*R*S \qquad \text{Equation 8}$$

In order to determine the influence of available rocky habitat and fishing regime on predicted potential egg production, we compared the predicted potential egg production (dependent variable), in 134 coastal units, across the values of percentage of coastline with rocky habitat (pR) and the percentage of coastline with rocky habitat associated to TURFs areas (pTURF) (both as independent variables). These comparisons were conducted using a GLM analysis with a quasipoisson family error distribution. Furthermore, to evaluate the influence of human impacts on propagules production we compared two scenarios: (a) a full restricted access scenario against a full open access and (b) the current system of TURFs against a full open access scenario.

In order to define the most critical determinant of potential egg production, we compared the mean egg production per site (dependent variable), across mean density and mean size (independent variables) obtained in each site using an ANCOVA analysis.

Results

Density and Potential Fecundity

The relationship between potential fecundity (F) and total length (L) was described by an exponential model function for both species, showing the expected increase of potential fecundity with size. Estimated potential fecundity was $F = 548{,}500\ (258{,}100)\ e^{L*0.31\ (\pm 0.05)}$ (df = 87, p-value < 0.01) for keyhole limpet and $F = 1{,}745\ (1{,}338)\ e^{L*0.74\ (\pm 0.08)}$ (df = 75, p-value < 0.01) for sea urchin.

Fishing regime showed a significant effect on mean size (L), density (D), potential fecundity (F) and potential egg production (P) of *F. latimarginata* (p-value always < 0.05) (Table 1A). On average, density of keyhole limpets was 65% higher in TURFs compared with OAAs (Fig. 2A). Size was also significantly different between fishing regimes, although the change was smaller (13%; Fig 2C). Potential fecundity was also 68% greater in TURFs in comparison to OAAs. Similarly, potential egg production was six-fold higher in TURFs than in OAAs (Figs 2E and 2G, Table 1). In contrast, no significant effect of fishing regime on density, size, potential fecundity and potential egg production was observed for *L. albus* (Table 1B). Although density of sea urchins in TURFs appeared to be two-fold higher than in OAAs, the large variability observed among sites in this species did not yield statistical differences (Fig. 2B). Sea urchin size was not significantly different between fishing regimes (Fig. 2D, Table 1B). No difference in potential fecundity and high variability were also observed between TURFs and OAAs (Fig. 2F, Table 1). Similarly, the influence of fishing regime on potential egg production was not significant despite an apparent two-fold larger potential egg production in TURFs (Fig. 2H, Table 1).

Table 1. Generalized linear models. Statistical results of the generalized linear models (GLM) applied to density, individual size, potential fecundity and potential egg production, across two fishing regime: TURFs (Territorial Use Rights for Fisheries) and OAAs (Open Access Areas).

A. *Fissurella Latimarginata*					
Model: glm (Density ~ Fishing Regime, family= quasipoisson)					
Deviance Explained: 18.47 %					
	Df	Deviance	Resid. Df	Resid. Dev.	Pr (>Chi)
NULL			31	0.95	
Fishing Regime	1	0.20	30	0.75	0.01
Model: glm (Size ~ Fishing Regime, family= gaussian)					
Deviance Explained: 14.20 %					
	Df	Deviance	Resid. Df	Resid. Dev.	Pr (>Chi)
NULL			251	440.99	
Fishing Regime	1	62.64	250	378.36	$1.25*10^{-10}$
Model: glm (Potential Fecundity ~ Fishing Regime, family= inverse.gaussian)					
Deviance Explained: 4.82%					
	Df	Deviance	Resid. Df	Resid. Dev.	Pr (>Chi)
NULL			251	$2.87*10^{-4}$	
Fishing Regime	1	$1.84*10^{-5}$	250	$2.73*10^{-4}$	$7.90*10^{-5}$
Model: glm (Potential Egg Production ~ Fishing Regime, family= inverse.gaussian)					
Deviance Explained: 57.71%					
	Df	Deviance	Resid. Df	Resid. Dev.	Pr (>Chi)
NULL			7	$9.43*10^{-4}$	
Fishing Regime	1	$5.44*10^{-4}$	6	$3.98*10^{-4}$	0.005
B. *Loxechinus albus*					
Model: glm (Density ~ Fishing Regime, family= quasipoisson)					
Deviance Explained: 6.93 %					
	Df	Deviance	Resid. Df	Resid. Dev.	Pr (>Chi)
NULL			15	1.99	
Fishing Regime	1	0.13	14	1.86	0.31
Model: glm (Size ~ Fishing Regime, family= gaussian)					
Deviance Explained: 1.47 %					
	Df	Deviance	Resid. Df	Resid. Dev.	Pr (>Chi)
NULL			143	214.90	
Fishing Regime	1	3.17	142	211.73	0.14
Model: glm (Potential Fecundity ~ Fishing Regime, family= inverse.gaussian)					
Deviance Explained: 0.17%					
	Df	Deviance	Resid. Df	Resid. Dev.	Pr (>Chi)
NULL			143	$2.22*10^{-6}$	
Fishing Regime	1	$3.64*10^{-9}$	142	$6.21*10^{-6}$	0.63

Model: glm (Potential Egg Production ~ Fishing Regime, family= inverse.gaussian)
Deviance Explained: 13.87 %

	Df	Deviance	Resid. Df	Resid. Dev.	Pr (>Chi)
NULL			3	$2.13*10^{-5}$	
Fishing Regime	1	$2.96*10^{-6}$	2	$1.83*10^{-5}$	0.43

Spatial Variability in Potential Egg Production

The spawning fraction (R) for *F. latimarginata* was 0.48 and for *L. albus* was 0.44. The fraction of mature individuals (S) was 0.84 for *F. latimarginata* and 0.69 for *L. albus*. The fraction of *F. latimarginata* in the keyhole limpet samples (K) was 0.43 (S1 Table). These estimates were used as constants in Eqs. 2 and 3. The linear models selected to describe the relationship between density (D) and potential fecundity (F) against the indicator Spatial Var were statistically significant (Table 2).

Using the coefficients estimated by the linear regressions in the study sites, P (potential egg production) was predicted for the 134 units in the regional domain of our study as follows:

$$P_{(F.latimarginata)}=(\text{Spatial Var}*11{,}977)*(\text{Spatial Var}*0.00108)*0.48*0.84*0.43 \qquad \text{Equation 9}$$

$$P_{(L.albus)}=(\text{Spatial Var}*123{,}780)*(\text{Spatial Var}*0.00035)*0.44*0.69 \qquad \text{Equation 10}$$

In the study zone, 379 of 795 km of coastline (47.7%) between 31.57°S and 36.00°S showed rocky habitat suitable for each species under study. We estimated that 21.27% (169 km) of coastline exhibited restricted access, distributed in 75 operative TURFs. The highest percentage of rocky habitat under TURF was found between 31.57°S and 33.50°S (49.94% of the coastline), while in the southern section of the study region (33.50°S to 36.00°S) fewer TURFs associated to suitable rocky habitat were present (27.79% of the coastline; Fig 3A).

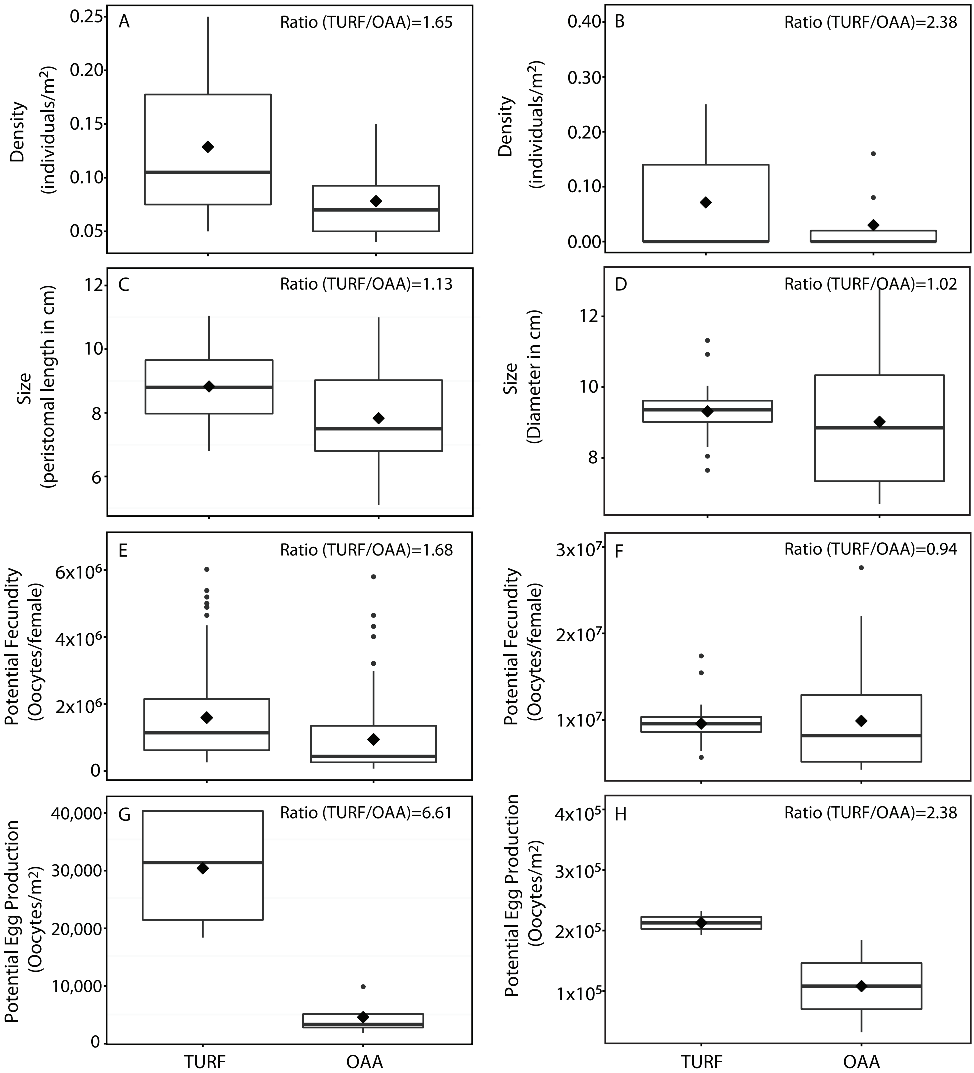


Fig. 2. Biological variables between fishing regimes. Box plots showing density, size, potential fecundity and potential egg production in areas under different fishing regimes: Territorial Use Rights for Fisheries (TURF) and Open Access Areas (OAAs; not limiting the entry of fishers). The number in the right corner in each plot indicates the ratio between fishing regimes (TURF/OAA) for each variable. Black diamonds' indicate mean: (A) *Fissurella latimarginata* density; (B) *Loxechinus albus* density; (C) *F. latimarginata* size; (D) *L. albus* size; (E) *F. latimarginata* potential fecundity; (F) *L. albus* potential fecundity; (G) *F. latimarginata* potential egg production; and (H) *L. albus* potential egg production.

The spatial distribution of potential egg production predicted by the model showed similar patterns for both species, driven by the distribution of suitable habitat. Suitable habitat explained 91.57% (F=2652.60, df=1, p<0.001) and 94.78% (F=2788.02, df=1, p<0.001) of total variability in potential egg production of keyhole limpets and sea urchins, respectively. The highest percentage of potential egg production occurred in the north region of studied domain, where about 80% of potential egg production of both species were concentrated between 31.57°S and 33.50°S (Fig. 3). In the southern region of the studied domain (33.50°S to 36.00°S), where suitable rocky habitat is present only along 24% of the coastline, egg production was lower. However, fishing regime influenced potential egg production in suitable habitats. The system of TURFs in our study region increased potential egg production of *F. latimarginata* by 67% against the predicted production under a complete OAAs scenario (Fig. 4A). The increase was smaller for *L. albus* (52%; Fig. 4B). Our predictions also showed the enormous influence

Table 2. Linear regressions. Linear models relating density and potential fecundity, both dependent variables and Indicator (Spatial Var; independent variable). Linear regressions were used to obtain the relationship between the indicator (Spatial Var) and the variables studied (potential fecundity and density).

A. Fissurella latimarginata				
Model: lm (Density ~ Spatial Var- 1)				
R^2= 0.86				
	Estimate	Std. Error	T value	Pr (>| t |)
Slope (β_D)	$1.08*10^{-3}$	$1.52*10^{-4}$	7.17	$1.8*10^{-4}$
Model: lm (Potential Fecundity ~ Spatial Var - 1)				
R^2= 0.56				
	Estimate	Std. Error	T value	Pr (>| t |)
Slope (β_F)	11977	3592	3.33	0.01
B. ***Loxechinus albus***				
Model: lm (Density ~ Spatial Var - 1)				
R^2= 0.87				
	Estimate	Std. Error	T value	Pr (>| t |)
Slope (β_D)	$3.52*10^{-4}$	$6.53*10^{-5}$	5.39	0.01
Model: lm (Potential Fecundity ~ Spatial Var - 1)				
R^2= 0.88				
	Estimate	Std. Error	T value	Pr (>| t |)
Slope (β_F)	123780	15395	8.04	$8.83*10^{-5}$

of fishing in reducing potential egg production of both species. Potential egg production showed more than a twofold reduction when the complete TURFs scenario was compared against complete OAAs condition in both species (Figs. 4A and B).

Size explained a similar proportion of the variability in potential egg production in both species (keyhole limpet: 23.09%, sea urchin: 20.22%; Table 3). However, the contribution of density to explain the variability in egg production potential was different between both species. Density explained 37.26% of the total variability in potential egg production in keyhole limpets and 79.77% in sea urchins (Table 3).

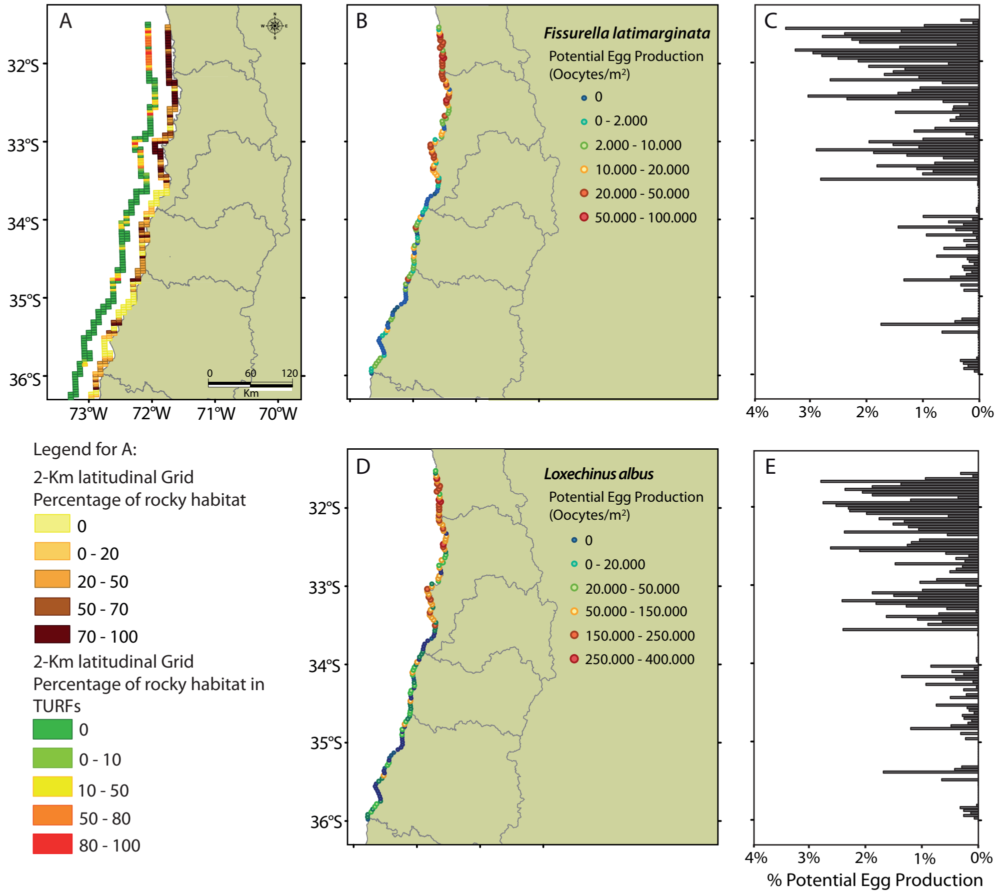


Fig. 3. Spatial distribution of habitat, restricted access areas and potential egg production. Spatial maps showing (A) percentage of coastline with rocky habitat and restricted access (Territorial Use Rights for Fisheries, TURFs) and (B, D) predicted potential egg production (oocytes/m2) along a latitudinal gradient with a 2-km grid resolution. Plots C and E show the contribution (percentage) of oocytes/m2 (potential egg production) of each grid to the regional (study area) production.

Discussion

In a global context, our main results show the influences of TURFs in enhancing size and density of exploited species and the direct consequences of enhanced size and density on potential egg production, thereby suggesting an important role of partially protected areas in producing propagules to seed exploited areas. Our results show further influences of management regime, as potential egg production was up to 200% lower in open access areas. Finally, although we did not find consistent results for both species we were able to determine enhanced potential egg production. Locally, our results are relevant for identifying the main regions along the coast of central Chile that exhibit higher potential for egg production in two important, exploited resources, the keyhole limpet (*F. latimarginata*) and the red sea urchin (*L. albus*).

In accordance with published evidence, our results show the general benefits of protection enhancing relevant biological variables, such as abundance and/or adult size inside TURFs boundaries (Lester & Halpern 2008, Gelcich et al. 2012). Although fully protected areas offer greater benefits than partially protected areas

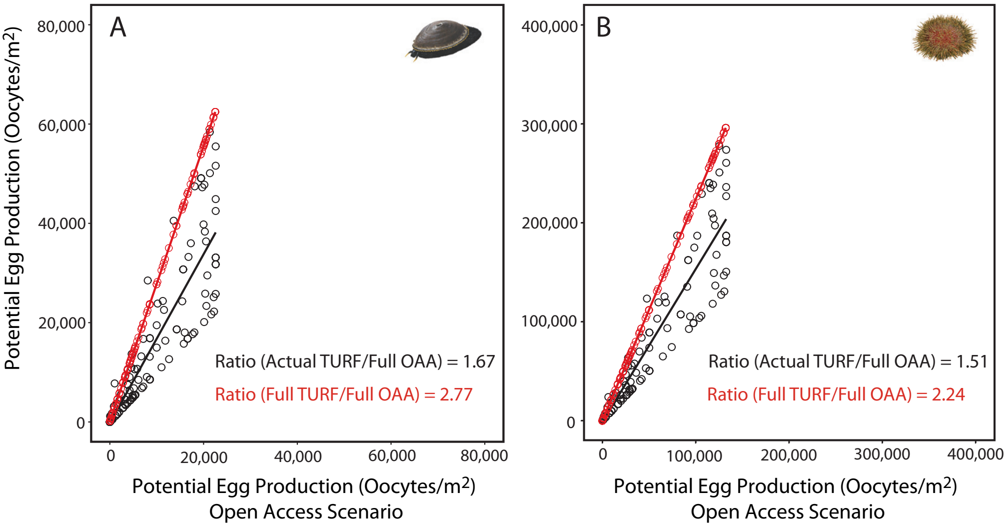


Fig. 4. Influence of fishing on potential egg production. Comparison of potential egg production between the open access areas (OAAs) scenario against (a) current scenario (existing Territorial Use Rights for Fisheries, TURFs; black line and symbols) and (b) full protection (all TURFs; red line and symbols) for (A) *Fissurella latimarginata* and (B) *Loxechinus albus*. The numbers in the lower right corner in each plot show the ratio in potential egg production from the two scenarios.

(74% greater density and 30% larger sizes, (Lester & Halpern 2008)), partially protected areas, such as TURFs, also generally showed significant effects in these two biological variables. Our results comparing TURFs and OAAs show similar patterns in density and size of exploited resources as expected from a synthesis of empirical studies comparing these biological variables in partially protected and background areas across a range of geographic locations worldwide (on average, 36% higher density, and 10% larger sizes in protected areas than in background areas (Lester & Halpern 2008)). We found that sizes were between 2% and 13% larger, and density between 65% and 238% higher (although non-significant for sea urchin) in TURFs than in open access areas. The large variability in density of sea urchins both in TURFs and open access areas may have precluded us from identifying a clear and significant pattern of higher density in TURFs for both species. Previous studies have also reported a lower impact of protection on *L. albus*, and larger variability in abundance, probably related to the patchy distribution of suitable microhabitats (Gelcich et al. 2012). *L. albus* is predominantly associated with highly wave exposed zones, where they are frequently found forming aggregations.

Our results also suggest that the enhanced biological variables can potentially amplify the benefits of protection outside the boundaries of protected areas by increasing individual production of dispersive propagules (Roberts et al. 2001,

Table 3. Influence of size and density on potential egg production. Statistical results of the effect of density and size on potential egg production.

A. *Fissurella latimarginata*					
Model: ANCOVA (Potential Egg Production ~ Density + Size)					
	Df	Sum Sq	Mean Sq	Pr (>| F |)	Exp Var (%)
Density	1	$6.62*10^{8}$	$6.62*10^{8}$	0.08	37.26
Size	1	$4.10*10^{8}$	$4.10*10^{8}$	0.15	23.09
Residuals	5	$7.04*10^{8}$	$1.42*10^{8}$		
B. *Loxechinus albus*					
Model: ANCOVA (Potential Egg Production ~ Density + Size)					
	Df	Sum Sq	Mean Sq	Pr (>| F |)	Exp Var (%)
Density	1	$1.86*10^{10}$	$1.86*10^{10}$	$1.47*10^{-3}$	79.77
Size	1	$4.72*10^{9}$	$4.72*10^{9}$	$2.92*10^{-3}$	20.22
Residuals	1	$9.92*10^{4}$	$9.92*10^{4}$		

Halpern 2003, Lester et al. 2009). First, the models we used to analyze potential fecundity showed an exponential increase in fecundity with size in both species. Second, the 13% differences in keyhole limpets´ size in TURFs compared to OAAs produced a 68% greater potential fecundity of females. The size increase between TURFs and OAA is smaller than the average 30% increase in size reported in a worldwide analysis comparing individual size between no-take and open access areas (Lester et al. 2009). Since small changes in size can have tremendous impact on potential fecundity, even the contribution of partially protected areas (10% larger sizes) to potential egg production through size enhancement of reproductive individuals might be substantial (Lester et al. 2009). Worldwide evidence shows that on average, the greater sizes in no-take areas, up to 200% larger than in partially protected areas (Lester et al. 2009), can disproportionally influence dependent variables such as potential egg production. Therefore, it is important to further explore the relevance of enhanced size on potential fecundity in fully and partially protected areas. We recognize that effective larval spillover requires a broader approach, including other factors not considered in this study, from fertilization success to processes affecting planktonic larval phases and local adaptation of early recruits (Fogarty & Botsford 2007, Prado et al. 2009). However, enhanced fertilization success can also be predicted in areas of higher population density (Levitan 1991) such as TURFs or no-take areas. It is also important to keep in mind the variability among species. Our analysis also suggests that differences in mean size of 2% between TURFs and OAAs of sea urchins do not produce significant differences in average potential fecundity.

The relevance of density in determining gonad production per unit of area has been clearly shown in the literature (Kelly et al. 2000, Willis et al. 2003, Pelc et al. 2009). However, the interplay between the combined effects of density and size is less clear and our results did not yield clear conclusions in this direction. In the case of keyhole limpets, for which density and size were enhanced in TURFs areas, a significant difference in potential egg production was recorded. The comparison between the two species showed that potential egg production of *F. latimarginata* increased by protection 277% more than *L. albus* due to the combined influence of larger size and higher densities in TURFs. In spite of the fact that we did not find significant differences in sea urchin density and size associated to fishing regime, the spatial variability in potential egg production of sea urchin is mainly explained by density (80%) and secondly by size (20%). Size differences ranging between 2 and 13% between open access and TURFs areas seem to explain about 20% of the variability in potential egg production. Thus, our results suggest that density might have a larger influence on variability in potential egg production than individual size. However, a third factor to consider is the direct influence of protection on reproductive investment, and therefore egg production. So far, most evidence is insufficient for determining the relative importance of protection indirectly on adult size and density, and directly on gonad investment in enhancing reproductive potential in protected areas. Direct estimates of gonad weight in scallops (Pecten maximus) suggest that there can be an additional benefit of protection directly on gonad investment, with differences of gonad weight ranging between 20 and 25% in protected areas (Kaiser et al. 2007). Therefore, it is important to increase the available information in general, to assess the direct influence of protection on gonad production. Further explorations, however, are needed to understand the most relevant determinants of egg production in protected areas, and to advance in strategies to enhance the benefits of protection outside the boundaries of protected areas (e.g., placing protected areas in sites assuring spill over, based on circulation patterns).

Our results show that the system of TURFs areas in our study region enhanced potential egg production of *F. latimarginata* by 67% in comparison to a complete open access scenario. In the case of sea urchins, a 52% greater potential egg production was estimated. Although a similar trend towards increasing potential egg production has been observed in other invertebrate species (Kelly et al. 2000, Rogers-Bennett et al. 2002, Pelc et al. 2009), the magnitude of the change is substantially different. Empirical evidence predicts between 2 to 5 times greater egg production in pink abalone (Haliotis corrugata) (Rogers-Bennett et al. 2002). A 10% increase in egg production of lobster (Jasus edwarsii) per year after closure was estimated, suggesting a 4 fold increase over 15 years (average age of the partially protected areas studied here). We relate the smaller changes in the two species studied here to the fact that the protected areas used in this study are also fishing areas (partially protected). Consistently, the comparison of our results of egg production against studies conducted with invertebrates in no-take areas in other regions show that fully protected areas can provide higher benefits than partially protected areas, such as TURFs. However, partial protection may be the only possible form of protection in highly populated regions (Tognelli et al. 2009), and can still have significant positive influence in potential seeding.

In our case, the influence of fishing is so high, that a 277% greater potential egg production of *F. latimarginata* can be expected between a complete OAAs scenario in comparison with a TURFs scenario. This hypothetical comparison against a no-take scenario is more similar to the studies comparing no-take areas in other invertebrate species (Kelly et al. 2000, Rogers-Bennett et al. 2002, Pelc et al. 2009). In the case of *L. albus* a 224% increase can be expected. In our study region, we did not have enough no-take areas to include a set to compare the three levels of human impact (fishing regime) to really evaluate the influence of a gradient in fishing effort on potential egg production. However, our results suggest that the intermediate effect of TURFs can still contribute substantially to enhancing egg production in the study area and potentially contribute to seeding exploited areas.

Our results also provide insights for management and conservation at the local level. The highest percentage of potential egg production was estimated in the north region of studied domain for both species, following the distribution of suitable habitat. More than 80% of potential egg production of *F. latimarginata* and *L. albus* were produced between 31.57ºS and 33.50ºS. It is worth noticing that the northern part of our study area also concentrates more than 90% of landings of both species (SERNAPESCA 2013). This pattern may be driven not only by abundance of resources (and habitat), but also by differences in fishing pressure among sites (de Juan et al. 2015). The map of potential egg production, combined with other processes, such as coastal circulation patterns, can be a key element to design a network of partially and fully protected areas in one of the most productive, yet exploited coastal regions of the world. Our results show the relevance of focusing conservation efforts in the most important area for potential egg production, the northern domain of our study area, although it may imply restricting fishing effort. However, the potential distribution of propagules needs to be coupled with hydrodynamic and biological models would allow to improve our understanding of larval supply to different areas of the coast, by identifying source and sink populations (Metaxas & Saunders 2009).

Acknowledgments

We thank B. Bularz, S. López, R. Calderón, M. Figueroa, C. Ruano and M. Andreu for their help in data collection and processing samples in the laboratory. S. Tapia and N. Godoy also helped conducting subtidal surveys to assess density. We also thank G.R. Finke for final revision of the manuscript and C. Styan and two anonymous reviewers for their helpful comments.

References

Aburto-Oropeza O, Erisman B, Galland GR, Mascareñas-Osorio I, Sala E, Ezcurra E (2011) Large Recovery of Fish Biomass in a No-Take Marine Reserve. PLoS One 6:e23601

Afflerbach JC, Lester SE, Dougherty DT, Poon SE (2014) A global survey of “TURF-reserves”, Territorial Use Rights for Fisheries coupled with marine reserves. Glob Ecol Conserv. 2: 97-106

Anger K, Moreira GS (1998) Morphometric and Reproductive Traits of Tropical Caridean Shrimps. J Crustac Biol 18:823–838

Brown G. DI, Gonzalez M, Lopez D, Duran L, Rivero R, Collado G, Betancourt C (1997) Informe Final Proyecto FIP-IT/94-33. Estudio de los ciclos vitales de las especies comerciales de lapas del genero *Fissurella sp*, en las regiones I a X. :196

Castilla JC (1999) Coastal marine communities: trends and perspectives from human-exclusion experiments. Trends Ecol Evol 14:280–283

Castilla JC (2000) Roles of experimental marine ecology in coastal management and conservation. J Exp Mar Bio Ecol 250:3–21

Castilla JC, Durán LR (1985) Human exclusion from the rocky intertidal zone of central Chile: the effects on *Concholepas concholepas* (Gastropoda). Oikos:391–399

Castilla J, Fernández M (1998) Small-scale benthic fisheries in Chile: on co-management and sustainable use of benthic invertebrates. Ecol Appl 8:S124

Costello C, Ovando D, Hilborn R, Gaines SD, Deschenes O, Lester SE (2013) Status and solutions for the world’s unassessed fisheries. Science (80-) 517

Denny CM, Willis TJ, Babcock RC (2004) Rapid recolonisation of snapper *Pagrus auratus*: Sparidae within an offshore island marine reserve after implementation of no-take status. Mar Ecol Prog Ser 272:183–190

Edgar GJ, Barrett NS (1999) Effects of the declaration of marine reserves on

Tasmanian reef fishes, invertebrates and plants. J Exp Mar Bio Ecol 242:107–144

FAO (2014) Countries recognize vital role of small-scale fishers.

Fernández M, Castilla JC (2005) Marine conservation in Chile: Historical perspective, lessons, and challenges. Conserv Biol 19:1752–1762

Fogarty MJ, Botsford LW (2007) Population connectivity and spatial management of marine fisheries. Oceanography 20:112–123

Freire J, García-Allut A (2000) Socioeconomic and biological causes of management failures in European artisanal fisheries: The case of Galicia (NW Spain). Mar Policy 24:375–384

Gelcich S, Fernández M, Godoy N, Canepa A, Prado L, Castilla JC (2012) Territorial user rights for fisheries as ancillary instruments for marine coastal conservation in Chile. Conserv Biol 26:1005–15

Gelcich S, Hughes TP, Olsson P, Folke C, Defeo O, Fernández M, Foale S, Gunderson LH, Rodríguez-Sickert C, Scheffer M, Steneck RS, Castilla JC (2010) Navigating transformations in governance of Chilean marine coastal resources. PNAS 107:16794–9

Gell FR, Roberts CM (2003) Benefits beyond boundaries: the fishery effects of marine reserves. Trends Ecol Evol 18:448–455

González L, Castilla J, Guisado C (1987) Effects of larval diet and rearing temperature on metamorphosis and juvenile survival of the sea urchin *Loxechinus albus* (Molina, 1782) (Echinodermata: Echinoidea). J Shellfish Res 6:109–115

Goñi R, Quetglas A, Reñones O (2006) Spillover of spiny lobsters *Palinurus elephas* from a marine reserve to an adjoining fishery. Mar Ecol Prog Ser 308:207–219

Halpern BS (2003) The impact of marine reserves: Do reserves work and does reserve size matter? Ecol Appl 13:S117–S137

Halpern BS, Walbridge S, Selkoe KA, Kappel C., Micheli F, D'Agrosa C, Casey K., Ebert C, Fox H., Fujita R, Heinemann D, Lenihan H., P.Madin E., Perry M., Selig E., Spaldin M, Steneck R, Watson R (2008) A Global Map of Human Impact on Marine Ecosystems. Science (80-) 319:948–952

Halpern BS, Warner RR (2003) Matching marine reserve design to reserve objectives. Proc R Soc Lond B 270:1871–8

Jennings S, Marshall SS, C. Polunin NV (1996) Seychelles marine protected areas: comparative structure and status of reef fish communities. Biol Conserv 75:201–209

Juan S de, Gelcich S, Ospina-Alvarez A, Perez-Matus A, Fernández M (2015) Applying an ecosystem service approach to unravel links between ecosystems and society in the coast of central Chile. Sci Total Environ 533:122–132

Kaiser MJ, Blyth-Skyrme RE, Hart PJB, Edwards-Jones G, Palmer D (2007) Evidence for greater reproductive output per unit area in areas protected from fishing. Can. J. Fish. aquat. Sci. 64: 1284-1289

Kelly S, Scott D, MacDiarmid AB, Babcock RC (2000) Spiny lobster, *Jasus edwardsii*, recovery in New Zealand marine reserves. Biol Conserv 92:359–369

Lester SE, Halpern BS (2008) Biological responses in marine no-take reserves versus partially protected areas. Mar Ecol Prog Ser 367:49–56

Lester SE, Halpern B., Grorud-Colvert K, Lubchenco J, Ruttenberg BI, Gaines SD, Airamé S, Warner RR (2009) Biological effects within no-take marine reserves: a global synthesis. Mar Ecol Prog Ser 384:33–46

Levin PS, Fogarty MJ, Murawski SA, Fluharty D (2009) Integrated Ecosystem Assessments: Developing the Scientific Basis for Ecosystem-Based Management of the Ocean. PLoS Biol 7:e1000014

Levitan DR (1991) Influence of Body Size and Population Density on Fertilization Success and Reproductive Output in a Free-Spawning Invertebrate. Biol Bull 181:261–268

Lowerre-Barbieri SK, Barbieri LR (1993) A new method of oocyte separation and preservation for fish reproduction studies. Fish Bull 91:165–170

Manríquez PH, Castilla JC (2001) Significance of marine protected areas in central Chile as seeding grounds for the gastropod *Concholepas concholepas*. Mar Ecol Prog Ser 215:201–211

Metaxas A, Saunders M (2009) Quantifying the "bio-" components in biophysical models of larval transport in marine benthic invertebrates: advances and pitfalls. BiolBull 216:257–72

Murray SN, Ambrose RF, Bohnsack JA, Botsford LW, Carr MH, Davis GE, Dayton PK, Gotshall D, Gunderson DR, Hixon MA, Lubchenco J, Mangel M, MacCall A, McArdle DA, Ogden JC, Roughgarden J, Starr RM, Tegner MJ, Yoklavich MM (1999) No-take Reserve Networks: Sustaining Fishery Populations and Marine Ecosystems. Fisheries 24:11–25

Myers RA, Worm B (2003) Rapid worldwide depletion of predatory fish communities. Nature 423:280–283

Pauly D, Christensen V, Dalsgaard J, Froese R, Torres Jr. F (1998) Fishing down the food webs. Science (80-) 279:860–863

Pelc R, Baskett M, Tanci T, Gaines S, Warner R (2009) Quantifying larval export from South African marine reserves. Mar Ecol Prog Ser 394:65–78

Prado P, Romero J, Alcoverro T (2009) Welcome mats? The role of seagrass meadow structure in controlling post-settlement survival in a keystone sea-urchin species. Estuar Coast Shelf Sci 85:472–478

R DCT (2013) R: A Language and Environment for Statistical Computing.

Roberts CM, Bohnsack JA, Gell F, Hawkins JP, Goodridge R (2001) Effects of marine reserves on adjacent fisheries. Science (80-) 294:1920–1923

Rogers-Bennett L, Haaker PL, Karpov KA, Kushner DJ (2002) Using Spatially Areas Explicit for Data to Marine Protected Abalone in California. Conserv Biol 16:1308–1317

Russ GR, Alcala AC, Maypa AP, Calumpong HP, White AT (2004) Marine reserve benefits local fisheries. Ecol Appl 14:597–606

Sale PF, Cowen RK, Danilowicz B., Jones GP, Kritzer JP, Lindeman KC, Planes S, Polunin NVC, Russ GR, Sadovy YJ, Steneck RS (2005) Critical science gaps impede use of no-take fishery reserves. Trends Ecol Evol 20:74–80

Shears NT, Grace RV, Usmar NR, Kerr V, Babcock RC (2006) Long-term trends in lobster populations in a partially protected vs. no-take Marine Park. Biol Conserv 132:222–231

Tognelli MF, Fernández M, Marquet PA (2009) Assessing the performance of the existing and proposed network of marine protected areas to conserve marine biodiversity in Chile. Biol Conserv 142:3147–3153

Walters CJ, Hilborn R, Parrish R (2007) An equilibrium model for predicting the efficacy of marine protected areas in coastal environments. Can J Fish Aquat Sci 64:1009–1018

Willis TJ, Millar RB, Babcock RC (2003) Protection of exploited fish in temperate regions: high density and biomass of snapper. J Appl Ecol 40:214–227

Wood CL, Micheli F, Fernández M, Gelcich S, Castilla JC, Carvajal J (2013) Marine protected areas facilitate parasite populations among four fished host species of central Chile. J Anim Ecol 82:1276–87

Worm B, Hilborn R, Baum JK, Branch TA, Collie JS, Costello C, Fogarty MJ, Fulton EA, Hutchings JA, Jennings S, Jensen OP, Lotze HK, Mace PM, McClanahan TR, Minto C, Palumbi SR, Parma AM, Ricard D, Rosenberg AA, Watson R, Zeller D (2009) Rebuilding Global Fisheries. Science (80-) 325:578–585

Chapter 3

Influence of larval traits on dispersal and connectivity patterns of two exploited marine invertebrates in central Chile

Chapter 3

This Chapter is based on:

Blanco, M., Ospina-Álvarez, A., Aiken, C.M., Navarrete, S.A., Fernández, M. (Submitted). Influence of larval traits on dispersal and connectivity patterns of two exploited marine invertebrates in central Chile.

Núcleo Milenio - Centro de Conservación Marina CCM, Estación Costera de Investigaciones Marinas ECIM, LINC-Global, Departamento de Ecología, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Santiago, Chile.

Abstract

The interaction between environmental variability and larval biological traits is relevant to identify critical processes determining marine population dynamics. Knowledge of connectivity patterns in marine populations is also fundamental for defining management and conservation plans. We developed a biophysical individual-based larval dispersal model to assess the effect of oceanographic variability and biological traits (larval diel vertical migration and temperature-dependent larval development) on recruitment success, dispersal distances, and connectivity patterns. We selected two species exploited by the artisanal fisheries in Chile: the red sea urchin (*Loxechinus albus*; 20 days of planktotrophic development) and the keyhole limpet (*Fissurella latimarginata*; 5 days of lecitotrophic development). We found that geographically and temporally-varying circulation processes dominate transport and effective dispersal of larvae in the region, rendering 'release location' and 'time of release' as the primary determinants of recruitment success, dispersal distance and connectivity patterns for both species, regardless of larval biological traits. Most recruitment to local population was allochthonous, with low levels of self-recruitment and local retention even for the species with short planktonic larval duration. Similar geographic patterns of source and destination strengths were observed in both species, showing a geographic mosaic of source and sink populations with relatively higher importance towards the north region of the studied domain. Our findings allow identifying primary determinants of recruitment success and dispersal distance for two important exploited species in Chile, and to make recommendations for management and conservation in one the most productive, but also exploited coastal regions in the world.

Keywords

Numerical model, Individual Based Model, Source-sink Dynamics, Larval Migration, Larval Behavior, Management.

Introduction

The complex processes affecting the movement of individuals within or among subpopulations (Crooks & Sanjayan 2006) are crucial to understand the regulation and persistence of wild populations (Possingham & Roughgarden 1990). In marine ecosystems, the complex life cycles involving very small dispersing pelagic larval phases (Cowen 2006) impose major challenges to understand patterns of connectivity among 'subpopulations'. A wide variety of larval responses (e.g., physiological, nutritional, behavioral) interacting with environmental conditions, (e.g., temperature), patterns of adult reproduction (e.g., egg production), and the physical characteristics of the fluid environment (e.g., ocean currents) have been identified as the major determinants of effective dispersal, patterns of subpopulation connectivity, and the successful onshore recruitment needed to replenish coastal populations (Cowen & Sponaugle 2009; Levin 2006; Metaxas & Saunders 2009; Morgan 2014; Ospina-Alvarez et al. in press; Werner et al. 2007). In addition, marine coastal populations are usually spatially fragmented or highly heterogeneous over space, either due to natural or human caused habitat patchiness (e.g., Halpern et al. 2008), or because of the highly spatially-structured management and conservation strategies (Fogarty & Botsford 2007, Gaines, et al. 2010b, Gaines, et al. 2010a, Defeo & Castilla 2012), imposing further challenges to our understanding of source and sink dynamics of marine populations. There is an urgent need to improve our knowledge on larval dispersal and connectivity, accounting for the complexity of processes involved, in order to design conservation and management strategies for marine species.

Diverse approaches have been applied to study connectivity in marine species (Cowen & Sponaugle 2009, Levin 2006, Munguia-Vega et al. 2014). Since it is impracticable to follow the small, highly diluted larvae in large water masses in the field (but see Worcester 1994), micro chemical and genetic markers have been applied to infer general spatio-temporal patterns of connectivity among specific subsets of populations (Hedgecock et al. 2007, Thorrold et al. 2007, Carson et al. 2010, 2011) but none of them can reproduce a 'connectivity matrix', i.e. the quantitative pattern of connection among all subpopulations within a region and over some ecologically - or evolutionarily - relevant period of time. It is the character of this connectivity matrix that determines dynamics, resilience and persistence of a metapopulation (Aiken et al. 2011, Jacobi & Jonsson 2011, Jacobi et al. 2012) as well as possibilities of species coexistence through dispersal (Aiken & Navarrete 2014). Spatially explicit coupled hydrodynamic individual based models (SEIBMs) are useful tools that allow recreation of 'realistic' connectivity patterns and the simultaneous evaluation of the role of biological and environmental factors on larval dispersal (Aiken et al. 2007, Cowen & Sponaugle 2009, Metaxas & Saunders 2009, Werner et al. 2007). How realistic is the recreation of connectivity matrices among subpopulations depends on how well the models reproduce key hydrodynamic features of the coastal ocean, as well as the knowledge of larval behavior and general larval performance while developing in the ocean. Temperature is one of the main factors affecting larval performance in the ocean through its effects on most biological rates and, particularly, on the rate of larval development (Planktonic Larval Duration, PLD; Gillooly et al. 2002, Hoegh-Guldberg 1995, O'Connor et al. 2007). Inter annual, seasonal and intra-seasonal variability in water temperature can thus deeply affect larval development and, in consequence, larval recruitment onshore (Hart & Scheibling 1988). The interaction between larval behavior (e.g., Diel Vertical Migration, DVM) and environmental conditions (e.g., buoyancy fronts, vertical currents) is also deemed critically important in modulating larval dispersal and eventual recruitment (Paris & Cowen 2004, Woodson & McManus 2007, Metaxas & Saunders 2009, Morgan 2014). Indeed, larvae can move vertically across water layers and modify their swimming behavior in response to fluctuations in flow velocities and direction (Metaxas & Saunders 2009, Ospina-Álvarez et al. 2012). DVM sometimes increases larval retention of coastal species near the shore (Aiken et al. 2011), and likely increases the chances of self-recruitment (Morgan 2014), although this is not always the case (Ospina-Alvarez et al. in press). DVM is particularly important in areas influenced by oceanographic conditions that favor baroclinic circulation (coastal upwelling, estuarine tidal currents) (Poulin et al. 2002, Aiken et al. 2011, Sundelöf & Jonsson 2012). In coastal upwelling areas, the concentration of larvae of some species below the Ekman layer has been linked to DVM, which seems to prevent offshore transport during upwelling events that could otherwise entrain larvae at the upwelling front and transport them to offshore waters (Peterson 1998, Morgan et al. 2009). However, larvae remaining in surface waters can be moved towards the shore during upwelling relaxation events (Roughgarden et al. 1991). The inclusion of larval biological traits when examining dispersal and onshore recruitment through biophysical models is therefore important as it provides a better representation of the spread of connectivity patterns that may be expected, and better inform species-specific or ecosystem based management plans.

Management and conservation plans for many exploited species are still based primarily on estimates of adult abundance, without explicit consideration of replenishing patterns (Szuwalski et al. 2015). Moreover, the spatial scales of regulatory measures (e.g., spatial regulation of fishing effort) on natural resources are not usually coupled with spatial scales of dispersal and recruitment success (Botsford et al. 2001, Gaines et al. 2010b, White & Costello 2011). Processes affecting the spatial distribution of sources and sinks, produced, for instance, by fluctuations in adult fecundity or heterogeneous circulation are still poorly evaluated, despite their pivotal importance on metapopulation dynamics and persistence (Roughgarden et al. 1985, Roughgarden & Iwasa 1986, Salomon et al. 2010). We must therefore move towards the explicit consideration of the interplay of processes operating during the larval phase coupled with patterns of adult distribution and reproduction (Watson et al. 2011, Aldana et al. 2017, Fernández et al. 2017), if we are to inform management and conservation plans.

From conceptual and applied perspectives, the central coast of Chile is a good model to examine how connectivity through larval dispersal changes depending on environmental and biological factors. A number of exploited species, exhibiting a wide range of larval traits, inhabit this coastal border, and their larvae are exposed to spatially heterogeneous advective and thermal conditions induced primarily by upwelling variability (Strub et al. 1998, Aiken et al. 2008). An additional important condition is the mosaic of regulatory and territorial management areas that generate spatial patterns of adult mortality and abundance, which in turn determine total reproductive output along the coast (Blanco et al. 2017). Thus, the simultaneous identification of critical areas for larval production and onshore recruitment may help identify local sources within the regional metapopulation, where there is high potential to contribute to marine conservation and management (Tognelli et al. 2009). This type of information becomes particularly critical nowadays, as many stocks are overexploited. To advance in this direction, we developed a SEIBM to, first, assess the interplay between larval biological traits (DVM behavior, temperature-dependent PLD) and spatio-temporal variability in hydrodynamic processes, during the period larvae are in the water column, on larval dispersal distance and recruitment success (see Table 1 for definitions). Second, we characterize patterns of potential connectivity (Table 1) and, using empirical information on abundance and estimates of reproductive output, we estimate 'realized connectivity' to identify the most important areas, in terms of spawning and settlement along the study region, which allowed us to define areas of increased self-recruitment, retention and source/sinks. We focus on two rocky reef invertebrates as models of heavily exploited species by the artisanal fishery, the keyhole limpet, *Fissurella latimarginata*, and the red sea urchin, *Loxechinus albus*, which have contrastingly planktonic larval traits.

Table 1. Constants and parameters set to the Spatial Explicit Individual Based Model (SEIBM) configurations.

Constants		
	Fissurella latimarginata	***Loxechinus albus***
Transport duration (PLD_{fixed} scenarios)	5+5 days	20+5 days
Temperature dependent PLD equation (PLD_{Temp} scenarios)	$L_{t+dt} = L_t + GR*(T)*dt$	$PD_{t+dt} = PD_t + K*(T)*dt$
Record frequency	24 (0.5 days)	48 (2.5 days)
Time step (seconds)	1800	
Lethal temperatures (upper/lowest)	23 °C/7°C	
Lag before target depth	Onset of vertical behavior, subsequent to hatching, was set at 3 days	
Vertical migration	Based on sunset/sunrise, depth at daytime: -30m; depth at night time: -1m	
Parameters		
Studied Domain (recruitment)	from 31.5°S to 36.0°S	
Date	The dates of spawning were set to: 5th, 10th, 15th, 20th, 25th and 30th every month	
Months	Spawning season (from September to November)	
Years	2010, 2011, 2012 and 2013	
Depth	Larvae were uniformly released between 0 and 30 m	
Release	20,000 particles with random release	
Scenarios		
LAG + PLD_{fixed}	Behavior: Passive Lagrangian transport/PLD: fixed Planktonic Larval Duration	
LAG + PLD_{Temp}	Behavior: Passive Lagrangian transport/PLD: Temperature Dependent PLD	
DVM + PLD_{fixed}	Behavior: Dial Vertical Migration/PLD: fixed Planktonic Larval Duration	
DVM + PLD_{Temp}	Behavior: Dial Vertical Migration /PLD: Temperature Dependent PLD	

Variables	
Recruitment success	Number of virtual larvae that are successfully transported and are found on an onshore recruitment area (initial number is constant) at the end of PLD+competency
Dispersal distance	Orthodromic distance (i.e., the shortest distance between any two points on the surface of a sphere) travelled from spawning (release) to recruitment locations in km
Potential connectivity	Probability of larval transport between two local settlement areas
Realized connectivity*	The product of potential connectivity, egg production and habitat availability
Realized source strength*	Larvae released at particular location that will disperse and successfully recruit anywhere in the metapopulation (also known as the 'footprint' of a given location)
Realized destination strength*	Is the strength of a location to have larvae delivered to it
Local retention	Defined as the ratio between locally produced settlement and local egg production (self-persistence of individual sites) (estimated by the diagonal element of the connectivity matrix)
Relative local retention	Defined as the ratio between local retention and all settlement of local origin (estimated by the diagonal element of the connectivity matrix divided by the sum of the corresponding column)
Self-recruitment	Defined as the ratio between local retention and settlement of all origins at a site (estimated by the diagonal element of the connectivity matrix divided by the sum of the corresponding row)
Allochthonous recruitment	Defined as the proportion of settlers in a location that comes from a different location which they were released (estimated by subtracting the diagonal element of the connectivity matrix from the sum of the corresponding row)

*Variables calculated only for the scenario DVM + PLD_{Temp}

Material and methods

Model species and the fisheries management system

Two management regimes have regulated benthic artisanal fisheries in Chile for approximately 25 years: a co-management system based on Territorial Use Rights for Fisheries (TURF), which is interspaced with Open Access Areas (OAAs) where traditional fisheries restriction apply (size limit, closed reproductive season). As a result, high heterogeneity in adult sizes and density is observed (Gelcich et al. 2012), which can lead to large variability in propagule production (Manríquez

& Castilla 2001, Blanco et al. 2017). This spatial variability on spawning areas interacts with the heterogeneous hydrodynamics conditions characterizing this region influenced by coastal upwelling.

The two harvested species used as models in our study, *Fissurella latimarginata* and *Loxechinus albus*, inhabit wave exposed rocky shores from the lowest intertidal zone down to 30 m depth. Size at first maturity of *F. latimarginata* ranges between 4 and 5 cm in length, while 7 cm in diameter has been reported for *L. albus* (Brown et al. 1997, Buckle et al. 1978). In central Chile, more than one gonad maturation cycle per year has been reported for both species, although the largest peak occurs during austral spring (Brown et al. 1997; Buckle et al. 1978). The species are free spawners, releasing their gametes into the water column, where the fecundation occurs. Three days after fertilization, the echinopluteus larvae of *L. albus* starts feeding (Arrau 1958), and develops in the plankton between 20 to more than 33 days (González et al. 1987). Competent larvae can remain in the plankton several days before reaching suitable settling habitat (Bustos et al. 1992). In contrast, *F. latimarginata* larvae are lecitotrophic, developing in the plankton for 5 to 10 days before settling (Chavez 2004). Three days after fertilization, and prior to a short period of encapsulated development, a free veliger swimming larvae develops in the plankton (Pérez et al. 2007, Reynoso-Granados et al. 2007).

Ocean dynamics in the region

The study region (31.50ºS to 36.00ºS and 71.50ºW to 74.00ºW), located within the coastal region of the Humboldt Current System (HCS), is characterized by the Chile Coastal Current (CCC), which flows primarily northward close to the coast forced by the southerlies (Strub et al. 1998, Aiken et al. 2008), which also produce the upwelling of sub-superficial, nutrient-rich cold water near the shore, a process strongly modified by coastal topography (Strub et al. 1998, Rutllant et al. 2004, Aiken et al. 2008, Tapia et al. 2009). In winter months south of 35.00°S, the CCC flow mostly poleward (Thiel et al. 2007) (Fig. 1A). Superimposed upon the mean flow there is a relatively energetic mesoscale eddy field, fed by baroclinic instability of the upwelling fronts (Aguirre et al. 2014, 2012, Hormazabal et al. 2013; Letelier et al. 2009). In the region of interest, the seasonal cycle is strongly marked and coastal upwelling occurs predominantly during spring and summer (Narváez et al. 2006, 2004).

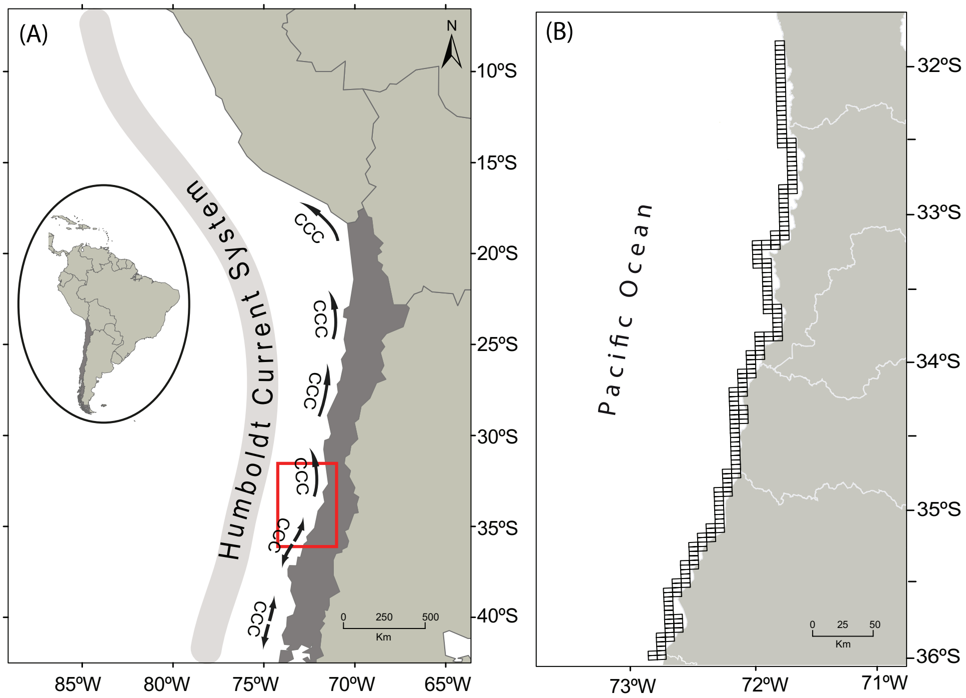


Fig. 1. Map of the study system. (A) Overview of the Chile Coastal Current (CCC) in the Humboldt Current System. The red square indicates the study domain (from 31.50ºS to 36.00ºS and from 71.50ºW to 74.00ºW). (B) Map of the study domain, release cell of 2 km of latitude and 4 km of longitude are shown in black squares.

3D HYCOM Hydrodynamic model

To reproduce the pattern of circulation in the study region we used the Hybrid Coordinate Ocean Model (HYCOM) (http://www.hycom.org) which is available in a 1/12° resolution for the region. HYCOM is a hybrid isopycnal coordinate ocean model (i.e., isopycnal in the stratified open ocean, fixed 10 m depths in the unstratified surface layers, and terrain-following in shallow coastal waters), that allows for better simulation of both coastal and open ocean features than fixed-coordinate systems (Chassignet et al. 2007). The model is data assimilative, using real time observations of the ocean's surface obtained by satellite altimetry, as well as vertical profile information from CTDs, the ARGO observation program, and other sources (http://www.hycom.org). The HYCOM reanalysis used in our study provides a unique 20 year record that solves well the upwelling and instability processes that dominate mesoscale variability in central Chile (Aiken 2017, Ospina-Alvarez et al. in press). Aiken (2017) provides a comparison of HYCOM and an unconstrained ROMS model for the region of the Humboldt Upwelling Ecosystem (HUE) considered in our study, showing that the circulation reproduced by HYCOM is close to that of ROMS simulations, representing well the regional scale ocean variability and surface and subsurface circulation (e.g. polar under current) observed in the HUE. It is important to note, however, that HYCOM suffers from an occasional false surface current that flows around 30°S (Aiken 2017), which is apparently caused by a numerical artifact of the atmospheric model used to provide the wind fields (Allan Wallcraft pers. comm.). This problem occurs to the north, outside the domain used in our study.

The netCDF HYCOM files were downloaded from HYCOM consortium, transformed to Regional Ocean Modeling System (ROMS) format, and coupled with ICHTHYOP software for offline particle tracking (see below).

Spatially Explicit Individual Based Model (SEIBM)

A SEIBM was developed to reproduce larval transport in the realistic ocean reproduced by HYCOM and assess the importance of two key larval biological traits on recruitment success and dispersal distance: temperature-dependent pelagic development time, and vertical swimming behavior, associated to the natural variability imposed by spatio-temporal variability in hydrodynamic circulation (Table 1). Particles mimicking larvae were released in a cell of 2 km of latitude times 4 km of longitude at the surface (first 30 m water column) (Fig. 1B). These cells were also used to define successful 'onshore' recruitment. To analyze the effect of different explanatory variables on model outputs we binned the shoreline cells into 0.3° latitudinal bands, named here release latitude.

Offline particle (individual larvae) tracking and statistics were conducted using a customized version of the open source modeling tool ICHTHYOP (Lett et al. 2008) (http://www.eco-up.ird.fr/projects/ichthyop/) on the hydrographic fields produced by the HYCOM model described above. We used a reflective boundary condition at the coast, and applied a filter to remove particles that stopped moving for more than 1.5 consecutive days, which were considered beached. This filter ensured that larval transport had occurred before tallying onshore recruitment. To establish the appropriate number of particles to be released, we performed repeated trials increasing release numbers (1,000, 5,000, 10,000, 15,000, 20,000, 50,000 and 100,000), and looked for the point at which these statistics stabilized (Brickman & Smith 2002). A total of 20,000 released particles were then used in all spawning events. The HYCOM fields were interpolated in time and space in the SEIBM to determine the values of the environmental state variables at any individual location. One-time step represents 1,800 seconds, and the simulations were run until the nominal larval PLD time plus a period of competency for settlement of 5 days were reached.

We reproduced adult spawning throughout the spring season by releasing virtual larvae uniformly distributed along the coast at a depth between 0 and 30m, every five days from September to November for four consecutive years (2010-2013). At each site, each release event represented a spawning of 20,000 larvae, 1,440,000 in total (20,000 virtual larvae per day x 6 dates x 3 months x 4 years). This approach makes several assumptions about the larval release process. First, the modeled species (keyhole limpet and red sea urchin) are broadcasters which release eggs and sperms into the water where fertilization occurs. This process takes place over timescales of minutes to hours and is not included in our model, which assumes that pelagic life starts at time zero with a fertilized egg. Second, the spatial location of the spawning fraction is identical for both model species along the central Chile coast, from 31.50ºS to 36.00ºS. Third, the spawning locations do not change over time, i.e. the adult spawning population is insensible to environmental or recruitment variability at the resolution scale.

Using the coupled SEIBM model, we explored the effects of (a) temperature-dependent development times, (b) larval behavior, and (c) lethal temperatures based on larval exposure to temperature thresholds, in addition to larval waste due to advection. Connectivity matrices from the circulation model were used to calculate 'Realized' connectivity (sensu Watson et al. 2010) which considered the pattern of larval production (based on oocyte production, Blanco et al. 2017) and suitable habitat availability (see also Table 1). Specifically, we simulated four scenarios for each species: (i) passive Lagrangian transport (LAG) and fixed (temperature insensitive) PLD (5 days for *F. latimarginata* and 20 days for *L. albus*), named LAG + PLDFixed, (ii) fixed PLD and DVM behavior from 0 to 30 m depth (DVM + PLDFixed), (iii) LAG and species-specific temperature-dependent PLD (LAG + PLDTemp) and (iv) larval DVM behavior and temperature-dependent

PLD (DVM + PLDTemp) (Fig. 2). Successful recruitment was tallied as the number of larvae found in the costal cells at the end of the fixed or temperature dependent PLD.

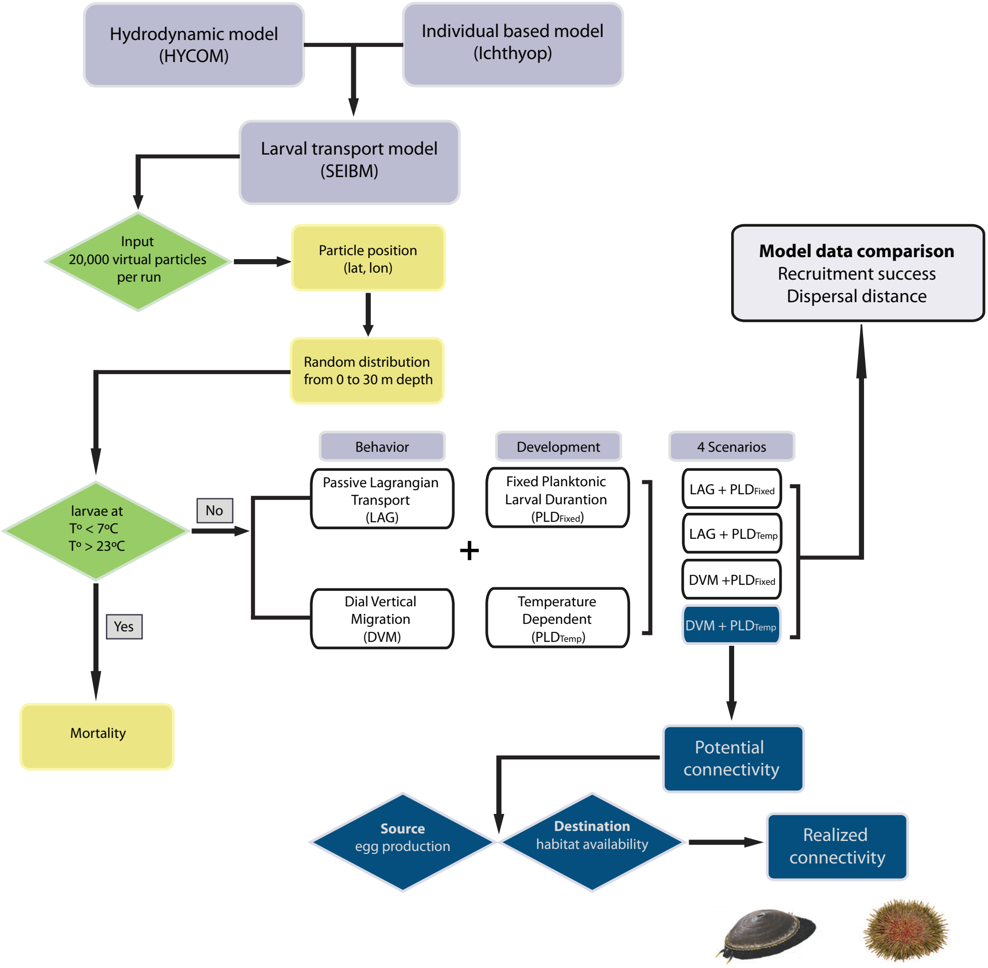


Fig. 2. Flow diagram of the Spatially Explicit Individual Based Model (SEIBM) for *Fissurella latimarginata* and *Loxechinus albus* in central Chile coast.

Larval behavior and lethal temperatures for larvae

As explained above two basic larval behaviors were explored in the models. In the LAG scenario the virtual larvae are assumed to be neutrally buoyant and behave as passive particles that track water movement in the vertical and horizontal velocity components. This scenario assumes that, whichever movement behaviors larvae have while developing in the water column, they are not capable of overcoming ocean current velocities. In the DVM scenario larvae displayed typical DVM, moving to deeper waters down to 30m during daytime and up to the surface (1m) at night, following the sunset/sunrise schedule. Maximum depth was defined based on limited observation of *L. albus* and other invertebrate species (Tremblay & Sinclair 1990, Molinet et al. 2010). Although many invertebrate larvae perform DVM, not all of them do (McLaren 1963). Unfortunately, the information is not available for the model species and, therefore, we contrast putative DVM against LAG behavior. In the model, larvae of both species started DVM behavior three days after release, which accounted for the three day period of pelagic intracapsular development of *F. latimarginata* trochophore larvae (Reynoso-Granados et al. 2007). Similarly, since sedimentation velocity was equal or higher than ciliary movement velocity for early larval stages (blastula and gastrula) of *L. albus* (McDonald 2004), we considered that DVM started at the echinopluteus stage, which appears, on average (depending on temperature), three days after fertilization (personal observation).

Since there is evidence that severe growth retardation of eggs and larvae of most temperate invertebrates and fish, as well as that high mortality (Rumrill 1990) occurs at temperatures lower than 7ºC and above 23°C, we considered that larvae exposed these thresholds for more 0.5 hours (one time step) would die. Since these threshold temperatures are rarely observed in central Chile, this mortality source had virtually no consequences on the patterns reported here, but imposing such restriction preventing us from including spuriously long or short larval development times in the PLDTemp condition. This temperature-induced mortality was imposed in addition to and independent of "larval waste" produced when larvae are found too far from appropriate settling habitat by the end of the competency period.

Temperature dependent pelagic larval development

The universal effects of temperature in determining larval development times were incorporated in ICHTHYOP through the positive effects of temperature on larval growth (which in turn reduce development times). The strategy for parameterization differed between the two species.

Parameterization for *Fissurella latimarginata*

For *F. latimarginata*, the time to complete PLD was reduced with increasing temperature, it was modeled according to the universal relationship proposed by O'Connor et al (2007):

$$\ln(PLD) = \beta - 1,34 * \ln(T/15) - 0,28 * (\ln(T/15))2 \qquad \text{Equation 1}$$

where PLD is expressed in days, T is temperature in Celsius degrees and β (β = 1.78) is a species-specific parameter (see O'Connor et al., 2007 supplementary information), and 15 is the reference temperature expressed in Celsius degrees. A developmental time of 5 days was reported for *F. latimarginata* at 17°C under laboratory conditions (Chavez 2004) and was used in equation 1 to obtain PLDs across a wide temperature range (from 9ºC to 20ºC), which rendered a PLD range between 4 and 13 days.

To model PLDTemp within ICHTHYOP we first transformed PLDs into daily growth rates (GR, um/day). We assumed linear growth from a hatching size of 190 um to a settlement size of 210 um (Chavez 2004),

$$GR(T) = (210-190) / PLD(T) \qquad \text{Equation 2}$$

and then calculated growth rate GR(T) considering the temperature experienced by the larvae at each time step (i.e. the growth function was updated at each time step). Temperature fields to which larvae were exposed to were obtained from the hydrodynamic model and larval size in each time step (L in um) were calculated following equation 3.

$$Lt+dt = Lt + GR * (T) * dt \qquad \text{Equation 3}$$

Parameterization for *Loxechinus albus*

In the case of *L. albus*, parameterization of temperature effects on larval development times was obtained through laboratory rearing experiments. To this end, we collected 33 mature urchin individuals (>7 cm) from subtidal areas around Las Cruces, central Chile and took them to the Estación Costera de Investigaciones Marinas where they were injected in the celomic cavity with 3 ml of 0.5M KCl to stimulate gamete release, following the protocol by Bustos et al. (1992). Eggs and sperm were washed with UV filtered seawater and sieved with 500 µm and 170 µm nylon mesh. Then, eggs from each female (n=4) were retained in 55 µm nylon mesh and divided into separate glass petri dishes, one for each female, where they were fertilized in an egg-sperm proportion of 1:100, from sperms of one male. The fertilized embryos were then divided in different batches, which were randomly assigned to experimental temperature treatments. Three temperature treatments were used: 10ºC, 13ºC and 17ºC, encompassing the range observed in the study area (Thiel et al. 2007). The experiments started at the blastula stage and finished at the pre-metamorphic, competent larval stage. We recorded larval arm length under a microscope every 2 days until the 8-arms stage was reached. Thereafter, a reduction in arm length was observed until the pre-metamorphic stage was reached.

Considering the developmental characteristic of echinopluteus larvae, we used the proportion of time larvae remained in each developmental stage, with respect to total developmental time. Therefore, to model temperature effects on development we

$$DPt+dt = DPt + K * (T) * dt \qquad \text{Equation 4}$$

where DP is Development Proportion, T is temperature in Celsius, dt is the time increment in days and K is a coefficient obtained from the relationship between growth rate and temperature (K= 0.38) through linear fitting. To incorporate the development proportion into the SEIBM, we followed the degree-day concept applied by Hinckley et al. (1996). At every time step, larvae advanced a fraction of the total development proportion depending on the temperature experienced during the time interval, until completing the entire PLD.

Analysis of model results

To obtain mean field approximations we performed 48 simulations for each model species (3 months x 4 years x 2 particle behaviors x 2 larval growth patterns). The analyses on these simulations were conducted using a multifactor analysis of variance from the Generalized Additive Model (GAM), in which we evaluated the effect on recruitment success and dispersal distances of (a) larval behaviors (LAG versus DVM), (b) fixed PLD (5 days for keyhole limpets and 20 days for red sea urchins) versus temperature dependent PLD (PLDTemp) and (c) initial conditions: (1) depth of larval release (6 levels, intervals of 5 m from 0 to 30 m), (2) release latitude (16 levels, intervals of 0.3°, from 31.50°S to 36.00°S), and (3) release date (day/month/year). A GAM with quasipoisson family error distribution was used for both dependent variables (recruitment and dispersal distance). To compare recruitment success and dispersal distance between years, and behavior and temperature-dependent PLD scenarios, as well as interaction terms, we used a Generalized Linear Model (GLM) analysis with a quasipoisson family error distribution. The choice of the most appropriate link function and error distribution was made based on residual analyses. We tested the goodness of fit of the model with a Chi-Squared test based on residual deviance and degrees of freedom (significance level 0.05). All statistical analyses were performed using R software v.3.1.3 (R 2013).

From the potential connectivity matrix, we calculated three retention indicators following Lett et al. (2015): (a) local retention (the diagonal element of the connectivity matrix; Table 1), (b) relative local retention (the diagonal element of the connectivity matrix divided by the sum of all released larvae in that latitude which successfully recruit anywhere in the metapopulation (sum of the corresponding column), and (c) self-recruitment (the diagonal element of the connectivity matrix divided by the sum of all larvae successfully recruiting at that latitude (sum of the corresponding row) (Table 1). These metrics were calculated using the R package ConnMatTools (Kaplan & Andrello 2016). In addition, we calculated allochthonous recruitment in each location, estimated by subtracting the diagonal element from the sum all recruits at that latitude (sum of the corresponding row), and the origin of recruits (north or south of target location) (Table 1). These metrics were compared among scenarios using a GLM analysis with a quasipoisson family error distribution.

Potential and realized connectivity

A multi-annual (2010-2013) mean connectivity matrix was obtained for each of the four modeled scenarios. These matrices contained all needed information for metapopulation dynamics and time-varying processes (Aiken & Navarrete 2014), but they can be visualized as representing potential connectivity, before spatial variation in larval production, since habitat availability and adult abundance are taken into account. Thus, a realized larval connectivity can be estimated using potential connectivity weighted by relevant biological and environmental information (following Watson et al. (2010) (Table 1).

To estimate larval production along the shore we assumed that all eggs produced become viable larvae. Modeled egg production, expressed as the number of oocytes per square meter, for each model species, were obtained from information on adult density, size structure, sex ratio and size-specific fecundity (oocytes/female of a given size), which are available for eight sites along the study area (Blanco et al. 2017). Following the egg production model described in Blanco et al. (2017), we used the spatial distribution of suitable habitat (hard bottoms) and fishing regime (no-take marine protected areas, TURFs, and OAAs), which affect size distribution and adult density (through harvesting), to obtain estimates of egg production for both model species in each release cell.

Realized connectivity was then calculated by multiplying the potential connectivity matrix by egg production and, subsequently, adjusting the proportion of available rocky habitat. Realized connectivity matrices were calculated only for the scenario with DVM and PLDTemp because they probably represent the more realistic larval attributes of the species (DVM; Molinet et al. 2010; temperature dependent PLD; Bustos et al. 1992, Chavez, 2004). Following Watson et al. (2010), we calculated realized source strength of each location (its ‘footprint’), summing all released larvae per location (sum across columns) that reached a settlement location in the realized connectivity matrix (Table 1). In the same way, we calculated the realized destination strength of each location summing the fractions of recruited larvae per location (sum across rows) in realized connectivity matrix (Table 1). To compare the spatial structure of potential and realized connectivity matrices, we conducted a mantel test using the R package ape (Paradis et al. 2017). The information from the connectivity matrix was used to construct direction linkage between release locations and larval recruitment locations, and the potential connectivity matrix defined the strength of connectivity.

Results

Recruitment success

Recruitment success ranged between 32.23% and 12.50% in the species exhibiting shorter PLD (*Fissurella latimarginata*), considering all scenarios, and decreased between 6.26% and 3.15% in the species showing larger PLD (*Loxechinus albus*) (Table 2).

Significant effects of release latitude, release depth, release date, larval behavior and temperature-dependent PLD were observed on recruitment success in both model species ($p\text{-value} < 0.001$). Release latitude explained most of the variability on recruitment success in both species (24.30% in keyhole limpets and 34.80% in red sea urchins) (Table 3), rendering similar spatial patterns of recruitment success for both species and across the four modeled scenarios (Fig. 3). Three small shoreline sections (latitudes) concentrated more than 80% of recruitment success: (a) 34.8% of all keyhole limpet and 17.7% of all red sea urchin recruitment (averaged across scenarios) was concentrated between 31.5ºS and 32.5ºS, (b) 33.2% of keyhole limpet and 60.6% of red sea urchin recruitment occurred between 33.0ºS and 33.5ºS, and (c) 12.15% of keyhole limpet and 8.09% of all sea urchin recruited to the shore was observed between 34.0ºS and 34.5ºS (Fig. 3). South of 34.5°S recruitment success was low in both species (8.96% in keyhole limpet and 7.76% in red sea urchin) (Fig. 3).

The spatial pattern on recruitment success was similar under the four modeled scenarios for both species (Fig. 3), highlighting the importance of topography and hydrography-driven dispersal on the spatial patterns of recruitment. Southern connectivity was higher for *L. albus* under LAG scenarios (recruitment success percentage below the matrix diagonal), contrastingly in DVM scenarios only northward connectivity was observed (recruitment success percentage above the matrix diagonal) (Fig. 3).

Recruitment success also varied significantly over time. Release date explained 5.54% of variability observed on recruitment success in keyhole limpets and 4.19% in red sea urchins (Table 3). Larval biological traits considered in this study (PLD and behavior) also had significant effects on recruitment success in both species, although the variance explained was low (< 3.95%) (Table 3).

For *F. latimarginata* average PLD ranged between 5.83 and 5.70 days under fixed PLD scenarios (Table 2), and between 8.03 and 8.10 days under PLDTemp scenarios (Table 2) showing an extension of precompetency time of 39% under PLDTemp scenarios. Conversely for *L. albus* average PLD varied between 22.92

Table 2. Summary of model results obtained for all modeled simulation scenarios; (i) passive Lagrangian transport (LAG), (ii) passive Lagrangian transport with a species-specific temperature dependent PLD (LAG + PLDTemp), (iii) virtual larvae with Diel Vertical Migration behavior (DVM) and (iv) virtual larvae with Diel Vertical Migration behavior and temperature dependent PLD (DVM + PLDTemp). For recruitment success, results were obtained by calculating the mean from each simulation (each spawning month and year, 12 simulations per scenario), for the other measures results were obtained by calculating the mean from all virtual larvae recruited in each experiment.

Fissurella latimarginata				
	LAG + PLD$_{\text{fixed}}$	**LAG + PLD**$_{\text{Temp}}$	**DVM + PLD**$_{\text{fixed}}$	**DVM + PLD**$_{\text{Tempè}}$
Mean dispersal distance ± se (km)	57.10 ± 0.11	75.84 ± 0.21	54.92 ± 0.09	64.09 ± 0.12
Median dispersal distance (km)	48.50	66.59	46.23	56.15
Maximum dispersal distance (km)	323.79	327.03	274.36	243.97
Minimum dispersal distance (km)	0.00	0.04	0.01	0.03
Larval waste + Mortality (%)	74.44	87.50	67.77	75.72
Recruitment success (%)	26.56	12.50	32.23	24.28
Local retention (%)	2.64	1.79	2.33	1.49
Relative local retention (%)	4.74	3.39	4.83	3.57
Self-recruitment (%)	5.25	4.39	5.34	3.53
Allochthonous recruitment (%)	97.36	98.21	97.67	98.51
Average days to settlement	5.83	8.03	5.70	8.10
Loxechinus albus				
Mean dispersal distance ± se (km)	49.41 ± 0.49	56.96 ± 0.59	76.98 ± 0.41	70.29 ± 0.40
Median dispersal distance (km)	21.29	26.45	53.66	58.49
Maximum dispersal distance (km)	407.44	409.56	378.59	383.50
Minimum dispersal distance (km)	0.02	0.01	0.34	0.07
Larval waste + Mortality (%)	96.19	96.85	93.74	93.99
Recruitment success (%)	3.81	3.15	6.26	6.01
Local retention (%)	6.13	5.13	1.17	1.81
Relative local retention (%)	3.60	4.58	0.50	0.77
Self-recruitment (%)	4.45	4.42	1.84	3.52
Allochthonous recruitment (%)	93.87	94.87	98.83	98.19
Average days to settlement	22.92	23.28	22.67	22.23

se = standard error

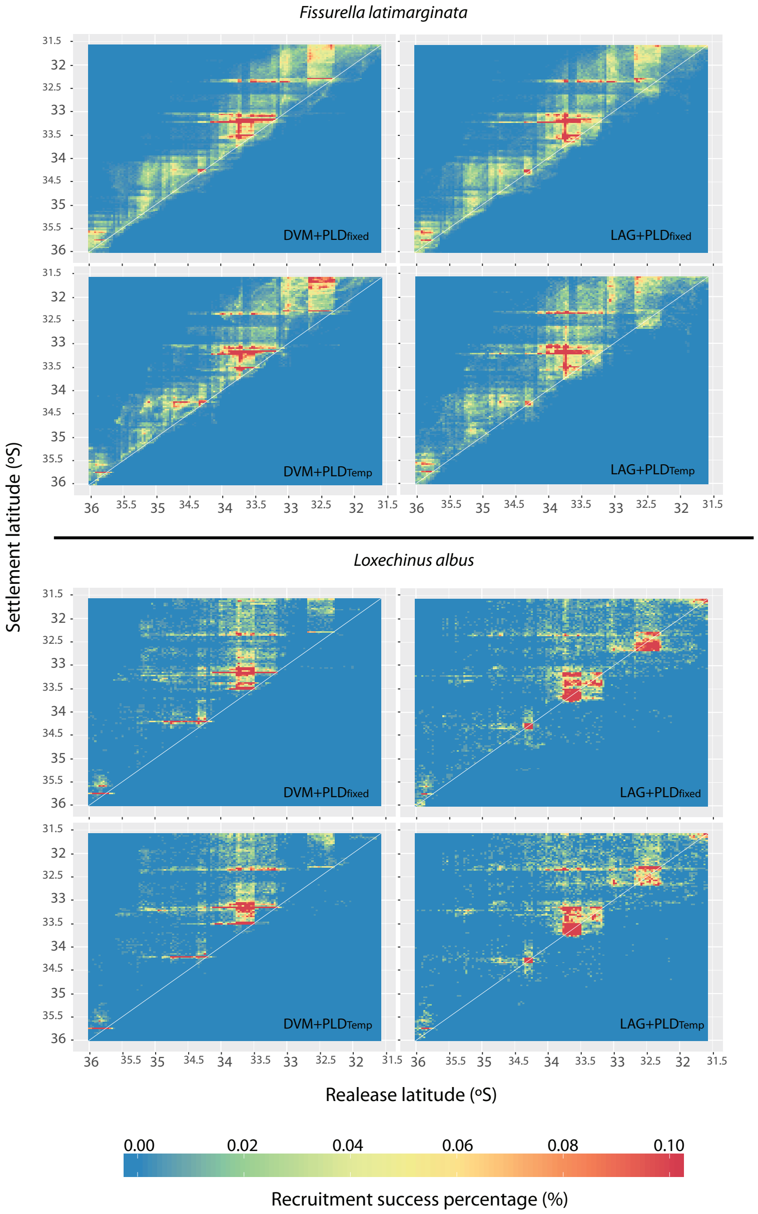


Fig. 3. Potential connectivity matrices obtained from the "HYbrid Coordinate Ocean Model" (HYCOM) coupled with ICHTHYOP Lagrangian particle (larval) tracking model, for *Fissurella latimarginata* (upper panel) and *Loxechinus albus* (bottom panel). Potential connectivity matrices show the mean accumulated recruitment from 2010 to 2013 during spring (September, October and November). The simulation scenarios are: (DVM + PLDfixed) Dial Vertical Migration (DVM) and fixed Planktonic Larval Duration (PLD), (LAG + PLDfixed) passive Lagrangian transport (LAG) and fixed PLD, (DVM + PLDTemp) DVM and PLD based on species-specific temperature dependent PLD and (LAG + PLDTemp) LAG and PLD based on temperature dependent PLD. Color scale shows the proportion of total recruited virtual larvae with respect to the total number of virtual larvae released from all locations.

and 22.67 under fixed PLD scenarios (Table 2), and between 23.28 and 22.23 days under PLDTemp scenarios (Table 2), not showing differences of precompetency time between PLD scenarios, even a reduction of 1% under PLDTemp scenarios.

Significant among-year differences were observed in terms of recruitment success for both species (X^2=20809.9, df=3, p<0.01 for *F. latimarginata* and X^2=5516.0, df=3, p<0.01 for *L. albus*). The highest mean recruitment success in both species was observed in 2012 (Fig. 4A, B), while the lowest in 2011 for keyhole limpets (16.95%, Fig. 4A) and 2013 for red sea urchins (Fig. 4B). Larval DVM had significant effects on recruitment success in both species (behavior: X^2= 18609.9, df= 1, p-value<0.01, for keyhole limpet and X^2=9609.0, df= 1, p-value<0.01 for red sea urchin), generally increasing onshore recruitment in both species (Fig. 4A, B). However, the effect of larval behavior on red sea urchin recruitment disappeared in 2011 (Fig. 4B). Consequently, the interaction term (year: behavior) was significant for red sea urchin (X^2= 1972.0, df= 3, p-value< 0.01) and not significant for keyhole limpets (X^2= 153.8, df= 3, p-value= ns), indicating that the effect of DVM depends on the year only for long PLD species (*L. albus*). Having a temperature dependent larval development time (PLDTemp) significantly reduced recruitment success with respect to fixed development time in keyhole limpets and sea urchins (X2= 29910.6, df= 1, p-value<0.01, for keyhole limpet and X2=278.5, df= 1, p-value<0.01 for red sea urchin), but the effect was much smaller and constant among years in red sea urchins (Fig. 4B). Therefore, the interaction term (year: PLD) was significant for keyhole limpet (X2= 2874.9, df= 3, p-value< 0.01) and not significant for red sea urchin (X2= 95.0, df= 3, p-value= ns), suggesting that temperature effects on PLD vary more among years for short PLD species than long PLD species.

The interactive effects of larval traits on recruitment success was apparent for the short PLD species (*F. latimarginata*) (Fig 4A), which rendered significant the (behavior: PLD) interaction term (X^2= 7026.2, df= 1, p-value< 0.01). For longer PLD species (*L. albus*) the interaction (behavior: PLD) was not significant (X^2= 90.4, df= 1, p-value= ns), indicating that larval behavior had similar effects on recruitment in all years, regardless of the small fluctuations in time of PLD induced by temperature (Fig. 4B). Despite among year variation in average recruitment, the second order interaction term (year: behavior: PLD) was not significant in either species (X^2= 207.2, df= 3, p-value= ns, for keyhole limpet and X^2= 97.4, df= 3, p-value=ns for red sea urchin).

Spatial patterns of larval retention from variability in connectivity

Spatial variation in dispersal process lead to high spatial variation in connectivity among local populations (e.g. Aiken et al. 2007), also demonstrated here by most

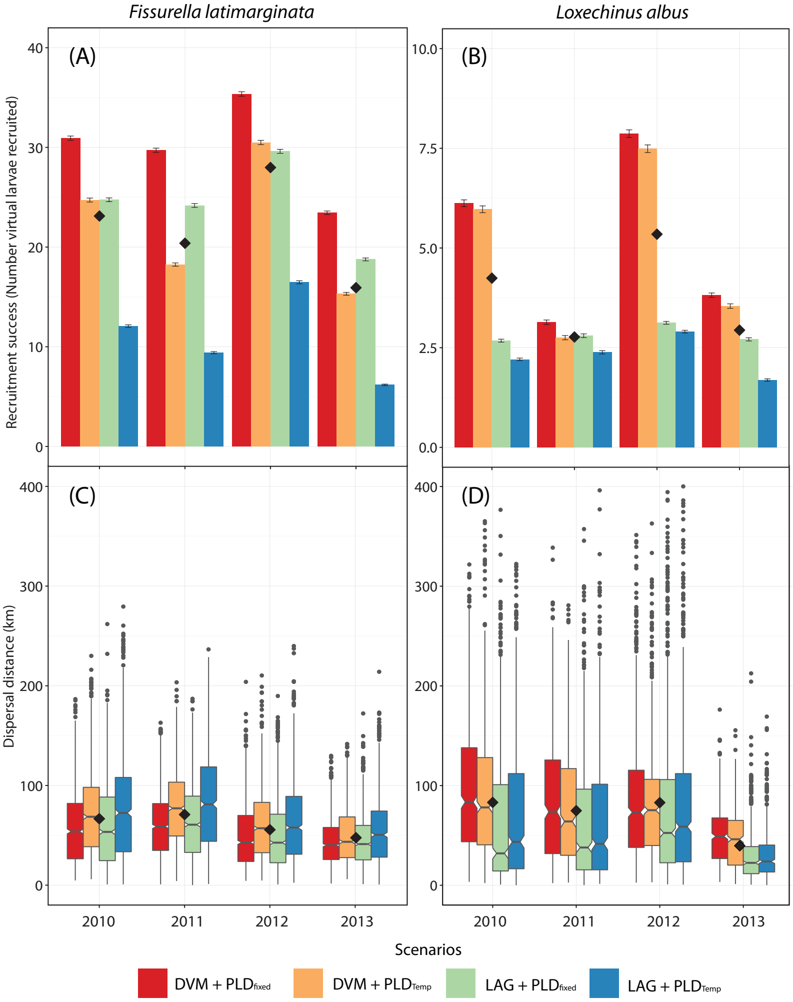


Fig. 4. Barplots showing average recruitment success (A and B) and boxplots showing dispersal distance (C and D) for *Fissurella latimarginata* (A and C) and *Loxechinus albus* (B and D) in the different years simulated under the four scenarios: Diel Vertical Migration behavior and fixed Planktonic Larval Duration (PLD) (DVM + PLDfixed), DVM behavior and PLD based on a species-specific temperature dependent PLD (DVM + PLDTemp), passive Lagrangian transport (LAG) behavior and fixed PLD (LAG + PLDfixed) and LAG and PLD based on temperature dependent PLD (LAG + PLDTemp). The black diamond's show the average between experiments per year.

indicators of larval retention and contribution of local populations to the regional metapopulation (Fig. 5). First, allochthonous recruitment (AR) was high across most local populations and generally higher than local retention (LR) at most latitudes (Fig. 5), highlighting the importance of inter-population recruitment subsidies on local population dynamics. Interestingly, this broad pattern was stronger for keyhole limpets, with shorter PLD, than for red sea urchins (compare top and bottom panels in Fig. 5). In the case of the keyhole limpet, AR and LR, as well as relative local retention (RLR), showed a mosaic structure across the region and all larval trait scenarios, with a slight regional (latitudinal) trend to increase

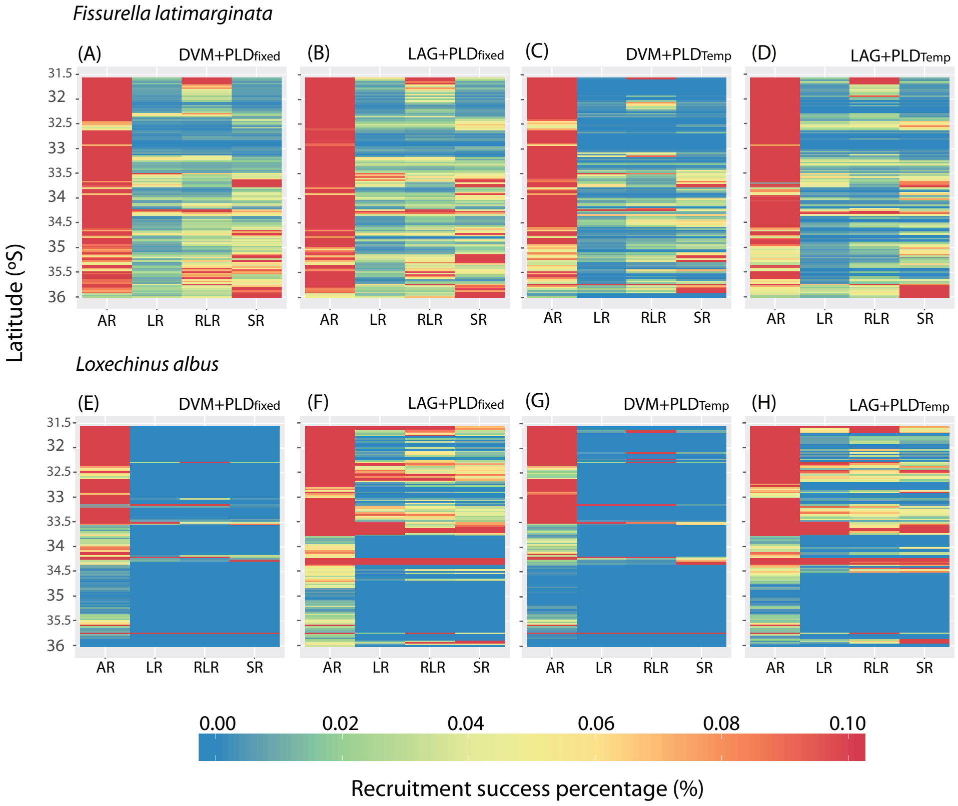


Fig. 5. Potential connectivity metrics calculated for *Fissurella latimarginata* and *Loxechinus albus* across the study area. AR indicates allochthonous recruitment (for the latitudinal variability in allochthonous recruitment we log transform and sum 1 in AR in all latitudes). LR is local retention, RLR is relative local retention and SR is self-recruitment. The simulation scenarios, shown for *Fissurella latimarginata* and *Loxechinus albus* are, respectively: (A and E) virtual larvae with Diel Vertical Migration (DVM) behavior and fixed Planktonic Larval Duration (PLD) (DVM + PLDfixed) (B and F) passive Lagrangian transport and fixed PLD, (C and G) DVM behavior and PLD based on a species-specific temperature dependent PLD and (D and H) LAG behavior and PLD based on temperature dependent PLD. Color scale shows the percentage obtained for the metrics calculated.

inter-population connectivity (AR) towards the northern end of the region (Fig. 6). In the case of red sea urchins, stronger regional patterns were observed in all indicators of larval local retention and self-recruitment (LR, RLR, SR) as well as AR, with generally higher values towards the northern end of the region, across larval trait scenarios and regardless of geographic (north/south) origin (Fig. 6). Note that most of AR was northward in both species (more than 80% in all *F. latimarginata* scenarios and more than 60% in *L. albus*) (Fig. 7). Southward AR was lower than 10% in all scenarios for keyhole limpet (Fig.7B).

Some larval traits, but not all of them, had significant effects on connectivity patterns and, these changes affected some but not all indicators of retention

Table 3. Analysis of deviance for the Generalized Additive Models (GAMs) with quasipoisson error structure applied to the SEIBM output for the dependent variables, number of larvae recruited and dispersal distance for *Fissurella latimarginata* and *Loxechinus albus*. Deviance explained (DE) were calculated for each factor individually (GAM: dependent variable ~ term + spline(term)). Note that the sum of DE of each factor is not equal to the total DE obtained for the model.

Fissurella Latimarginata				
Recruitment success ~ PLD + behavior + depth + spline(release latitude) + spline(date) R-sq. (adj.) = 0.36; Total DE = 37.30%				
Parametric terms	**df**	**F**	**p-value**	**DE (%)***
PLD	1	1246.87	$2x10^{-16}$	3.95
Behavior	1	664.40	$2x10^{-16}$	2.46
Release depth	5	37.93	$2x10^{-16}$	0.82
Smooth terms	**edf**	**F**	**p-value**	**DE (%)***
spline(release latitude)	8.98	807.70	$2x10^{-16}$	24.30
spline(release date)	8.99	183.80	$2x10^{-16}$	5.54
Dispersal distance ~ PLD + behavior + depth + spline(release latitude) + spline(date) R-sq. (adj.) =0.35; Total DE = 35.70%				
Parametric terms	**df**	**F**	**p-value**	**DE (%)***
PLD	1	719.70	$2.00x10^{-16}$	3.25
Behavior	1	121.10	$2.00x10^{-16}$	0.09
Release depth	5	140.60	$2.00x10^{-16}$	2.95
Smooth terms	**edf**	**F**	**p-value**	**DE (%)***
spline(release latitude)	8.98	652.30	$2.00x10^{-16}$	23.80
spline(release date)	8.94	214.20	$2.00x10^{-16}$	6.94

Loxechinus albus				
Recruitment success~ PLD + behavior + depth + spline(release latitude) + spline(date) R-sq. (adj.) =0.35; DE = 42.40%				
Parametric terms	**df**	**F**	**p-value**	**DE (%)***
PLD	1	22.51	$2.10x10^{-6}$	0.10
Behavior	1	573.42	$2.00x10^{-16}$	3.84
Release depth	5	16.75	$2.00x10^{-16}$	0.03
Smooth terms	**edf**	**F**	**p-value**	**DE (%)***
spline(release latitude)	8.98	672.81	$2.00x10^{-16}$	34.80
spline(release date)	8.99	89.45	$2.00x10^{-16}$	4.19
Dispersal distance ~ PLD + behavior + depth + spline (release latitude) + spline (date) R-sq. (adj.) = 0.39; DE = 39.10%				
Parametric terms	**df**	**F**	**p-value**	**DE (%)***
PLD	1	2.51	0.11	$9.33x10^{-3}$
Behavior	1	121.72	$2.00x10^{-16}$	1.23
Release depth	5	35.15	$2.00x10^{-16}$	1.50
Smooth terms	**edf**	**F**	**p-value**	**DE (%)***
spline (release latitude)	8.97	269.90	$2.00x10^{-16}$	26.10
spline (release date)	8.83	172.70	$2.00x10^{-16}$	19.60

Depth: correspond to release depth (0-5m, 5-10m, 10-15 m, 15-20m, 20-25m, 25-30m)
Release latitude: from 31.5ºS to -40ºS
Date: correspond to release date (day/month/year)
df: degree of freedom
edf: effective degree of freedom

recruitment in keyhole limpets and/or red sea urchins. A significant effect of temperature dependent PLD was observed on self-recruitment (SR) and LR in keyhole limpet (Table 4 & S1), which can be visually appreciated comparing panels C and D of Fig. 5. Higher larval LR and SR were observed under fixed PLD (Table 2) than when PLD was allowed to vary with temperature, probably due to increased dispersal distance (see below) and larval waste. No significant effect of behavior was detected on SR or LR in keyhole limpet (S1), nor did behavior modify the effect of type of PLD (interaction term behavior: PLD was not significant, Table 4). In contrast, significant effects of larval behavior were observed on larval LR and SR in the case of the red sea urchin (S1), while the type of PLD and the interaction with behavior were not significant (Table 4). Interestingly, generally lower red sea urchin LR and SR were observed under DVM (Table 2). AR was not affected by larval PLD or behavior in both species (Table 4).

Table 4. Analysis of deviance for the Generalized Linear Models (GLMs) with quasipoisson error structure applied to the potential connectivity metrics calculated for self-recruitment, local retention, relative local retention and allochthonous recruitment for *Fissurella latimarginata* and *Loxechinus albus*.

Fissurella latimarginata					
Self-recruitment ~ Behavior * PLD, family= quasipoisson Deviance Explained: 1.82%					
	Df	Deviance	Resid. Df	Resid. Dev.	Pr (>Chi)
NULL			555	26.34	
Behavior	1	0.03	554	26.30	0.49
PLD	1	0.39	553	25.92	0.01
Behavior * PLD	1	0.06	552	25.86	0.33
Local retention ~ Behavior * PLD, family= quasipoisson Deviance Explained: 3.47%					
NULL			555	11.42	
Behavior	1	$4.63*10^{-2}$	554	11.37	0.23
PLD	1	0.35	553	11.02	$8.99*10^{-4}$
Behavior * PLD	1	$1.80*10^{-3}$	552	11.02	0.81
Relative local retention ~ Behavior * PLD, family= quasipoisson Deviance Explained: 1.52%					
NULL			555	27.51	
Behavior	1	$4.28*10^{-3}$	554	27.50	0.86
PLD	1	0.41	553	27.09	0.08
Behavior * PLD	1	$8.80*10^{-4}$	552	27.09	0.94
Allochthonous recruitment ~ Behavior * PLD, family= quasipoisson Deviance Explained: 0.00%					
NULL			555	345.37	
Behavior	1	$9.74*10^{-4}$	554	345.37	0.97
PLD	1	$7.28*10^{-3}$	553	345.36	0.93
Behavior * PLD	1	$0.03*10^{-4}$	552	345.36	0.99
Loxechinus albus					
Self-recruitment ~ Behavior * PLD, family= quasipoisson Deviance Explained: 17.52%					
NULL			555	33.15	
Behavior	1	5.63	554	27.51	$3.17*10^{-12}$
PLD	1	0.16	553	27.35	0.23
Behavior * PLD	1	$0.97*10^{-3}$	552	27.34	0.77
Local retention ~ Behavior * PLD, family= quasipoisson Deviance Explained: 8.85%					
NULL			555	60.47	
Behavior	1	5.12	554	55.35	$2.37*10^{-4}$
PLD	1	$0.96*10^{-2}$	553	55.34	0.87
Behavior * PLD	1	0.22	552	55.12	0.45

Relative local retention ~ Behavior * Growth, family= quasipoisson Deviance Explained: 2.63%					
NULL			555	53.85	
Behavior	1	0.88	554	52.97	0.09
PLD	1	0.19	553	52.78	0.43
Behavior * PLD	1	0.34	552	52.43	0.29
Allochthonous recruitment ~ Behavior * Growth, family= quasipoisson Deviance Explained: 0.00%					
NULL			555	964.94	
Behavior	1	0.18	554	964.76	0.86
PLD	1	$3.53*10^{-4}$	553	964.76	0.99
Behavior * PLD	1	$7.05*10^{-3}$	552	964.75	0.97

Dispersal distances

As expected, dispersal distances were generally longer for red sea urchins than keyhole limpets, but on some years (2013) such a pattern reversed, with red sea urchins mean dispersal distances being lower than those of keyhole limpets across all larval traits (Fig. 4C,D, average of 47.39 km for keyhole limpet and 39.52 km for red sea urchins). Consequently, we observed that release year had a significant effect on dispersal distance in both species (X^2=26214.9, df=3, p<0.01, for *F. latimarginata* and X^2=42066, df=3, p<0.01 for *L. albus*). Averaging across the four years of simulations showed increased mean dispersal distances in the much shorter PLD species, keyhole limpets, under some larval trait scenarios (Table 2). The year with highest mean dispersal distance was different between species; 2011 for keyhole limpet (79.85 km) and 2010 for red sea urchin (83.11 km) (Fig. 4C and D). Larval behavior had a significant effect on dispersal distance in both species (X^2=463.3, df=1, p-value<0.01 for *F. latimarginata* and X^2=6720, df=1, p-value<0.01 for *L. albus*), but in opposite direction and generally larger effects on red sea urchins than keyhole limpets (Fig. 5C, D, Table 2). Consistently longer mean distances under DVM scenarios were observed for red sea urchin (Fig. 4D), increasing average dispersal distance across years from 49.41 to 76.98 under fixed PLD and from 56.96 to 70.29 km under PLDTemp (Table 2). In the keyhole limpet, DVM generally and slightly decreased mean dispersal distance across years (Fig. 4C, average 75.84 km in LAG and 64.09 km under DVM; Table 2).

When averaging across years, the type of PLD had significant main effect on dispersal distance only for keyhole limpet (X^2=14901.7, df=1, p-value<0.01, for *F. latimarginata* and X^2=2, df=1, p-value= ns for *L. albus*), increasing dispersal when PLD was temperature dependent (Fig. 4C, Table 2). In this short PLD species, an extension of two days of planktonic development increased dispersal distance from 57.10 to 75.84 km under LAG scenarios and from 54.92 to 64.09 km under DVM scenarios (Table 2). In contrast, the effect of PLD type on the red sea urchin was small and varied in direction depending on larval behavior: a slightly negative effect under DVM and slightly positive effect under LAG behaviors (Fig. 4D, Table 2). The interaction term (year: behavior) was statistically significant on dispersal distance for red sea urchin but not for keyhole limpet (X^2= 32.6, df=3, p-value= ns, for *F. latimarginata* and X^2=2523, df=3, p-value< 0.01 for *L. albus*). The interaction term (year: PLD) was statistically significant on dispersal distance for both species (X^2= 283.8, df=3, p-value<0.01, for *F. latimarginata* and X^2= 49, df=3, p-value< 0.01 for *L. albus*). The interaction term (behavior: PLD) was statistically significant on dispersal distance for red sea urchin and not for keyhole limpet (X^2= 102.8, df=1, p-value= ns, for *F. latimarginata* and X^2= 530, df=1, p-value< 0.01 for *L. albus*). The third level interaction term (year: behavior: PLD) was not significant in either species (X^2= 33.9, df=3, p-value= ns, for *F. latimarginata* and X^2= 15, df=3, p-value= ns for *L. albus*).

Beyond the inter-annual variation shown above, the date of release had significant effects on mean dispersal and explained 6.94% of model variability in keyhole limpets and 19.60% in red sea urchins (Table 3). Behavior (DVM or LAG) was statistically significant in both model species, although the variance explained was extremely low (0.09% on keyhole limpets and 1.23% on red sea urchins) (Table 3). The type of PLD in the model was statistically significant only in keyhole limpets and explained 3.25% of model variability (Table 3).

Release latitude and release date, as well as depth of release, have also significant effects on mean dispersal distances of both model species (p-value < 0.001). The factor that explained most variance in dispersal distance was release latitude (23.80% on keyhole limpets and 26.10% on red sea urchin) (Table 3). The geographic pattern of dispersal distances was similar among larval trait scenarios and also generally similar between species (Fig. 7). Mean red sea urchin dispersal distance was negative in some latitudes (at 36.0ºS, between 34.4ºS and 34.8ºS

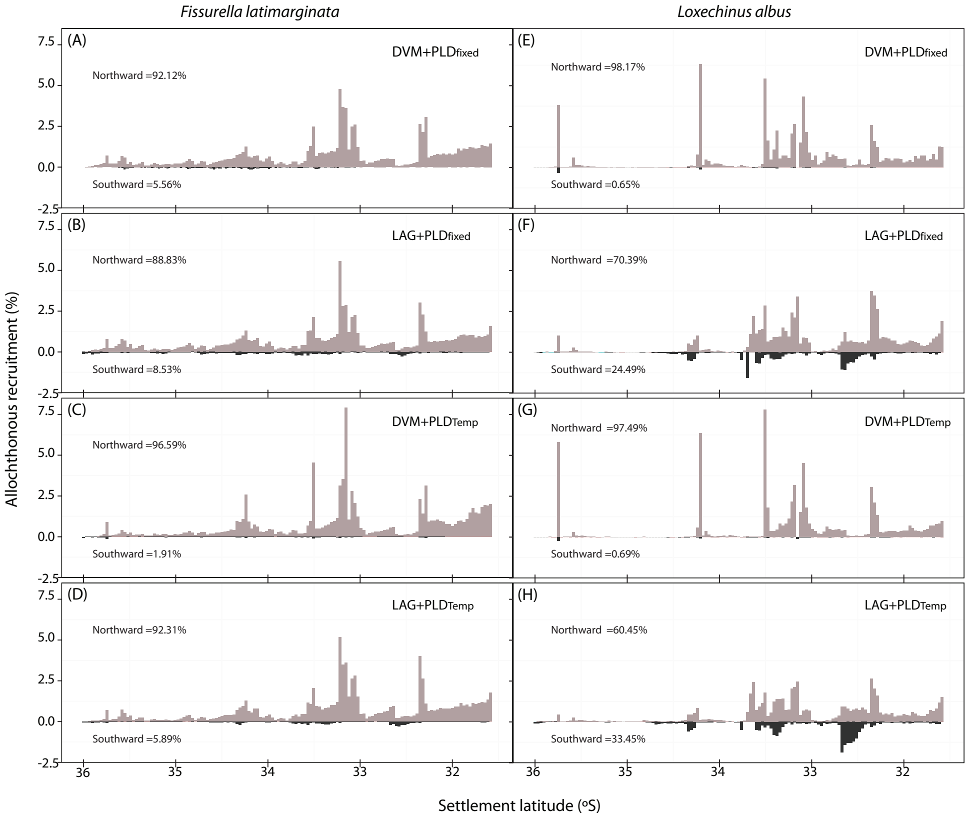


Fig. 6. Spatial variability of allochthonous recruitment across the study area, showing also the origin, northward (positive values in gray bars) or southward (negative values in black bars) from the recruitment site for *Fissurella latimarginata* and *Loxechinus albus* under different scenarios: (A and E) virtual larvae with Diel Vertical Migration (DVM) behavior and fixed Planktonic Larval Duration (PLD) (DVM + PLDfixed) (B and F) passive Lagrangian transport and fixed PLD (LAG + PLDfixed), (C and G) DVM behavior and PLD based on a species-specific temperature dependent PLD (DVM + PLDTemp) and (D and H) LAG behavior and PLD based on temperature dependent PLD (LAG + PLDTemp).

and between 33.6ºS and 33.8ºS), only in LAG scenarios, indicating southern connectivity (Fig.7; F and H). However mean dispersal distance was always positive in DVM scenarios (Fig.7; E and G).

Realized connectivity

Significant differences in the spatial structure of connectivity were observed between potential and 'realized' connectivity in both species (Mantel test; p-value < 0.001), indicating that the spatial patterns of reproductive output and available habitat have a clear signal on connectivity among local populations. However and

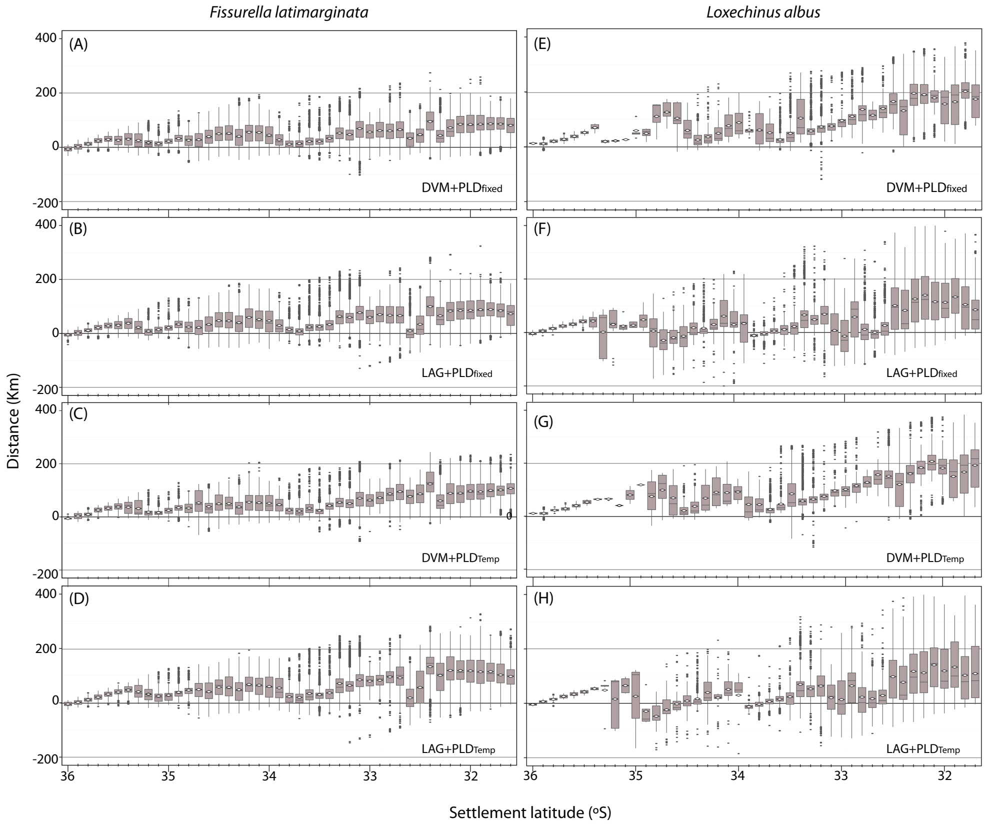


Fig. 7. Boxplots showing orthodromic distance traveled by recruited virtual larvae in each latitude for *Fissurella latimarginata* and *Loxechinus albus* under different scenarios: (A and E) virtual larvae with Diel Vertical Migration (DVM) behavior and fixed Planktonic Larval Duration (PLD) (DVM + PLDfixed) (B and F) passive Lagrangian transport and fixed PLD (LAG + PLDfixed), (C and G) DVM behavior and PLD based on a species-specific temperature dependent PLD (DVM + PLDTemp) and (D and H) LAG behavior and PLD based on temperature dependent PLD (LAG + PLDTemp).

as expected, the latitudes with high successful recruitment were unaltered in both species (Fig. 8). The most important source locations for overall recruitment in the metapopulation (considering the DVM and PLDTemp scenarios) were observed between 32.3ºS and 32.6ºSºS and between 33.2ºS and 33.6ºS for *F. latimarginata* (Fig. 8A). Very similar results were obtained for the longer PLD species, the red sea urchin, with the most important realized source locations between 32.4ºS and 32.5ºS and between 33.2ºS and 33.5ºS (Fig. 8B). Therefore, for both species we identified the same geographic region as main source locations (between 33.0ºS and 33.5ºS and at 32.5ºS) for the metapopulations (Fig. 4); these latitudes contributed in 72% to the overall recruitment. The most important realized larval destination (locations receiving larvae from multiple source populations) were found mainly at the northern end of the studied domain for both species, between 33.0ºS to 33.2ºS and north of 32.2ºS (Fig. 8; D, E and F), these latitudes contributed in 94% to the overall recruitment in the study region.

Discussion

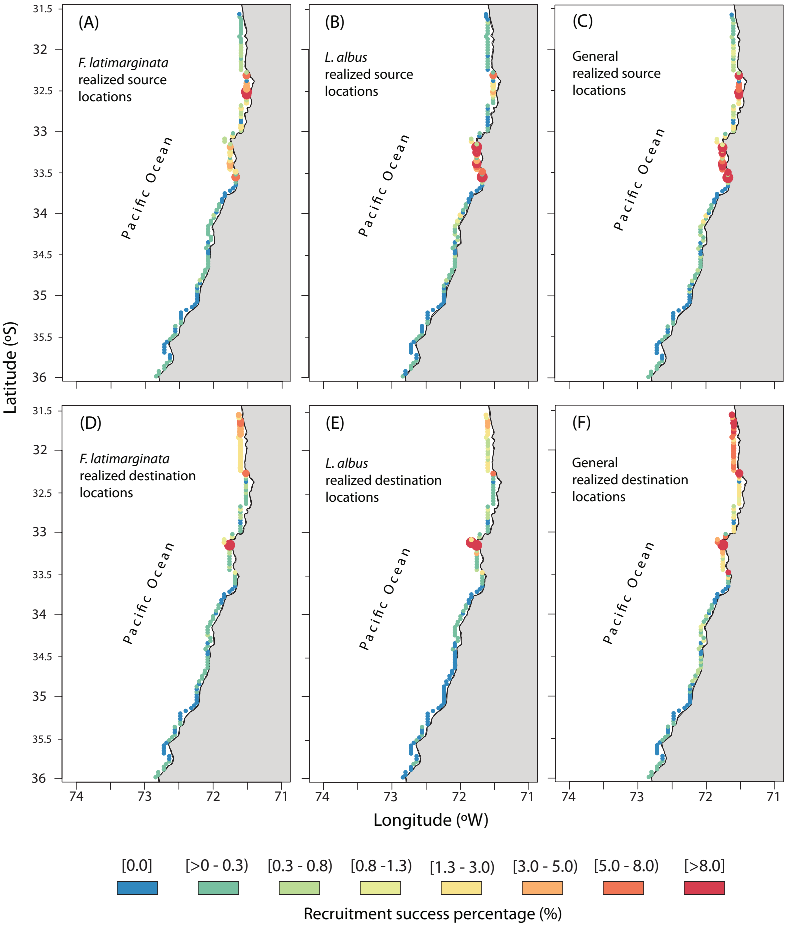


Fig. 8. Metrics for the realized connectivity matrix, calculated weighting the potential connectivity matrix with the modeled egg production and, subsequently, adjusted by the proportion of available rocky habitat. The upper three maps showed realized source strength of each location, estimated by sum of all the fractions of released larvae per location (sum across columns) of the realized connectivity matrix, for *Fissurella latimarginata* (A), *Loxechinus albus* (B) and both model species (C). The lower three maps showed realized destination strength of each locations, estimated by sum of all the fractions of recruited larvae per location (sum across rows) of realized connectivity matrix, for *F. latimarginata* (D), *L. albus* (E) and both model species (F). Color scale shows for maps (A, B and C) the proportion of larvae recruited that have released in each location and for maps (D, E, F) shows the proportion of larvae recruited in each location from all larvae released on the study domain.

Globally, our results allow us to conclude that geographically and temporally-varying circulation processes dominate transport and effective dispersal of putative larvae in the coastal ocean, rendering 'release location' and 'time of release' as the primary determinants of recruitment success, dispersal distance, and population connectivity patterns for both invertebrate species modeled, regardless of larval biological traits. Larval swimming behavior, as modeled in this study (DVM), had significant, but rather minor influence on most response variables examined. However, in both species, DVM enhanced recruitment success as compared to passive Lagrangian particles (LAG). Once a pelagic larval development time is defined for a species, realistic variability in this time imposed by the variable temperatures to which larvae are exposed in the ocean (PLDTemp) also had significant, but comparatively minor effects on response variables, and the direction of the effect changed between species and even between modeled years. Within the studied area of central Chile, most recruitment to local populations was allochthonous, with low levels of self-recruitment and local retention at the scale of a latitudinal degree, even for the species with short PLD, the heavily harvested keyhole limpet. Our analyses also show the existence of a geographic mosaic of potential sources and sink populations across the region, with few regional breaks and weak latitudinal trends that suggest increasing importance of 'realized sources' and 'realized destinations' towards the northern end of the domain (central Chile) for both modeled species. We discuss the extent to which these patterns can be used as a template for management and conservation planning in the region, and the broad contribution of these results to our views of larval dispersal in the ocean.

Processes driving larval dispersal in a realistic ocean

The identification of the release location and date of larval release as the primary determinant of recruitment success, conferring similar patterns of source and destination strengths in species with widely different development times is striking, but consistent with previous studies in other geographic regions. Indeed, several modeling studies have shown that the spawning locations, the dates when spawning occur, and the number of adult reproductive individuals are the main factors explaining recruitment variability (Parada et al. 2008, Brochier et al. 2009, Ospina-Alvarez et al. 2015). Equally important is the fact that, despite inter-annual variability in recruitment success, the spatial pattern remains fairly unchanged for both species, a result that should be corroborated over longer timescales encompassing 'anomalous' years (e.g. El Niño) and over a finer spatial scale using models able to capture small scale coastal dynamics like eddies (e.g., high spatial resolution or nested models). As we discuss below, these findings are of great importance for the applicability of territory-based protection schemes and spatial management (e.g. TURFs, protection of reproductive adults, MPAs). Spatial variability and persistence in recruitment contribution of geographic locations is associated to the relationship between release latitude and topographically-modified oceanographic features leading to variability in larval transport, dispersal and eventual recruitment success on the shore (Navarrete et al. 2005, Cowen et al. 2007, Lagos et al. 2008). For instance, our results show that three latitudes concentrate most of recruitment success observed in the region for both species and there is a general spatial coincidence between locations exhibiting higher recruitment success and topographic headlands (A1), although our results are constrained by model resolution (latitudinal bands of 2 km). Several studies developed in the study region have shown that topographic effects are more important than variation in wind-driven offshore Ekman flux explaining the intensification of upwelling around these points (Figueroa & Moffat 2000, Aiken et al. 2008). Therefore, coastal topography can play a critical role in determining locations with higher/lower recruitment success by modifying the intensity of oceanographic processes such as upwelling circulation, and it seems to also influencing realized dispersal distance. Several studies have shown that temporal and spatial variability in upwelling circulation can affect larval recruitment through: (a) retention of water masses, and larvae, into bays (upwelling shadows), usually found downstream of capes and headlands (upwelling centers) (Graham & Largier 1997, Poulin et al. 2002, Aiken et al. 2008), (b) collision of upwelling fronts with exposed shore locations during upwelling relaxation events (Roughgarden et al. 1988, 1991, Wing et al. 1995, Shanks et al. 2000) and (c) complex stratified alongshore and cross-shore circulation patterns generated during relaxation (Kirincich et al. 2005, Kirincich & Barth 2009). Whichever the mechanism, our model results suggest that topography plays a major role in defining recruitment patterns and determining temporal inter-annual persistence across this upwelling region, which is generally supported by empirical observations of intertidal invertebrate recruitment along central Chile and Oregon (Lagos et al. 2005, Wieters et al. 2008), and by inferred patterns of red sea urchin recruitment along the coast of California (Ebert & Russell 1988).

While location of origin and spawning date played major roles on dispersal distance and successful onshore recruitment, environmental conditions affecting larval development and larval behavior did have significant, albeit lower effects on these important population variables. Much has been speculated about the effect of increased sea surface temperature on larval dispersal and resulting recruitment and population connectivity, both in the context of latitudinal variation in mean temperatures (Thorson 1950, Bradbury et al. 2008, Ayata et al. 2010, Leis et al. 2013) and in the context of impinging climate change (O'Connor et al. 2007, 2012, Munday et al. 2009, Lacroix et al. 2018). Indeed, the dominant effect of temperature on metabolic and development rates (Gillooly et al. 2002, Brown et al. 2004) leads to highly predictable and universal reduction in larval development times (O'Connor et al. 2007), which is expected to generally reduce effective dispersal distances. However, since the actual thermal regimes experienced by developing larvae in a complex realistic ocean will depart very significantly from laboratory controlled conditions, it is critical to examine temperature effects under realistically variable thermal conditions and in different regions of the world. In our model, temperature dependent development had an important effect on recruitment success through changes in PLD, but surprisingly, the impact was greater on the short PLD species (keyhole limpets), than on longer PLD species (red sea urchin). For red sea urchin, development time was extended more than 2 days under all scenarios (PLDfixed and PLDTemp), showing a reduction of 1% in PLDTemp scenarios compared to PLDfixed, leading to marginal effects on recruitment success (Fig. 4B) and no consistent effect on dispersal distances (Fig. 4D). For keyhole limpets temperature dependent development increased the average time to reach the settlement size by two days, which represents 39% increase from the nominal development time. Hence in this species we observed increased larval waste leading to lower recruitment (Fig. 4A) and slight but very consistent increase in average dispersal distances (Fig. 4C). It is remarkable that the relative impact of temperature dependent development is stronger on species exhibiting shorter larval developmental times. This is not because development in this species is more sensible to temperature, but because of the differences in the actual thermal regimes and temperature ranges experienced in a realistic ocean, even when larvae are released at the same time. The longer the PLD, the more variable the thermal environment experienced through development. Long PLDs will necessarily extend beyond the warm water season and be exposed to colder waters that could have important effects on development times. Lacroix et al. (2018) predicts a PLD increase of 22% in the a flatfish species in the North Sea in a Climate Change scenario, but our results suggest a complex interaction between the effect of temperature on different developmental times and probably also across regions since variability in temperature depends on the oceanographic conditions determining temperature (e.g., dominance of upwelling). Moreover, a rise on ocean temperature is expected to not only decrease larval duration, other consequences needs to be considered: changes on spawning period (Fincham et al. 2013), changes on reproductive output (Shama 2015) and also changes on larval mortality (Madeira et al. 2016). Thus, we submit that predicting consequences of increased sea surface temperature on dispersal and recruitment, and be counter intuitive, is much more complex than simply projecting mean ocean temperature increases (O'Connor et al. 2007, Byrne 2011, McLeod et al. 2015, Lacroix et al. 2018).

Laval behavior, especially the ability to perform diel vertical migration, has been pinpointed as the most important missing information in studies of larval dispersal (Levin 2006, Metaxas & Saunders 2009, Morgan 2014). Our results showed that DVM behavior enhances recruitment success in both model species and across all years modeled. For red sea urchin, DVM increase recruitment success 76% and for keyhole limpets the increase was lower (45%), so the magnitude of DVM enhancement was 30% higher for red sea urchins in comparison with keyhole limpets (Table 2). Thus, DVM behavior seems to be more relevant in species exhibiting longer PLDs (20 to 25 days; red sea urchin), probably because they can experience baroclinic circulation patterns for longer periods of time. While the effect of DVM on recruitment was rather minor in the context of spatial and temporal variation encounter along the modeled region, it is remarkable that it was consistently positive across all these conditions and for both species. In many modeling and observational studies conducted in upwelling regions DVM behavior has been proposed as a mechanism promoting larval retention into the shore (Aiken et al. 2011, Marta-Almeida et al. 2006, Morgan 2014, Morgan et al., 2009a). The offshore currents at the surface and onshore currents at deeper depths during upwelling events (Kirincich et al. 2005, Morgan et al. 2009, Strub et al. 1998) allow organisms performing DVM to migrate below the Ekman layer, and reduce offshore transport (Aiken et al. 2011, Marta-Almeida et al. 2006, Morgan et al. 2009, Queiroga et al. 2007). This general mechanism may play a role in the observed increased recruitment rates in our model. However, in contrast to the idea that DVM behavior may enhance recruitment through reducing dispersal and increasing larval retention nearshore during development, DVM had positive effects on dispersal distance (see also Ospina-Alvarez et al. in press), negatively impacting local retention and self-recruitment, specially of red sea urchins. In a previous study conducted in Monterey Bay, Carr et al. (2008) observed that DVM did not substantially lead to nearshore retention as the return flow during daytime did not compensate offshore nighttime transport. In our study, for red sea urchin we also observed that allochthonous recruitment under DVM was mainly northward, compared to LAG where more than 20% was southward (Fig. 7). This result reinforces the idea that larvae that vertically migrate were advected northward and then a fraction returned to nearshore locations, possibly by the mechanisms described above. Thus, our results suggest that for species with moderate PLD (20 to 25 days), like the red sea urchins, in the upwelling ecosystem of central Chile, vertical migration is not a behavior promoting local retention, nor self-recruitment, but it increases the probability of successful onshore transport of competent larvae and, probably increases alongshore dispersal distances in a coastal band across the region. Increased onshore recruitment and reducing dispersal have been suggested as some of the many factors that may favor the evolution of DVM in invertebrate and fish larvae (Batchelder et al. 2002, Marta-Almeida et al. 2006, Morgan 2014). Our results show that there might be an adaptive advantage as higher recruitment is observed in both species under the DVM across all scenarios, but this comes at the expense of increased dispersal, rather than reduced dispersal distances. Moreover, DVM represents less than 5% of the explained variance in recruitment success. Further studies are needed to determine increased recruitment can be a sufficiently strong selective force leading to DVM behavior in competent larvae.

Despite the persistence of the spatial pattern of sources and sinks, our results showed high inter-annual (Fig.4) (and also intra-annual (A2)) variability on mean dispersal distance and recruitment. Upwelling intensifies during austral spring and early summer, which is the period when most species exhibit a peak in larval release (Reitzel et al. 2004), producing high variability in alongshore transport (Aguirre et al. 2012). Byers & Pringle (2006) noted a discrepancy between warmest boreal month and dates with the calculated highest larval release, which occurs earlier in the year, and proposed that spring release could be a tradeoff not for faster development, but because in this season mean currents (advection) are minimal and variability (contributing to diffusion) is maximal. Indeed, in our study larval development time during the spawning season was not reduced from experimental development time (20 days for red sea urchins and 5 days for key-hole limpets) (González et al. 1987, Chavez 2004), but actually increased. In highly advective environments, like most costal ocean and especially in upwelling shores, spawning over several months or the entire year enhances retention probability by increasing the variation in the currents encountered (Byers & Pringle 2006). Therefore, larvae released in different times of the year will contribute very differently to metapopulation dynamics simply because of temporal variability in hydrodynamic features (see also Ayata et al. 2010). But it is uncertain to what extent the tradeoffs of development times or future recruitment success plays a significant role in spawning strategies of marine invertebrates. Energetic constraints on female reproduction, mating behavior, or availability of food for the developing larvae clearly are important determinants of spawning (Leslie et al. 2005, Lester et al. 2007). Thus, reproduction during spring months could be a reproductive-larval dispersal tradeoff for many marine invertebrates inhabiting nearshore environments, although will reduce physically-driven onshore recruitment.

Regardless of this large difference in the magnitude of recruitment success between species, attributable to differences in PLD, the spatial pattern of connectivity was consistent between species and also among scenarios (Fig. 3). This is not entirely surprising considering that release location was the main factor explaining the variability in recruitment and dispersal distances. Many studies have shown apparently high self-recruitment in shorter PLD species. For instance, Ayata et al. (2010) report 1.82 times higher larval exchange between adjacent populations for a PLD of 2 weeks than one of 4 weeks. In contrast, our results showed high allochthonous recruitment (>90%) in both modeled species, with high exchange rates between non-adjacent locations. This suggests that timing and location of release may have greater impact on population connectivity than reproductive adult demography.

Consequences for Conservation and Management

Despite the short duration of our simulations and relatively coarse spatial resolution (limited by availability of HYCOM product), our modeling results offer important insights for future management and conservation studies. First, despite the large differences in PLD, the pattern of sources and sinks, and the specific locations of recruitment success along the shore, were very similar between the two species (at the scale of latitudinal bands), and remarkably persistent among years. This means that territory-based planning to protect species (MPAs) could be effective for sets of species with contrasting development times (White & Costello 2011). Our finding that the best spawning and recruitment locations remain the same, despite inter-annual variation in recruitment success, means that protections of these sites for fisheries benefits or conservation value, respectively, may be an effective strategy, at least over ecological timescales. Thus, frequent rotation of areas, as suggested for some species (Game et al. 2009), may not be necessarily the strategy. Second, while increasing PLD had the expected large negative effect on recruitment, attributable to increased larval waste, mean dispersal distances surpassed most scales of management instruments (e.g. TURFs, (White & Costello 2011)), even in the short PLD species. The observed importance of allochthonous recruitment throughout the region for both species. are sort of good news and bad news for management and conservation. On the one hand, this means that most marine reserves will never be large-enough to protect self-maintained populations of threatened species, even those with low dispersal potential. For this and many other reasons (Gaines et al. 2010a, Aiken & Navarrete 2011), a network of reserves is necessary to guarantee species persistence. On the other hand, connectivity among TURF management areas is inevitable, even for these short PLD exploited species, calling into question the single-TURF management approach followed so far in Chile (Tognelli et al. 2009, Gaines et al. 2010b) and highlighting the importance of regional management plans and cooperation among TURFs (White & Costello 2011). Third, although details of the larval behavior and environmental effects on larval development are important when it comes to study specific determinants of dispersal and recruitment, they appear to play minor roles in comparisons of spatio-temporal variation in coastal ocean circulation. Therefore, while further species-specific information in larval biology will allow us to improve model representations of connectivity (Sponaugle et al. 2006, Werner et al. 2007, Metaxas & Saunders 2009, Morgan 2014), in the short term it pays to improve the resolution of our models of coastal circulation (e.g. Nickols et al. 2012), especially in regions of the world for which basic physical information (bathymetry, high resolution winds) are not available.

The analyses of realized connectivity further suggest the importance of the northern domain of our study area, where the most relevant realized source (between 32.40ºS to 32.60ºS and between 33.20ºS to 33.60ºS) and destinations locations (between 33.00ºS to 33.20ºS) were identified. In fact, the northern region of the domain (central Chile) is where there is high proportion of rocky habitat and also a high number of TURFs. Therefore, it will be interesting to explore the relative importance of habitat distribution or effective management on the observed patterns. Previous studies have also described high recruitment potential (from models, Aiken et al. 2007) and observed recruitment (Navarrete et al. 2008) in central Chile. This highlights the need to increase effective protection actions (e.g. no-take reserves) in this region.

In general our findings provide relevant and new information to inform spatial patterns of management and conservation in one of the region's most impacted by human activities in Chile. It is clear that model limitations preclude us from providing more specific advice and future studies should address these limitations. First, the spatial model resolution (2 by 4 km model cells) does not allow us to resolve well the coastal boundary layer (Nickols et al. 2012) and to link recruitment observations with the co-management system of TURFs, which usually are smaller than 1-2 km long. Second, we only modeled four years (because of availability of HYCOM product at the time of this study) and longer timescales are necessary to capture potentially meaningful ecological variation. Third, we only consider mortality due to losses by advection and temperature limit thresholds. However other mortality causes may be important, such as predation, food availability and other density-dependent and density-independent (e.g. riverine plumes) factors. Despite these model limitations, the modeling approach followed here allow us to identify primary determinants of recruitment success and dispersal distances for two important species exploited by artisanal fisheries in Chile, and to make broad recommendations for management and conservation in one of the most productive, but also heavily exploited coastal regions in the world.

Acknowledgements

We thank Fundación Mutua Madrileña (MB) FONDECYT 3150425 (AO), Fondecyt 1160289 (SAN), Fondecyt 1130976 (MF) and the Iniciativa Científica Milenio CCM RC 1300004 from the Ministerio de Economía, Fomento y Turismo de Chile.

References

Aguirre C, Pizarro Ó, Strub PT, Garreaud R, Barth JA (2012) Seasonal dynamics of the near-surface alongshore flow off central Chile. J Geophys Res Ocean 117:1–17

Aiken CM (2017) A reanalysis of the Chilean ocean circulation: preliminary results for the region between 20 S to 40 S. Lat Am J Aquat Res 45:193–198

Aiken CM, Castillo MI, Navarrete SA (2008) A simulation of the Chilean Coastal Current and associated topographic upwelling near Valparaíso, Chile. Cont Shelf Res 28:2371–2381

Aiken C, Navarrete SA (2011) Environmental fluctuations and asymmetrical dispersal: generalized stability theory for studying metapopulation persistence and marine protected areas. Mar Ecol Prog Ser 428:77–88

Aiken CM, Navarrete SA (2014) Coexistence of competitors in marine metacommunities: Environmental variability, edge effects, and the dispersal niche. Ecology 95:2289–2302

Aiken CM, Navarrete SA, Castillo MI, Castilla JC (2007) Along-shore larval dispersal kernels in a numerical ocean model of the central Chilean coast. Mar Ecol Prog Ser 339:13

Aiken CM, Navarrete SA, Pelegrí JL (2011) Potential changes in larval dispersal and alongshore connectivity on the central Chilean coast due to an altered wind climate. J Geophys Res Biogeosciences 116:1–14

Aldana M, García-Huidobro MR, Pulgar VM, Pulgar J (2017) Upwelling promotes earlier onset and increased rate of gonadal development of four coastal herbivores. Bull Mar Sci 93:000–000

Arrau L (1958) Desarrollo del erizo comestible de chile *Loxechinus albus* Mol. Rev Biol Mar VII:39–60

Ayata S-D, Lazure P, Thiébaut É (2010) How does the connectivity between populations mediate range limits of marine invertebrates? A case study of larval dispersal between the Bay of Biscay and the English Channel (North-East Atlantic). Prog Oceanogr 87:18–36

Batchelder HP, Edwards CA, Powell TM (2002) Individual-based models of copepod populations in coastal upwelling regions: Implications of physiologically and environmentally influenced diel vertical migration on demographic success and nearshore retention. Prog Oceanogr 53:307–333

Blanco M, Ospina-Álvarez A, González C, Fernández M (2017) Egg production patterns of two invertebrate species in rocky subtidal areas under different fishing regimes along the coast of central Chile. PLoS One 12:1–18

Botsford LW, Hastings A, Gaines SD (2001) Dependence of sustainability on the configuration of marine reserves and larval dispersal distance. Ecol Lett 4:144–150

Bradbury IR, Laurel B, Snelgrove PV., Bentzen P, Campana SE (2008) Global patterns in marine dispersal estimates: the influence of geography, taxonomic category and life history. Proc R Soc B Biol Sci 275:1803–1809

Brickman D, Smith PC (2002) Lagrangian stochastic modeling in coastal oceanography. J Atmos Ocean Technol 19:83–99

Brochier T, Colas F, Lett C, Echevin V, Cubillos LA, Tam J, Chlaida M, Mullon C, Fréon P (2009) Small pelagic fish reproductive strategies in upwelling systems: A natal homing evolutionary model to study environmental constraints. Prog Oceanogr 83:261–269

Brown G. DI, Gonzalez M, Lopez D, Duran L, Rivero R, Collado G, Betancourt C (1997) Informe Final Proyecto FIP-IT/94-33. Estudio de los ciclos vitales de las especies comerciales de lapas del genero *Fissurella sp*, en las regiones I a X. :196

Brown CA, Holt SA, Jackson GA, Brooks DA, Holt GJ (2004) Simulating larval supply to estuarine nursery areas: How important are physical processes to the supply of larvae to the Aransas Pass Inlet? Fish Oceanogr 13:181–196

Buckle LF, Guisad C, Tarifeñ E, Zuleta A, Cordova L (1978) Biological studies on the chilean sea-urchin *Loxechinus albus* (Molina) (Echinodermata; Echinoidea) IV- Maturation cycle ans seasonal biochemical changes in the gonad. Ciencias Mar 5:1–18

Bustos E, Olave S, Troncoso R, Godoy C (1992) Investigación repoblamiento de recursos bentónicos Area Piloto IV Región.Etapa IV. 5. Investigaciones en erizo *Loxechinus albus* (Molina. 1782).

Byers JE, Pringle JM (2006) Going against the flow: Retention, range limits and invasions in advective environments. Mar Ecol Prog Ser 313:27–41

Byrne M (2011) Impact of ocean warming and ocean acidification on marine invertebrate life history stages: vulnerabilities and potential for persistence in a changing ocean. Oceanogr Mar Biol An Annu Rev 49:1–42

Carr SD, Capet XJ, McWilliams JC, Pennington JT, Chavez FP (2008) The influence of diel vertical migration on zooplankton transport and recruitment in an upwelling region: Estimates from a coupled behavioral-physical model. Fish Oceanogr 17:1–15

Carson HS, Levin LA, Cook GS, López-Duarte PC (2011) Evaluating the importance of demographic connectivity in a marine metapopulation. Ecology 92:1972–1984

Carson HS, López-Duarte PC, Rasmussen L, Wang D, Levin LA. (2010) Reproductive timing alters population connectivity in marine metapopulations. Curr Biol 20:1926–1931

Chassignet EP, Hurlburt HE, Smedstad OM, Halliwell GR, Hogan PJ, Wallcraft AJ, Baraille R, Bleck R (2007) The HYCOM (HYbrid Coordinate Ocean Model) data assimilative system. J Mar Syst 65:60–83

Chavez LHP (2004) FONDEF DOOI1141d. Innovaciones tecnológicas para repoblamiento y producción de lapas chilenas de explotación (*Fissurella latimarginata* y *Fissurella cumingi*) en áreas de manejo y centros de cultivo. :255

Cowen RK (2006) Scaling of Connectivity in Marine Populations. Science (80-) 311:522–527

Cowen R, Gawarkiewicz G, Pineda J, Thorrold S, FE W (2007) Population Connectivity in Marine Systems an overview. Oceanography 20:14–21

Cowen R, Sponaugle S (2009a) Larval dispersal and marine population connectivity. Ann Rev Mar Sci 1:443–466

Cowen RK, Sponaugle S (2009b) Larval Dispersal and Marine Population Connectivity. Ann Rev Mar Sci 1:443–466

Crooks KR, Sanjayan M (2006) Connectivity conservation (KR Crooks and M Sanjayan, Eds.), 14th edn. Cambridge University Press

Defeo O, Castilla JC (2012) Governance and governability of coastal shellfisheries in Latin America and the Caribbean: Multi-scale emerging models and effects of globalization and climate change. Curr Opin Environ Sustain 4:344–350

Ebert T, Russell M (1988) Latitudinal variation in size structure of the west coast purple sea urchin: A correlation with headlands. Limnol Oceanogr 33:286–294

Fernández M, Blanco M, Ruano-Chamorro C, Subida MD (2017) Reproductive output of two benthic resources (*Fissurella latimarginata* and *Loxechinus albus*) under different management regimes along the coast of central Chilea. Lat Am J Aquat Res 45:391–402

Figueroa D, Moffat C (2000) On the influence of topography in the induction of coastal upwelling along the Chilean coast. Geophys Res Lett 27:3905–3908

Fincham JI, Rijnsdorp AD, Engelhard GH (2013) Shifts in the timing of spawning in sole linked to warming sea temperatures. J Sea Res 75:69–76

Fogarty MJ, Botsford LW (2007) Population connectivity and spatial management of marine fisheries . Oceanography 20:112–123

Gaines SD, Lester SE, Grorud-Colvert K, Costello C, Pollnac R (2010a) Evolving science of marine reserves: New developments and emerging research frontiers. Proc Natl Acad Sci 107:18251–18255

Gaines S, White C, Carr M, Palumbi S (2010b) Designing marine reserve networks for both conservation and fisheries management. Proc Natl Acad Sci USA 107:18286–93

Game ET, Bode M, McDonald-Madden E, Grantham HS, Possingham HP (2009) Dynamic marine protected areas can improve the resilience of coral reef systems. Ecol Lett 12:1336–1345

Gelcich S, Fernández M, Godoy N, Canepa A, Prado L, Castilla JC (2012) Territorial user rights for fisheries as ancillary instruments for marine coastal conservation in Chile. Conserv Biol 26:1005–15

Gillooly JF, Charnov EL, West GB, Savage VM, Brown JH (2002) Effects of size and temperature on developmental time. Nature 417:70–73

González L, Castilla J, Guisado C (1987) Effects of larval diet and rearing temperature on metamorphosis and juvenile survival of the sea urchin *Loxechinus albus* (Molina, 1782) (Echinodermata: Echinoidea). J Shellfish Res 6:109–115

Graham WM, Largier JL (1997) Upwelling shadows as nearshore retention sites: The example of northern Monterey Bay. Cont Shelf Res 17:509–532

Halpern BS, Walbridge S, Selkoe KA, Kappel C., Micheli F, D'Agrosa C, Casey K, Ebert C, Fox H, Fujita R, Heinemann D, Lenihan H., P. Madin E., Perry M, Selig E, Spaldin M, Steneck R, Watson R (2008) A Global Map of Human Impact on Marine Ecosystems. Science (80-) 319:948–952

Hart M, Scheibling RE (1988) Heat waves, baby booms, and the destruction of kelp beds by sea urchins. Mar Biol 99:167–176

Hedgecock D, Barber PH, Edmands S (2007) Genetic approaches to measuring connectivity. Oceanography 20:70–79

Hinckley S, Hermann AJ, Megrey BA (1996) Development of a spatially explicit, individual-based model of marine fish early life history. Mar Ecol Prog Ser 139:47–68

Hoegh-Guldberg (1995) Temperature, Food Availability, and the Development of Marine Invertebrate Larvae. Am Zool 35:415–425

Jacobi MN, André C, Döös K, Jonsson PR (2012) Identification of subpopulations from connectivity matrices. Ecography (Cop) 35:1004–1016

Jacobi MN, Jonsson PR (2011) Optimal networks of nature reserves can be found through eigenvalue perturbation theory of the connectivity matrix. Ecol Appl 21:1861–1870

Kaplan D, Andrello M (2016) Package "ConnMatTools", Tools for Working with Connectivity Data. :1–50

Kirincich AR, Barth JA (2009) Alongshelf Variability of Inner-Shelf Circulation along the Central Oregon Coast during Summer. J Phys Oceanogr 39:1380–1398

Kirincich AR, Barth JA, Grantham BA, Menge BA, Lubchenco J (2005) Wind-driven inner-shelf circulation off central Oregon during summer. J Geophys Res C Ocean 110:1–17

Lacroix G, Barbut L, Volckaert FAM (2018) Complex effect of projected sea temperature and wind change on flatfish dispersal. Glob Chang Biol 24:85–100

Lagos NA, Castilla JC, Broitman BR (2008) Spatial environmental correlates of intertidal recruitment: A test using barnacles in northern chile. Ecol Monogr 78:245–261

Lagos NA, Navarrete SA, Véliz F, Masuero A, Castilla JC (2005) Meso-scale spatial variation on settlement and recruitmen of intertidal barnacles along the coast of central Chile. Mar Ecol Prog Ser 290:165–178

Leis JM, Caselle JE, Bradbury IR, Kristiansen T, Llopiz JK, Miller MJ, O'Connor MI, Paris CB, Shanks AL, Sogard SM, Swearer SE, Treml EA, Vetter RD, Warner RR (2013) Does fish larval dispersal differ between high and low latitudes? Proc Biol Sci 280:20130327

Leslie HM, Breck EN, Chan F, Lubchenco J, Menge BA (2005) Barnacle reproductive hotspots linked to nearshore ocean conditions. Proc Natl Acad Sci U S A 102:10534–10539

Lester SE, Gaines SD, Kinlan BP (2007) Reproduction on the edge: large-scale patterns of individual performance in a marine invertebrates. Ecology 88:2229–2239

Lett C, Nguyen-Huu T, Cuif M, Saenz-Agudelo P, Kaplan DM (2015) Linking local retention, self-recruitment and persistence in marine metapopulations. Ecology 33:1–32

Lett C, Verley P, Mullon C, Parada C, Brochier T, Penven P, Blanke B (2008) A Lagrangian tool for modelling ichthyoplankton dynamics. Environ Model Softw 23:1210–1214

Levin LA. (2006) Recent progress in understanding larval dispersal: New directions and digressions. Integr Comp Biol 46:282–297

Madeira D, Costa PM, Vinagre C, Diniz MS (2016) When warming hits harder: survival, cellular stress and thermal limits of Sparus aurata larvae under global change. Mar Biol 163

Manríquez PH, Castilla JC (2001) Significance of marine protected areas in central Chile as seeding grounds for the gastropod *Concholepas concholepas*. Mar Ecol Prog Ser 215:201–211

Marta-Almeida M, Dubert J, Peliz A, Queiroga H (2006) Influence of vertical migration pattern on retention of crab larvae in a seasonal upwelling system. Mar Ecol Prog Ser 307:1–19

McDonald K (2004) Patterns in early embryonic motility: Effects of size and environmental temperature on vertical velocities of sinking and swimming echinoid blastulae. Biol Bull 207:93–102

McLaren IA (1963) Effects of temperature on growth of zooplankton, and the adaptive value of vertical migration. J Fish Res Board Canada 20:685–727

McLeod I, McCormick M, Munday P, Clark T, Wenger A, Brooker R, Takahashi M, Jones G (2015) Latitudinal variation in larval development of coral reef fishes: implications of a warming ocean. Mar Ecol Prog Ser 521:129–141

Metaxas A, Saunders M (2009) Quantifying the "bio-" components in biophysical models of larval transport in marine benthic invertebrates: advances and pitfalls. BiolBull 216:257–72

Molinet C, Herrera C, Gebauer P, Landaeta MF, Moreno CA (2010) Estados tempranos de Echinoidea en canal Lagreze, Islas Guaitecas, sur de Chile. Rev Biol Mar Oceanogr 45:19–33

Morgan SG (2014) Behaviorally Mediated Larval Transport in Upwelling Systems. Adv Oceanogr 2014:1–17

Morgan SG, Fisher JL, Miller SH, McAfee ST, Largier JL (2009) Nearshore larval retention in a region of strong upwelling and recruitment limitation. Ecology 90:3489–3502

Munday PL, Leis JM, Lough JM, Paris CB, Kingsford MJ, Berumen ML, Lambrechts J (2009) Climate change and coral reef connectivity. Coral Reefs 28:379–395

Munguia-Vega A, Jackson A, Marinone SG, Erisman B, Moreno-Baez M, Girón-

Nava A, Pfister T, Aburto-Oropeza O, Torre J (2014) Asymmetric connectivity of spawning aggregations of a commercially important marine fish using a multidisciplinary approach. PeerJ 2:e511

Navarrete SA, Broitman BR, Menge BA (2008) Interhemispheric comparison of recruitment to intertidal communities: pattern persistence and scales of variation. Ecology 89:1308–1322

Navarrete SA, Wieters EA, Broitman BR, Castilla JC (2005) Scales of benthic-pelagic coupling and the intensity of species interactions: from recruitment limitation to top-down control. Proc Natl Acad Sci USA 102:18046–18051

Nickols KJ, Gaylord B, Largier JL (2012) The coastal boundary layer: Predictable current structure decreases alongshore transport and alters scales of dispersal. Mar Ecol Prog Ser 464:17–35

O'Connor MI, Bruno JF, Gaines SD, Halpern BS, Lester SE, Kinlan BP, Weiss JM (2007) Temperature control of larval dispersal and the implications for marine ecology, evolution, and conservation. Proc Natl Acad Sci USA 104:1266–71

O'Connor MI, Selig ER, Pinsky ML, Altermatt F (2012) Toward a conceptual synthesis for climate change responses. Glob Ecol Biogeogr 21:693–703

Ospina-Alvarez A, Catalán I a, Bernal M, Roos D (2015) From egg production to recruits : connectivity and inter-annual variability in the recruitment patterns of European anchovy in the northwestern Mediterranean. Prog Oceanogr 138: 431 - 447

Ospina-Alvarez A, Palomera I, Parada C (2012) Changes in egg buoyancy during development and its effects on the vertical distribution of anchovy eggs. Fish Res 117–118:86–95

Ospina-Alvarez A, Weidberg N, Aiken C, Navarrete S (in press) Larval transport in the upwelling ecosystem of central Chile: The effect of vertical migration for different larval development times and against the effect of environmental variability. Prog Oceanogr

Parada C, Mullon C, Roy C, Fréon P (2008) Does vertical migratory behaviour retain fish larvae onshore in upwelling ecosystems? A modelling study of anchovy in the southern Benguela. African J Mar Sci 30:437–45

Paradis E, Bolker B, Claude J, Cuong HS, Desper R, Durand B, Dutheil J, Gascuel O, Heibl C, Lawson D, Lefort V, Legendre P, Lemon J, Noel Y, Nylander J, Opgen-Rhein R, Popescu A-A, Schliep K, Strimmer K, Vienne D de (2017) Package "ape". Analyses of Phylogenetics and Evolution. :1–276

Paris CB, Cowen RK (2004) Direct evidence of a biophysical retention mechanism for coral reef fish larvae. Limnol Oceanogr 59:1964–1979

Pérez M. C, González ML, López D (2007) Breeding cycle and early development of the keyhole limpet *Fissurella nigra* (Lesson, 1831). J Shellfish Res 26:315–318

Peterson W (1998) Life cycle strategies of copepods in coastal upwelling zones. J Mar Syst 15:313–326

Possingham HP, Roughgarden J (1990) Spatial population dynamics of a marine organism with a complex life cycle. Ecology 71:973–985

Poulin E, Palma AT, Leiva G, Narvaez D, Pacheco R, Navarrete SA, Castilla JC (2002) Avoiding offshore transport of competent larvae during upwelling events: The case of the gastropod *Concholepas concholepas* in central Chile. Limnol Oceanogr 47:1248–1255

Queiroga H, Cruz T, Santos A dos, Dubert J, González-Gordillo JI, Paula J, Peliz Á, Santos a. MP (2007) Oceanographic and behavioural processes affecting invertebrate larval dispersal and supply in the western Iberia upwelling ecosystem. Prog Oceanogr 74:174–191

R DCT (2013) R: A Language and Environment for Statistical Computing.

Reitzel AM, Miner BG, McEdward LR (2004) Relationships between spawning date and larval development time for benthic marine invertebrates: A modeling approach. Mar Ecol Prog Ser 280:13–23

Reynoso-Granados T, Monsalvo-Spencer P, Serviere-Zaragoza E, Guzmán del Próo SA (2007) Larval and early juvenile development of the volcano keyhole limpet, *Fissurella volcano*. J Shellfish Res 26:65–70

Roughgarden J, Gaines S, Possingham H (1988) Recruitment dynamics in complex life cycles. Science (80-) 241:1460–1466

Roughgarden J, Iwasa Y (1986) Dynamics of a metapopulation with space-limited subpopulations. Theor Popul Biol 29:235–261

Roughgarden J, Iwasa Y, Blaxter C (1985) Demographic theory for an open population with space-limited recruitment. Ecology 66:54–67

Roughgarden J, Pennington JT, Stoner D, Alexander S, Miller K (1991) Collision of upwelling fronts with the intertidal zone: the cause of recruitment pulses in barnacles populations of central California. Acta Oecologica 12:35–51

Rumrill S (1990) Natural mortality of marine invertebrate larvae. Ophelia 32:163–198

Rutllant JA, Rosenbluth B, Hormazabal S (2004) Intraseasonal variability of wind-forced coastal upwelling off central Chile (30°S). Cont Shelf Res 24:789–804

Salomon Y, Connolly SR, Bode L (2010) Effects of asymmetric dispersal on the coexistence of competing species. Ecol Lett 13:432–441

Shama LNS (2015) Bet hedging in a warming ocean: Predictability of maternal environment shapes offspring size variation in marine sticklebacks. Glob Chang Biol 21:4387–4400

Shanks AL, Largier J, Brink L, Brubaker J, Hooff R (2000) Demonstration of the onshore transport of larval invertebrates by the shoreward movement of an upwelling front. Limnol Oceanogr 45:230–236

Sponaugle S, Grorud-Colvert K (2006) Environmental variability, early life-history traits, and survival of new coral reef fish recruits. Integr Comp Biol 46:623–33

Strub P, Mesías J, Montecino V, Rutlant J, Salinas S (1998) Coastal ocean circulation off western South America. In: Robinson A, Brink K (eds) (eds) The sea, Vol 11. JWiley & Sons, New York, p 273–314

Sundelöf A, Jonsson PR (2012) Larval dispersal and vertical migration behaviour - a simulation study for short dispersal times. Mar Ecol 33:183–193

Szuwalski CS, Vert-Pre KA, Punt AE, Branch TA, Hilborn R (2015) Examining common assumptions about recruitment: A meta-analysis of recruitment dynamics for worldwide marine fisheries. Fish Fish 16:633–648

Tapia FJ, Navarrete SA, Castillo M, Menge BA, Castilla JC, Largier J, Wieters EA, Broitman BL, Barth J a. (2009) Thermal indices of upwelling effects on inner-shelf habitats. Prog Oceanogr 83:278–287

Thiel M, Macaya EC, Acuna E (2007) The Humboldt Current System of northern and central Chile: oceanographic processes, ecological interactions and socioeconomic feedback. Oceanogr Mar Biol 45:195–344

Thorrold SR, Zacherl DC, Levin LA (2007) Population Connectivity and Larval Dispersal Using Geochemical Signatures in Calcified Structures. Oceanography 20:80–89

Thorson G (1950) Reproductive and larval ecology of marine bottom invertebrates. Biol Rev 25:1–45

Tognelli MF, Fernández M, Marquet PA (2009) Assessing the performance of the existing and proposed network of marine protected areas to conserve marine biodiversity in Chile. Biol Conserv 142:3147–3153

Tremblay M, Sinclair M (1990) Sea scallop larvae *Placopecten magellanicus* on Georges Bank: vertical distribution in relation to water column stratification and food. Mar Ecol Prog Ser 61:1–15

Watson JR, Hays CG, Raimondi PT, Mitarai S, Dong C, Mcwilliams JC, Blanchette

CA, Caselle JE, Siegel DA (2011) Currents connecting communities: Nearshore community similarity and ocean circulation. Ecology 92:1193–1200

Watson JR, Mitarai S, Siegel DA, Caselle JE, Dong C, McWilliams JC (2010) Realized and potential larval connectivity in the Southern California Bight. Mar Ecol Prog Ser 401:31–48

Werner FE, Cowen RK, Paris CB (2007) Coupled biological and physical models: present capabilities and necessary developments for future studies of population connectivity. Oceanography 20:54–69

White C, Costello C (2011) Matching spatial property rights fisheries with scales of fish dispersal. Ecol Appl 21:350–62

Wieters EA, Gaines SD, Navarrete SA, Blanchette CA, Menge BA (2008) Scales of dispersal and the biogeography of marine predator-prey interactions. Am Nat 171:405–417

Wing SR, Botsford LW, Largier JL, Morgan LE (1995) Spatial structure of relaxation events and crab settlement in the northern California upwelling system. Mar Ecol Prog Ser 128:199–211

Woodson CB, McManus MA. (2007) Foraging behavior can influence dispersal of marine organisms. Limnol Oceanogr 52:2701–2709

Worcester SE (1994) Adult rafting versus larval swimming: dispersal and recruitment of a botryllid ascidian on eelgrass. Mar Biol 121:309–317

Part III
Tercera parte

Discusión General

Discusión general

Los distintos capítulos de esta tesis han contribuido a ampliar el conocimiento de las distintas etapas de los ciclos de vida complejos de *L. albus* y *F. Latimarginata*, dos especies de invertebrados bentónicos objetivo de la pesca artesanal en la costa central de Chile, y han aportado información valiosa para el futuro diseño de estrategias de manejo y conservación adaptadas a la ecología de estas especies. Los principales resultados de esta tesis han sido: (a) demostrar que la condición y la inversión reproductiva individual de especies consideradas objetivo pesquero no siempre está condicionada por el nivel de protección y la productividad oceánica (afloramiento costero); (b) sumar evidencia a que si bien no parece haber un efecto directo de la protección sobre el valor reproductivo individual, si se observan efectos indirectos en la producción de propágulos mediados por el incremento en la talla y la densidad de individuos reproductores en áreas protegidas; (c) demostrar que para las dos especies estudiadas la localización geográfica y la fecha del desove parecen ser los principales determinantes del éxito de reclutamiento y la distancia de dispersión, (d) proporcionar más evidencias que refuerzan la idea que la modelización de rasgos biológicos individuales de las larvas (comportamiento de migración vertical y desarrollo larval dependiente de la temperatura) afectan significativamente el transporte y en consecuencia los patrones de dispersión y reclutamiento. Estos resultados son relevantes a nivel global, ya que han permitido entender la importancia relativa de los efectos directos e indirectos de la protección sobre un aspecto poco evaluado de la conservación: su impacto fuera de los límites de las zonas protegidas, a través de la producción de propágulos. Pero también constituyen importantes contribuciones a nivel local ya que han permitido: (a) identificar y cuantificar la contribución del sistema actual de áreas de manejo a la producción regional de huevos y larvas, el cual aumenta entre un 67% y un 57% la producción potencial de huevos de *F. latimarginata* y *L. albus*, respectivamente, respecto a un escenario de libre acceso, a lo largo de la costa central de Chile; (b) identificar las principales zonas de desove, que en la zona de estudio se concentran entre los 31.57ºS y los 33.50ºS, con un 80% de la producción potencial de huevos para ambas especies; (c) identificar las áreas que exportan una mayor proporción relativa de larvas que alcanzan un área de asentamiento y las áreas de asentamiento con mayor probabilidad relativa de captar larvas después de haber concluido su transporte, que interesantemente son coincidentes en ambas especies a pesar de sus diferencias en el periodo de desarrollo planctónico (5 días para la lapa y 20 días para el erizo); y (d) identificar la importancia relativa del reclutamiento alóctono y autóctono, que en la región de estudio es mayoritariamente alóctono, incluso para las especies con tiempos de desarrollo corto como la lapa. Estos hallazgos han permitido avanzar no solo hacia un mejor entendimiento de la influencia de la historia de vida temprana de dos especies de invertebrados bentónicos de una gran importancia a nivel pesquero, sobre los patrones de provisión de larvas en la costa central de Chile, sino también contribuir con información crítica para el diseño de programas de conservación y manejo. Esto es particularmente importante para la zona de estudio, la cual concentra la mayor densidad de población humana en Chile, lo que a su vez la convierte, a nivel país, en una de las zonas generadoras de mayor impacto antrópico al ecosistema costero (Tognelli et al. 2009). De tal manera, resulta de especial interés desarrollar estrategias de manejo y conservación que promuevan la extracción sostenible de los recursos en esta zona. A continuación, en esta discusión general, se discuten los principales resultados obtenidos y se proponen nuevas perspectivas de manejo.

El efecto de la protección y el afloramiento costero sobre la inversión reproductiva y la condición individual de los adultos reproductores

La presente investigación ha demostrado que la protección no tiene un efecto significativo sobre la inversión reproductiva y la condición individual, medidas a través del índice gonadosomático y el peso seco del cuerpo, respectivamente. Tradicionalmente la elección de sitios para el establecimiento de áreas protegidas se ha realizado siguiendo criterios de productividad (Leslie 2005). Se esperaría entonces que los efectos directos de la protección sobre la inversión reproductiva y la condición individual sean positivos si los sitios a proteger son particularmente productivos. Sin embargo, estos efectos pueden revertirse bajo situaciones de denso-dependencia considerando los aumentos de densidad observados en zonas protegidas (ej. alimentación o parasitismo denso-dependiente) (Loot et al. 2005, Wood et al. 2013). Así, bajo escenarios de denso-dependencia en disponibilidad de alimento, o castración por parasitismo, las reservas individuales de energía podrían verse condicionadas (Kaiser et al. 2007, Aldana et al. 2014) dificultándose la evaluación de los múltiples procesos que interactúan (productividad, denso-dependencia). Estudios desarrollados en la costa de Chile demostraron que la tasa de infección de numerosas especies de invertebrados, incluyendo la lapa Fissurella crassa, es significativamente más alta en áreas marinas protegidas respecto a áreas de libre acceso (Loot et al. 2005, Wood et al. 2013). Sin embargo, el mayor número de parásitos en las gónadas de Fissurella crassa en TURFs incrementó el valor del índice gonadosomático en estas áreas (Aldana et al. 2014). Los resultados obtenidos en esta tesis nos han permitido concluir que la selección de sitios más productivos para la instalación de TURFs no ejerce influencia significativa en la inversión reproductiva y condición individual. Nuestros resultados, abren la puerta a hipótesis alternativas que analicen la importancia relativa de los diferentes componentes denso-dependientes.

Una de las contribuciones de este trabajo ha sido la constatación de que en la escala espacial de análisis, el afloramiento costero, que actúa como el principal impulsor de la dinámica costera en el área de estudio, (Wieters et al. 2003, Navarrete et al. 2005, Wieters 2005, Tapia et al. 2009, 2014), no tiene un efecto significativo sobre los indicadores fisiológicos evaluados, condición e inversión reproductiva individual de las dos especies de herbívoros estudiadas. Un estudio reciente desarrollado en zonas con distinto nivel de influencia del afloramiento costero, a lo largo de la costa central de Chile, en el que se comparó la inversión reproductiva individual para cuatro especies de herbívoros, entre ellos *F. latimarginata*, demostró que los organismos que crecen en zonas influenciadas por el afloramiento invierten significativamente más energía en reproducción y que, además, el desarrollo de la gónada ocurre a edades más tempranas, en comparación con zonas de sombra del afloramiento costero (Aldana et al. 2017). Los resultados de Aldana et al. (2017) no concuerdan con los resultados obtenidos en este trabajo. Una posible explicación de la falta de concordancia tiene que ver con el diseño experimental, específicamente con la replicación de los niveles de afloramiento. El estudio de Aldana et al. (2017) está basado en una sola localidad por cada nivel de afloramiento, mientras que el presente estudio incorporó más de una localidad por cada nivel de afloramiento. Así, la replicación de localidades puede incorporar la variabilidad que ocurre en zonas de afloramiento. Si bien la zona de Chile central está caracterizada por afloramientos costeros, se han descrito importantes variaciones entre zonas de afloramiento (Figueroa & Moffat 2000, Tapia et al. 2014), las cuales pueden estar causadas por variaciones en la orientación de la costa (Tapia et al. 2009). La orientación de la costa influye en

la intensidad, temporalidad y dirección del oleaje, el cual influye en la inversión reproductiva y el crecimiento somático de los individuos sometidos a esta variabilidad. Por ejemplo, para el erizo *Paracentrotus lividus* se ha encontrado que la exposición al oleaje afecta positivamente la inversión reproductiva y negativamente al crecimiento somático (Lozano et al. 1995, Ouréns et al. 2012). Sin embargo, estas relaciones no son generalizables a todas las especies de invertebrados bentónicos, por ejemplo, en la lapa *Cymbula aculus* se encontró que la exposición al oleaje afecta negativamente la inversión reproductiva, la cual puede verse reducida de 10 a 25 veces respecto a las zonas protegidas del oleaje (Branch & Odendaal 2003). Adicionalmente, no hay un claro efecto sobre la inversión reproductiva de la relación entre el nivel de protección, la extracción de especies objetivo de la pesca y la exposición al oleaje (Branch & Odendaal (2003). En consecuencia, y volviendo a la comparación entre la presente investigación, en la cual la mayoría de las áreas muestreadas fueron áreas donde se permite la extracción pesquera (TURFs y ALAs), tan solo se incluyó un área de no acceso (AMP de las Cruces), y la investigación de Aldana et al. (2017), en la cual se incluyeron dos áreas marinas protegidas, no hay un consenso sobre los efectos conjuntos del nivel de protección y el afloramiento costero sobre la condición y la inversión reproductiva individual de especies de invertebrados bentónicos sometidos a extracción pesquera. Probablemente, en este punto, sea aconsejable proponer investigaciones que tratasen de dar respuesta exclusivamente a esta pregunta teniendo en cuenta las variaciones a nivel local, tanto en el nivel de explotación pesquera como otros factores ambientales que puedan generar respuestas complejas sobre el crecimiento y la inversión reproductiva.

Efectos indirectos de la protección sobre el potencial reproductivo

En esta investigación se ha constatado que las decisiones de gestión que establecen un mosaico de áreas total y parcialmente protegidas alternando con áreas de libre acceso afectan significativamente la talla de la lapa y el erizo rojo. En la mayoría de las localidades bajo estudio los individuos recolectados en áreas total y parcialmente protegidas fueron de mayor tamaño en comparación con las áreas libres adyacentes (Fig. 2, capítulo 1). Sin embargo, estos resultados no fueron consistentes en todas las localidades. Incluso, en dos de las localidades bajo estudio el patrón observado en la talla del erizo rojo fue inverso, es decir, la talla promedio de los individuos fue más grande en áreas libres que en áreas protegidas.

(a) *Fissurella latimarginata*

(b) *Loxechinus albus*

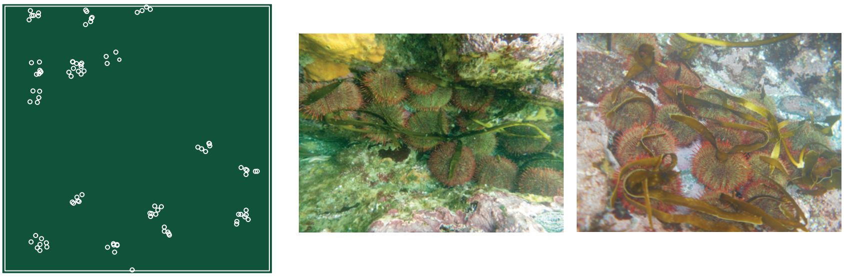


Figura 3.1. Patrón de distribución espacial de (a) *Fissurella latimarginata* y (b) *Loxechinus albus*, los individuos se han representado como círculos blancos. Los patrones de distribución para ambas especies se han representado a partir de simulaciones con datos obtenidos en muestreos de campo realizados en áreas de manejo. Para *F. latimarginata* se ha utilizado la herramienta "runifpoint", de la librería "spatstat" del software R (versión 3.1.3), esta herramienta permite generar una posición (x,y) de cada individuo, en un área predeterminada (en este caso, 15 x 15 m), dado un número de individuos por área (se han simulado 44 individuos). Para *L. albus* se ha utilizado la herramienta "rMatClust", que permite generar un patrón de distribución agregado, dada una densidad de parches (se han simulado 0.15 parches/m2), el radio de los parches (0.5 m) y el número de individuos por parche (6 individuos/parche). Las fotografías corresponden a individuos observados en muestreos de campo, para *L. albus* se observan agregaciones de varios individuos.

Una posible explicación puede ser la existencia de un esfuerzo pesquero variable en las áreas parcialmente protegidas (TURFs) de las distintas localidades. Por ejemplo, en la localidad de Laguna Verde (159.33 ha) la extracción de erizo rojo entre los años 2010 y 2013 alcanzó las 3 toneladas, mientras que en la localidad de Quintay (324.78 ha), en los mismos años, la extracción alcanzo las 68 toneladas (SUBPESCA 2013). Estás áreas se encuentran a una distancia lineal de unos 14 km y ambas corresponden a zonas de afloramiento costero. Sin embargo, aunque las condiciones medioambientales son similares, el esfuerzo pesquero en ambas localidades es evidentemente distinto. Este hecho pone en relieve que el nivel de explotación pesquera puede tener una mayor influencia en la talla media de los individuos que la que ejercen los factores ambientales. En el caso de la lapa (*F. latimarginata*), la diferencia en la extracción pesquera entre localidades fue menor, en la localidad de Quintay entre los años 2010 y 2013 los desembarques de lapa fueron 7 veces mayores que en Laguna Verde (14 y 2 toneladas, respectivamente; SUBPESCA 2013). Estos resultados mostraron la ausencia de un patrón regional en las tallas de ambas especies, esta observación refuerza la idea de que el esfuerzo pesquero es el mayor determinante de las diferencias observadas en la talla de la lapa y el erizo rojo, y esto puede condicionar de forma indirecta la inversión reproductiva a través de la producción de huevos (capítulo 2).

Esta investigación ha permitido evidenciar que a nivel global las áreas parcialmente protegidas tienen un efecto positivo sobre la talla y la densidad de los adultos reproductores de ambas especies modelo de estudio. Tanto para *F. latimarginata* como para *L. albus*, la talla de los individuos fue mayor en TURFs respecto a las áreas libres entre un 13 y un 2%, respectivamente. La densidad de individuos también fue más alta en TURFs, entre un 65 y un 238%, respectivamente, en comparación con las áreas de libre acceso. Sin embargo las diferencias en la talla y la densidad de individuos entre niveles de protección tan solo fueron significativas en el caso de la lapa. La gran variabilidad en la densidad de erizos tanto en TURFs como en áreas de libre acceso no ha impedido identificar un patrón claro y significativo de mayor densidad de individuos en TURFs para esta especie. Estudios previos también han reportado menor impacto de la protección en *L. albus* y mayor variabilidad en la abundancia y talla de los individuos, probablemente debido a la distribución parcheada que tiene el erizo rojo (Gelcich et al. 2012). En la zona de estudio, *L. albus* se encuentra predominantemente asociado a zonas expuestas, de difícil acceso para los pescadores, donde habitualmente se encuentra formando agregaciones (Figura 3.1B).

Los resultados sugieren que existe un potencial efecto reserva que podría amplificar indirectamente los efectos positivos de la protección sobre la exportación de larvas desde las áreas protegidas hacia las áreas aledañas, vía los efectos de la protección sobre la densidad y la talla de los adultos reproductores. En primer lugar, los resultados presentados han mostrado un incremento exponencial de la fecundidad potencial en relación con la talla para ambas especies (Figura 3.2). En segundo lugar, la diferencia en la talla de las lapas en TURFs respecto a las áreas de libre acceso fue del 13%, este incremento produjo un 68% mayor fecundidad en

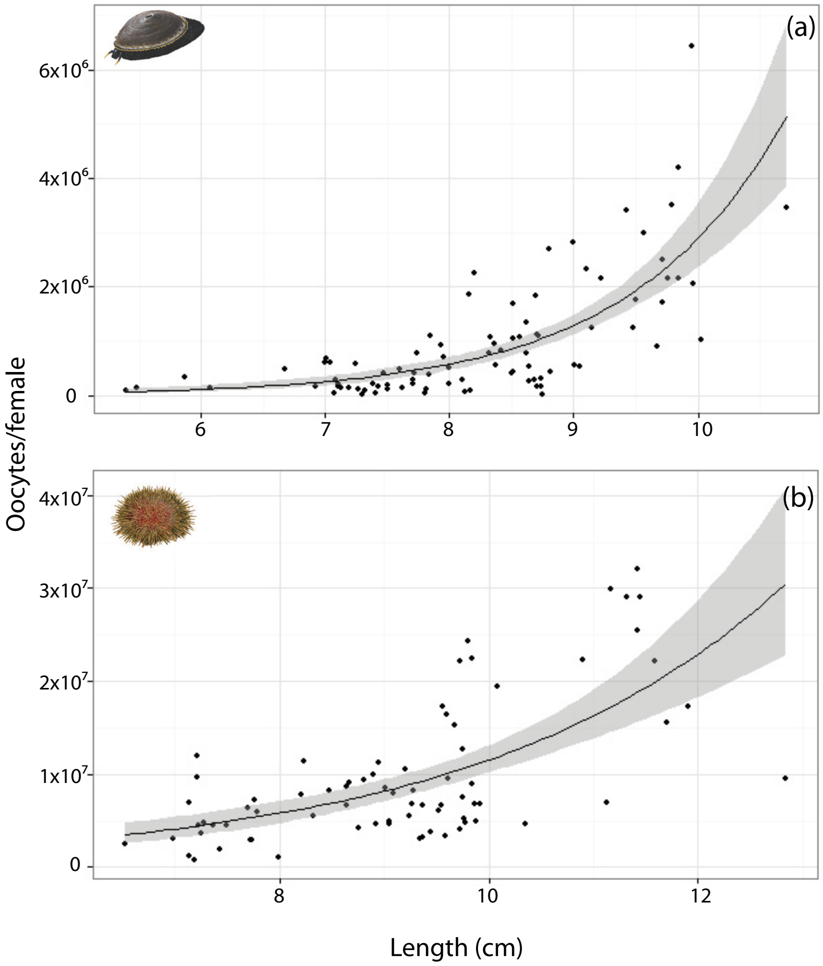


Figura 3.2. Relación entre la talla de la hembra y el número de ovocitos, ajustada a un modelo exponencial para (a) *Fissurella latimarginata* y (b) *Loxechinus albus*.

las hembras recolectadas en TURFs. Resultados que contrastan con los obtenidos para el erizo rojo, donde la diferencia en talla de tan solo un 2% no produjo diferencias significativas en la fecundidad potencial. Aun así, se podría afirmar que, dado que los individuos de mayor tamaño se encuentran en las TURFs (Figura 3.3), la talla podría generar un efecto en la fecundidad potencial y que esta última afecta la producción potencial de huevos. Los resultados de esta investigación han demostrado que las áreas parcialmente protegidas (TURFs) representa un incremento de la producción de huevos (661% para la lapa y del 238% para el erizo rojo), a través del incremento de talla y densidad de los individuos reproductores.

En otros estudios también se ha observado un mayor éxito de fertilización en áreas con una mayor densidad de individuos (Levitan 1991), tal y como lo pueden ser las áreas protegidas, lo que contribuiría positivamente a potenciar aun más el efecto reserva relacionado con la exportación de larvas. Sin embargo, la exportación de larvas de un área determinada a áreas adyacentes requiere de un enfoque más amplio, que incluya otros factores determinantes que afectan el transporte y la dispersión larval (capítulo 3) y la adaptación y sobrevivencia de los reclutas.

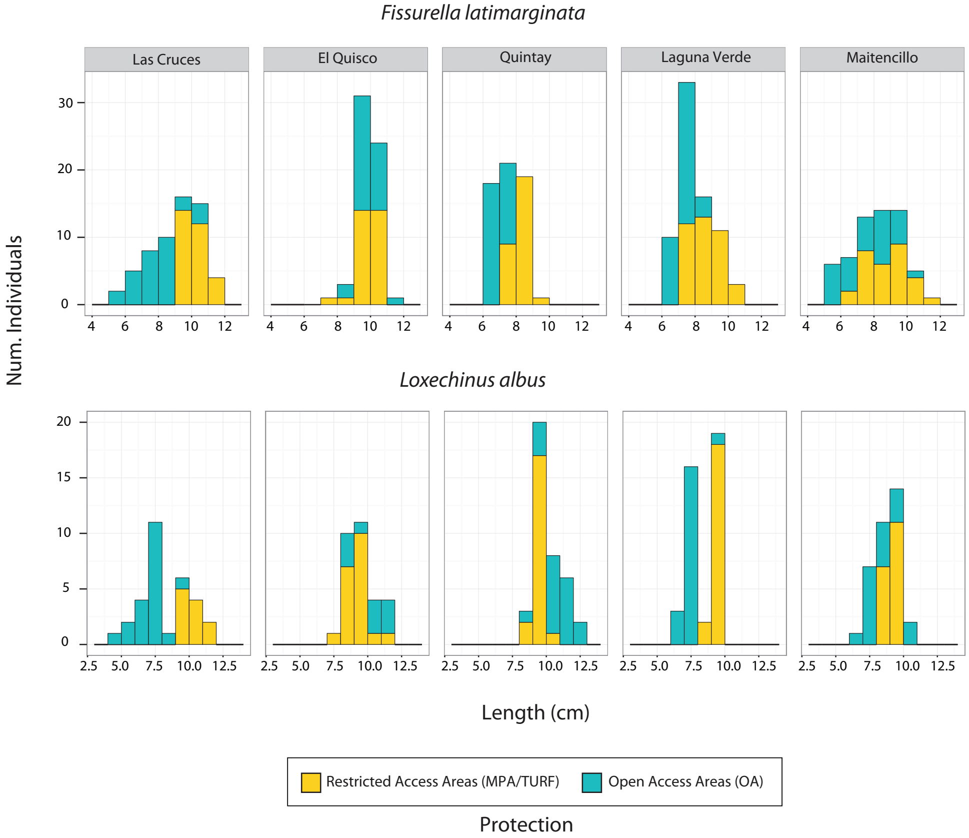


Figura 3.3. Distribución de tallas en áreas de acceso restringido a la pesca (barras amarillas) (áreas parcialmente protegidas (áreas de manejo (TURFs)) y áreas marinas totalmente protegidas (de áreas totalmente protegidas únicamente se ha considerado el área marina protegida de las Cruces (MPA))) y áreas de libre acceso (barras azules).

La relevancia de la densidad como determinante de la producción gonadal por unidad de área ha sido reportada previamente en la literatura (Kelly et al. 2000, Willis et al. 2003, Pelc et al. 2009). Sin embargo, la interacción de los efectos combinados de la densidad y talla de los organismos no han sido concluyentes y nuestros resultados tampoco permiten realizar ninguna aseveración. En *F. latimarginata* la diferencia en la producción potencial de huevos entre TURFs y áreas de libre acceso fue un 277% más elevada que en *L. albus*, además se encontraron diferencias significativas en la producción potencial de huevos al comparar ambos niveles de explotación pesquera, para el erizo rojo estas diferencias no fueron significativas. Se desarrolló un modelo lineal para relacionar la producción potencial de huevos con la densidad y la talla, en el erizo rojo la densidad explicó aproximadamente el 80% de la variabilidad observada seguido por la talla, que explicó aproximadamente el 20%. En cambio, para la lapa la densidad explicó un 37% de la variabilidad observada en la producción potencial de huevos y la talla el 23%. De acuerdo con estos resultados, podría afirmarse que la densidad podría tener una mayor influencia en la variabilidad observada en la producción potencial de huevos que la talla individual de los organismos. Si esta hipótesis fuese cierta, se deberían definir estrategias de manejo que tuviesen como objetivo el mantener o aumentar la densidad de individuos en las distintas áreas. Nuevos estudios son necesarios para confirmar o rechazar esta hipótesis y evaluar cuáles son los principales determinantes de la producción potencial de huevos en las áreas protegidas. Con estudios como estos se lograría avanzar en estrategias que consideren los efectos positivos de las áreas protegidas como zonas de producción de propágulos, como exportadoras de estos y resaltando su importancia en la dinámica poblacional mediante la conectividad de las distintas subpoblaciones.

Influencia de los factores hidrodinámicos y rasgos biológicos larvales en los patrones de transporte, dispersión, reclutamiento y conectividad larval

En las zonas costeras, los procesos de circulación son geográficamente y temporalmente variables (Narváez et al. 2004, Lagos et al. 2005, Aiken et al. 2008). Los resultados han demostrado que para ambas especies de invertebrados bentónicos e independientemente de los rasgos biológicos de las larvas, la localización y el momento de desove son los principales determinantes de la distancia de dispersión, el reclutamiento y los patrones de conectividad observados en la región de estudio. Es destacable que independientemente de las diferencias en PLD, aproximadamente 20 días para el erizo y 5 días para la lapa, la localización (latitud, longitud) y fecha en la cual se produce el desove son los factores que en mayor medida explican la variabilidad observada en el reclutamiento de ambas especies. Esta observación es consistente con resultados obtenidos en estudios realizados con otras especies y en diferentes zonas alrededor del mundo, en los cuales se destaca la importancia espacio-temporal del desove, además de la densidad de adultos reproductores (Parada et al. 2008, Brochier et al. 2009, Ospina-Alvarez et al. 2015). Los resultados presentados en esta disertación han demostrado que, en la región de estudio y para las dos especies, la mayor parte del reclutamiento se concentra alrededor de tres franjas latitudinales (Fig. 3, capítulo 3). Aunque la resolución espacial del modelo utilizado (2 km latitudinales) es baja para avanzar en mecanismos causales, se puede hipotetizar que existe una concordancia espacial entre las latitudes que muestran mayor reclutamiento y los salientes de la costa (Apéndice, Fig. A1). La concentración o retención de larvas en relación con accidentes geográficos a lo largo de la costa es un fenómeno que ha sido observado con anterioridad para otras especies y zonas de estudio (Roughan et al. 2005). En la costa central de Chile, algunos estudios señalan que los efectos de la topografía de la costa son más relevantes que las variaciones en las corrientes impulsadas por el viento, explicando la intensificación del afloramiento alrededor de salientes de la costa (Figueroa & Moffat 2000, Aiken et al. 2008). La influencia de la variación temporal y espacial en la intensidad del afloramiento costero sobre el reclutamiento larval podría estar relacionada con distintos mecanismos: la retención de las masas de agua (zonas de sombra de surgencia) (Graham & Largier 1997, Poulin et al. 2002, Aiken et al. 2008), la colisión de los frentes de afloramiento con las zonas expuestas de la costa durante eventos de relajación del afloramiento (Roughgarden et al. 1988, 1991, Wing et al. 1995, Shanks et al. 2000) y los complejos patrones de circulación que se desarrollan a lo largo y ancho de la costa generados durante los eventos de relajación del afloramiento (Kirincich et al. 2005, Kirincich & Barth 2009) (Figura 3.4B).

El comportamiento de migración vertical de las larvas (DVM), tuvo un efecto significativo en la distancia de dispersión y el éxito del reclutamiento. Sin embargo, la varianza explicada de este factor sobre la varianza total fue menor del 4%. Para ambas especies, el comportamiento de migración vertical aumentó el número de reclutas al final del proceso de transporte respecto a un transporte de tipo Lagrangiano pasivo. Los efectos del comportamiento de migración vertical sobre el reclutamiento son mayores en el erizo rojo, la especie con un PLD más largo (de 20 a 25 días). En numerosos estudios desarrollados en regiones de afloramiento costero, el comportamiento de migración vertical de las larvas es señalado como un mecanismo que promueve la retención de las larvas en la zona costera (Marta-Almeida et al. 2006, Morgan et al. 2009, Aiken et al. 2011, Morgan 2014). Las corrientes superficiales hacia fuera de la costa y las corrientes en profundidad hacia la costa que se generan durante los eventos de afloramiento costero, permiten que las larvas que realizan migración vertical por debajo de la capa de Ekman puedan reducir el transporte hacia afuera de la zona costera, y consecuentemente aumenten la probabilidad de reclutamiento (Figura 3.4A) (Marta-Almeida et al. 2006, Queiroga et al. 2007, Morgan et al. 2009, Aiken et al. 2011). Aunque el proceso arriba descrito puede explicar el incremento en el éxito del reclutamiento para las larvas con comportamiento de migración vertical, los resultados obtenidos, principalmente en el erizo rojo, también muestran que las larvas que realizan DVM presentan distancias de dispersión mayores que las larvas pasivas. Esto significa que el comportamiento de migración vertical afecta positivamente el reclutamiento, pero que igualmente reduce significativamente la retención local (LR) y el auto-reclutamiento (SR) (Figura 3.5). Estos resultados son coherentes con estudios realizados en la bahía de Monterey, donde observaron que el DVM no provocó una retención efectiva de las larvas en las zonas de desove (Carr et al. 2008). Esto se explicó debido a que el flujo de retorno durante el día no compensaba el transporte aguas afuera durante la noche (Carr et al. 2008). Los resultados de esta investigación además han demostrado que en el erizo rojo el reclutamiento alóctono (AR) en escenarios con DVM es mayoritariamente hacia el norte, comparado con los escenarios con larvas pasivas donde se observó más de un 20% de reclutamiento hacia el sur. Los resultados obtenidos refuerzan la idea de que, en el sistema de afloramiento de Chile central, las larvas que realizan una migración nictimeral aumentan la probabilidad de reclutamiento, sin embargo, este mecanismo no conlleva una retención de las larvas en los lugares de desove, sino que el DVM potencia el reclutamiento de las larvas en zonas alejadas de los hábitats parentales.

La temperatura que experimentan las larvas durante su desarrollo en la columna de agua condiciona la duración de su vida planctónica (O'Connor et al. 2007). Los

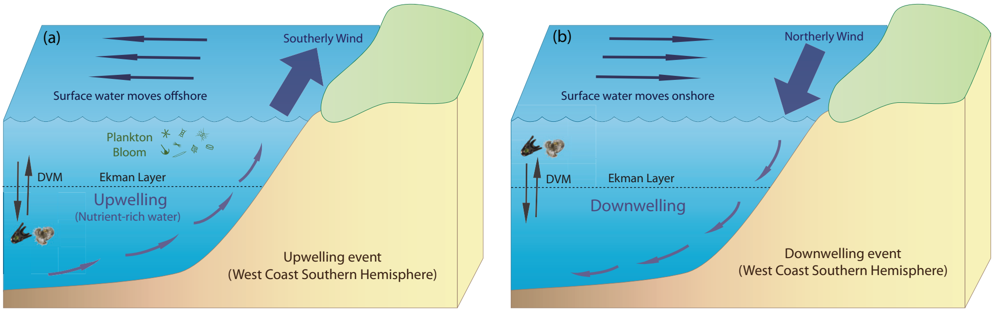


Figura 3.4. Esquema de la circulación costera en (a) eventos de afloramiento costero y (b) eventos de relajación de afloramiento. DVM indica migración nictimeral. El dibujo vectorial de la línea de costa se ha obtenido de la librería IAN (Symbol libraries, University of Maryland).

resultados obtenidos en estas simulaciones han confirmado que tanto la distancia de dispersión como el reclutamiento son variables sensibles a la duración de la vida planctónica de las larvas. Sin embargo, se observaron diferencias en las respuestas de ambas especies a este factor. Para la lapa, las simulaciones que incluyeron un PLD dependiente de la temperatura, el tiempo de desarrollo fue un 39% más largo, la distancia de dispersión fue un 24% mayor y el éxito del reclutamiento fue un 59% más bajo, se redujo significativamente el auto-reclutamiento y la retención local, en comparación con las simulaciones de PLD fijo. En cambio para el erizo rojo el tiempo de desarrollo larval se extendió más de dos días en todas las simulaciones (con y sin PLD dependiente de la temperatura) y la distancia de dispersión media no fue significativamente diferente entre simulaciones con y sin PLD dependiente de la temperatura. Aunque para el erizo rojo, el PLD dependiente de la temperatura tuvo un efecto significativo sobre el éxito del reclutamiento, disminuyendo esta variable un 9%, explicó un porcentaje marginal de la variabilidad observada (0.1%) (Tabla 3, capítulo 3), indicando una escasa significancia de este factor (White et al. 2014). Los resultados obtenidos en estas simulaciones mostraron que la inclusión de la parametrización del PLD dependiente de la temperatura en los modelos de transporte larval en la región de estudio tiene efectos significativos únicamente para la especie de PLD corto, como la lapa (PLD > 10 días). Esto no es debido a que las especies con PLD corto son más sensibles a la temperatura sino a las diferencias en los rangos de temperatura experimentados en un escenario realista, ya que cuanto más largo es el PLD, más variable es la temperatura que experimentan las larvas en el ambiente en el que se desarrollan. Las larvas con PLD más largo (20 días), generalmente pueden extender su período de desarrollo más allá de la estación cálida y pueden estar expuestas a temperaturas bajas y esto, puede tener importantes efectos en los tiempos de desarrollo. Estudios donde se han evaluado los efectos del cambio climático sobre distintos rasgos biológicos de las especies, han señalado que un aumento de la temperatura del océano no solo reducirá el tiempo de desarrollo larval, sino que tendrá otras consecuencias que deben ser consideradas como: los cambios en el período de desove (Fincham et al. 2013), cambios en la inversión reproductiva (Shama 2015) e incluso cambios en la mortalidad larval (Madeira et al. 2016). Así, evaluar los efectos del aumento de la temperatura del océano en la dispersión y el reclutamiento es un proceso complejo (O'Connor et al. 2007, Byrne & Selvakumaraswamy 2011, McLeod et al. 2015, Lacroix et al. 2018). De hecho estos efectos pueden variar enormemente entre regiones, especialmente en aquellas que presentan patrones estacionales contrastados, y entre especies que se reproducen en distintas épocas del año. Igualmente, estudios que tengan como finalidad el estudio del cambio climático en los procesos de transporte y dispersión larval también se beneficiarán al tener en cuenta la temperatura durante el desarrollo como un factor afectando la duración del transporte.

La matriz de conectividad potencial, definida como la probabilidad de transporte larval entre un área de reproducción y exportación de larvas hasta un área de asentamiento, y la matriz de conectividad realizada, donde se escala la probabilidad de transporte entre áreas con la producción potencial de huevos de cada especie y el hábitat disponible, difieren significativamente. Sin embargo, aunque la conexión entre las diferentes latitudes a lo largo de la costa no es la misma en las matrices de conectividad potencial y realizada, si que se observa que las latitudes de liberación de larvas (Fig. 8 A, B y C, capítulo 3) y las latitudes de asentamiento de larvas (Fig. 8 D, E y F, capítulo 3) que acumulan mayor porcentaje de éxito de reclutamiento son coincidentes para ambas matrices y especies (Fig. 3, capítulo 3). Estudios donde se ha evaluado empíricamente el reclutamiento respaldan los resultados de este estudio. Por ejemplo, se encontró una gran variabilidad en el reclutamiento de especies intermareales entre localidades a lo largo de la costa central de Chile, además no encontraron una correlación entre la abundancia promedio de adultos y la tasa de reclutamiento (Caro et al. 2010). En otro estudio desarrollado en la misma región y en la costa de Oregon, observaron una persistencia espacial del reclutamiento en escalas de 250 km (Navarrete et al. 2008). Se ha sugerido que la persistencia espacial del reclutamiento se debe a la escala espacial relativamente constante de los procesos oceanográficos (intensidad y distancia a los frentes de afloramiento y velocidad del viento) (Lagos et al. 2008). Sin embargo, estos procesos oceanográficos que operan a escalas de cientos de kilómetros no pueden explicar las variaciones del reclutamiento observadas en escalas espaciales más pequeñas, en esta escala otros factores deben ser considerados. De hecho, la orientación de la costa y la exposición al oleaje pueden variar en escalas de cientos de metros y causar diferencias en el reclutamiento (McCulloch & Shanks 2003, Pfaff et al. 2011). Independiente de los factores que explican el reclutamiento, los patrones espaciales recurrentes que se han observado, pueden tener importantes implicaciones para el diseño de áreas protegidas. Sin embargo, aunque los resultados han permitido identificar las áreas de salida y llegada de larvas que presentan mayor probabilidad de reclutamiento en la costa central de Chile, el siguiente paso debería considerar que significa la protección de cada una de estas áreas para asegurar la resiliencia de las subpoblaciones en la región de estudio para así diseñar una red de reservas efectiva (Watson et al. 2011).

Implicaciones para el manejo de los recursos bentónicos en Chile central

El sistema actual de TURFs a nivel regional, ha supuesto un incremento de la producción potencial de huevos de *F. latimarginata* y de *L. albus* (67% y del 52%, respectivamente). Aunque una tendencia similar hacia un incremento en la producción potencial de huevos relacionada con el nivel de protección se ha observado en otras especies de invertebrados (Kelly et al. 2000, Rogers-Bennett et al. 2002, Pelc et al. 2009), la magnitud de este cambio es sustancialmente menor en las dos especies de herbívoros aquí estudiadas. Esto puede deberse al hecho de que las áreas protegidas consideradas en este estudio son áreas parcialmente protegidas donde se permite la pesca. Sin embargo, algunos autores han argumentado que la protección parcial puede ser la única posibilidad en regiones con una elevada densidad de población humana (Tognelli et al. 2009), donde la pesca es una actividad de gran importancia para las comunidades locales, como lo es en la costa central de Chile. Independientemente de si se pudiese o no establecer áreas protegidas con restricción total a la pesca, nuestros resultados sugieren que en la costa central de Chile la protección parcial afecta positivamente la producción de huevos y que potencialmente estas áreas podrían estar actuando como

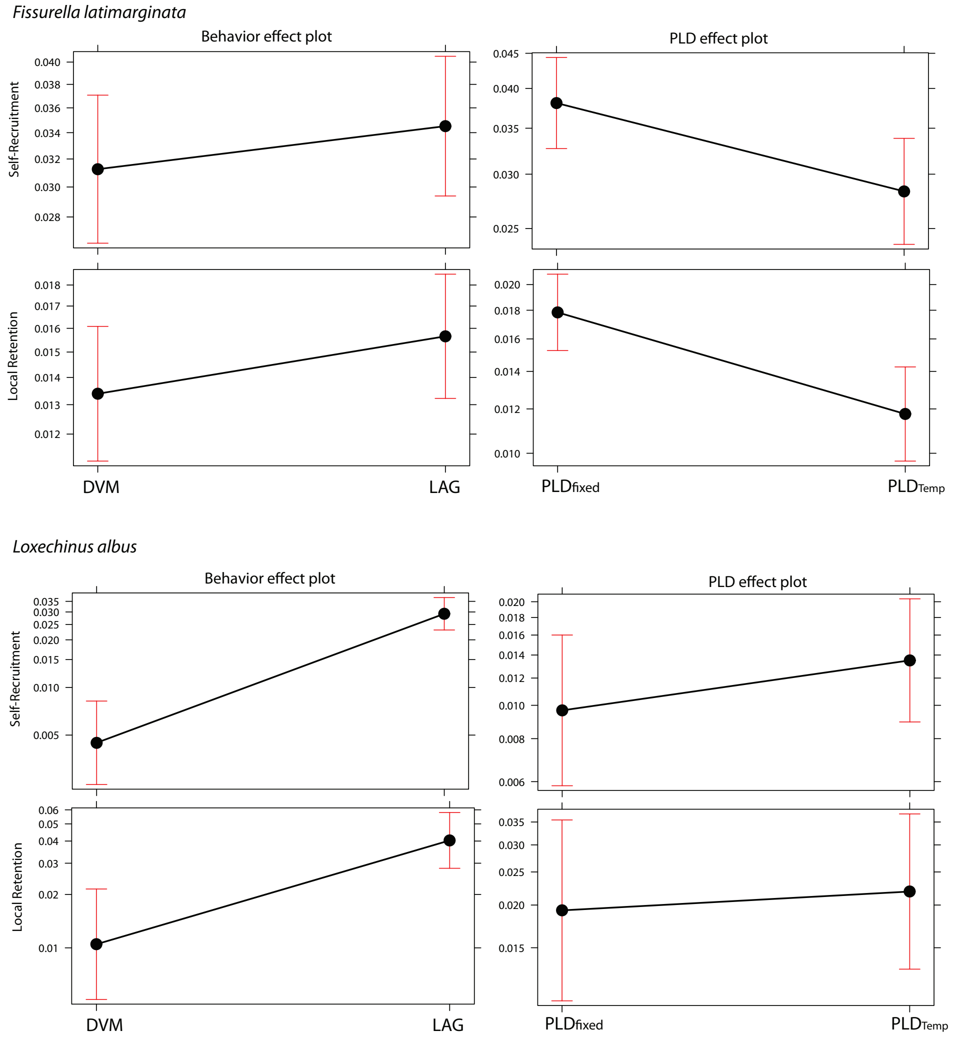


Figura 3.5. Tamaño del efecto del comportamiento (migración vertical (DVM) vs larvas con movimiento lagrangiano pasivo (LAG)), y el tiempo de desarrollo (tiempo de desarrollo dependiente de la temperatura (PLD_{Temp}) vs tiempo de desarrollo fijo (PLD_{fixed})) sobre las variables auto-reclutamiento (SR) y retención local (LR) en *Fissurella latimarginata* (panel superior) y en *Loxechinus albus* (panel inferior).

fuentes de repoblación de las áreas libres mediante la exportación de huevos y potencialmente larvas. En nuestro estudio se observó que el efecto de la protección en la producción potencial de huevos fue alto (entre un 661% para lapa y un 238% para el erizo rojo) (Fig. 2, Capítulo 2G,H). A nivel local estos resultados permiten afirmar que el sistema actual de áreas parcialmente protegidas (TURFs) podría contribuir en un programa regional de conservación, generando efectos positivos sobre variables que influyen en el potencial reproductivo local como la talla y la densidad de los individuos.

Si dividimos la zona de estudio en dos regiones delimitadas por los 33.50º de latitud sur, y las denominamos región norte y región sur, podemos afirmar que la producción potencial de huevos, para las dos especies estudiadas, es mayor en la región norte que en la región sur. A diferencia de la región sur, donde predominan los fondos y playas arenosas, la región norte presenta un mayor porcentaje de fondos y playas rocosas, que se consideran el hábitat esencial de las dos especies bajo estudio. Esta condición explica que más del 80% de la producción potencial de huevos para lapa y erizo rojo, en la zona de estudio, se concentre entre los 31.57ºS y los 33.50ºS (Figura 3, capítulo 2). Los resultados de la matriz de conectividad realizada (Figura 8, capítulo 3), en los que se incorporan los datos de la producción potencial de huevos y el hábitat disponible, muestran que las latitudes más exitosas para la llegada y salida de larvas en ambas especies se concentran también en el dominio norte de la región de estudio. Estos resultados ponen en relevancia la necesidad de establecer acciones de protección efectivas en esta región, ya que es también es donde se concentran el 90% de las capturas de ambas especies (Figura 1.7).

Los patrones de salida y llegada de larvas y las localidades específicas con mayor probabilidad de éxito del reclutamiento a lo largo de la costa, fueron similares entre las dos especies, aunque sus PLD fuesen diferentes (5 días lapa y 20 días erizo). Además estos resultados fueron persistentes entre los cuatro años de simulación. Esto implica que el planeamiento territorial para la protección y gestión de las especies explotadas, basado en áreas protegidas, no necesariamente debe ser específico para cada especie, sino que pueden desarrollarse planes efectivos para un conjunto de especies con tiempos de desarrollo contrastados. Aunque existen variaciones interanuales en el éxito del reclutamiento, el hecho de que se observe un patrón espacial persistente en el tiempo, significa que la protección de los lugares exitosos puede ser una estrategia efectiva que puede tener beneficios tanto desde el punto de vista pesquero como de la conservación.

El reclutamiento ha sido mayoritariamente alóctono en todas las localidades a lo largo de la región de estudio (Fig.5, capítulo 3), con una distancia de dispersión larval promedio mayor a los 50 km. Estos resultados han demostrado que las escalas de dispersión larval superan el tamaño de los instrumentos de manejo actuales (White & Costello 2011). Esto significa, que las áreas marinas protegidas que actualmente existen en la costa central de Chile no son suficientemente

grandes para asegurar un auto-reclutamiento que garantice la persistencia de las poblaciones de invertebrados bentónicos, intensamente explotadas en el litoral chileno, incluso para aquellas con un potencial dispersivo más bajo (5 días). Esta es una de las razones por las que se recomienda la necesidad de establecer una red de áreas marinas protegidas (totales y parciales) coordinada en la región a través de la cooperación entre los distintos sindicatos de pescadores involucrados, para así garantizar la persistencia de las poblaciones de las especies explotadas por la pesca artesanal. Además, estos resultados ponen en relieve que la conectividad entre TURFs es necesaria para asegurar la persistencia de las poblaciones, incluso para especies con PLD corto, poniendo en duda la efectividad, del sistema actual de manejo en Chile, basado en la gestión individualizada de las TURFs (Tognelli et al. 2009, Gaines et al. 2010).

Críticas y recomendaciones para futuros estudios

Los resultados obtenidos en este trabajo muestran importantes ideas para enfocar futuras estrategias de conservación y manejo de invertebrados bentónicos en la costa central de Chile. Sin embargo, el presente estudio presenta ciertas limitaciones para abordar dichas estrategias de forma concreta y pormenorizada. En primer lugar, si bien la resolución espacial de los datos oceanográficos es limitada (4 km), permiten una primera aproximación para identificar áreas importantes para la llegada y salida de larvas. No obstante, para diseñar estrategias de gestión a la escala espacial de las TURFs (menos de 1km), es necesaria una mayor resolución que permita resolver mejor los procesos de mesoescala (la circulación inducida por el viento, como vórtices, remolinos y filamentos), los procesos de microescala y la interacción de estos procesos oceanográficos con la topografía de la costa. Aunque se observa variabilidad inter-anual en el éxito del reclutamiento y en la distancia de dispersión, es destacable que el patrón espacial observado es persistente entre años. Sin embargo, este estudio solo incorpora cuatro años de simulación y dentro del período de simulación no hay ningún año anómalo (ej. períodos de el Niño). Así, en futuras investigaciones sería interesante considerar series de tiempo más largas que incorporen estos eventos de macroescala ya que pueden tener un impacto importante en el reclutamiento de las comunidades (Gaymer et al. 2010, Aravena et al. 2014).

El comportamiento de migración vertical y los efectos ambientales, como la temperatura, sobre el desarrollo de las larvas son importantes en el estudio del reclutamiento y la dispersión larval. Sin embargo, es necesario avanzar en el conocimiento de aspectos determinantes de la biología y ecología de las especies. Un aspecto importante es la sobrevivencia larval a determinadas condiciones ambientales, como por ejemplo: el efecto de la disminución de la concentración de oxígeno sobre las larvas, evento frecuente en zonas de afloramiento (Auel & Verheye 2007, Thomsen et al. 2016), o el efecto de la concentración de alimento sobre la sobrevivencia y reclutamiento de las larvas (Beaugrand et al. 2003), entre otros procesos. Sin embargo, aunque más información sobre la biología larval de las especies es necesaria, y esta puede ayudar a mejorar nuestra comprensión y representación de los patrones de conectividad (Sponaugle & Grorud-Colvert 2006, Werner et al. 2007, Metaxas & Saunders 2009, Morgan 2014), a corto plazo lo más relevante es mejorar la resolución de los modelos de circulación costera (Nickols et al. 2012), especialmente en aquellas regiones del mundo, como es el litoral chileno, donde información básica, como la batimetría de alta resolución no está aun disponible.

Aunque la causa o causas últimas de la migración vertical no han sido plenamente identificadas, este comportamiento ha sido sugerido como de significancia adaptativa para muchas especies de organismos marinos (Hays 2003). La interacción del comportamiento de migración vertical con el medio ambiente marino, especialmente con las corrientes, los remolinos de mesoescala, la temperatura de la columna de agua y la salinidad generan una variabilidad en la eficacia biológica de los individuos que lo exhiben (Batchelder et al. 2002, Marta-Almeida et al. 2006, Morgan 2014), la cual impacta directamente en propiedades a nivel de la población, como, por ejemplo, los patrones de abundancia en el espacio y el tiempo, la mortalidad, la dispersión y el reclutamiento larval. En este estudio, es claro que la probabilidad de reclutamiento ha sido considerada como una propiedad emergente que globaliza la eficacia biológica de todos los individuos modelados. Los resultados de este estudio sugieren que el comportamiento de DVM, como rasgo biológico, podría ser de significancia adaptativa para los individuos que lo exhiben. Sin embargo, este estudio ha demostrado que, aunque a nivel poblacional la migración vertical aumenta la probabilidad de reclutamiento, este comportamiento no produce una mayor retención en las zonas de reproducción. Es decir que el comportamiento de migración vertical aumenta la sobrevivencia de las larvas que se exportan fuera de las áreas de reproducción y que se asientan en zonas de la costa distintas a su lugar de origen. Estudios adicionales que centren su atención en la adaptabilidad y la plasticidad evolutiva de los individuos y como estas afectan el patrón de transporte general se hacen necesarios. Especialmente aquellos donde se obtenga información sobre la respuesta individual de las larvas a condiciones medioambientales contrastantes, sea mediante experimentos "in situ" o de mesocosmos.

En este estudio se ha observado que la protección tiene efectos sobre la talla y densidad de los individuos y sobre la producción potencial de huevos. Sin embargo, debido a la naturaleza de las especies estudiadas, invertebrados bentónicos que liberan sus gametos a la columna de agua, el número de larvas, dependerá en última instancia de la fertilización de los mismos. La fertilización de los gametos dependerá de la inversión reproductiva individual y de los patrones de distribución espacial dentro de las áreas y estos patrones pueden variar sustancialmente debido a la presión pesquera. Así, un aspecto que sería interesante abordar en futuras investigaciones es evaluar el efecto que tiene la densidad, nivel de agregación y talla de los individuos sobre el número de huevos fecundados. Este tipo de información podría ayudar a desarrollar planes de manejo en las TURFs que consideren tanto la información de la densidad mínima a mantener en un área como la información de los patrones de agregación y distancia entre individuos reproductores necesaria para poder asegurar una exportación efectiva de larvas.

Conclusiones

- La protección y el afloramiento costero no tienen un efecto directo sobre la inversión reproductiva ni sobre la condición individual de las especies modelo de estudio, esto sugiere que la selección de sitios para establecer áreas marinas protegidas parece ser menos relevante que las restricciones en la extracción pesquera, la cual promueve un incremento en la talla de los individuos, y esto puede influir de forma indirecta en la inversión reproductiva.

- La protección tiene un efecto significativo sobre la densidad, talla de los individuos, fecundidad de las hembras reproductoras y producción potencial de huevos con valores más elevados de estas variables en áreas protegidas en individuos de *F. latimarginata*, en *L. albus* estos efectos no son significativos.

- Los resultados sugieren que el efecto de protección parcial observado en las TURFs puede contribuir sustancialmente a aumentar la producción de huevos en el área de estudio y potencialmente contribuir a la repoblación de las áreas libres.

- La densidad de individuos es el principal determinante de la producción potencial de huevos en ambas especies y por ello, las regulaciones pesqueras que establecen cuotas de captura en todas las áreas deben ser promovidas para poder mantener la densidad de los adultos reproductores, para así fomentar la repoblación de las áreas libres.

- La localización y fecha del desove son los principales determinantes de la variabilidad observada en el éxito del reclutamiento y la distancia de dispersión en la región de estudio.

- El comportamiento de migración vertical tiene un efecto significativo en el éxito del reclutamiento y distancia de dispersión, sin embargo, el porcentaje de variabilidad explicada por este factor es baja, principalmente en la especie de PLD más corto (*F. latimarginata*).

- En el sistema de afloramiento de Chile central, las larvas que realizan una migración vertical tienen mayor probabilidad de reclutamiento, sin embargo, este mecanismo no conlleva una retención de las larvas en los lugares de desove sino que el DVM potencia el reclutamiento de las larvas en zonas alejadas de los hábitats parentales.

- El efecto de la temperatura sobre el desarrollo tiene un efecto significativo en el éxito del reclutamiento y distancia de dispersión en la especie de PLD más corto (*F. latimarginata*), sin embargo este efecto no es significativo en la especie de PLD más largo (*L. albus*).

- El reclutamiento para ambas especies modelo de estudio es mayoritariamente alóctono a lo largo de toda la región de estudio. Esto significa, que las áreas marinas protegidas que actualmente existen en la costa central de Chile no son suficientemente grandes para asegurar un auto-reclutamiento que garantice la persistencia de las poblaciones de invertebrados bentónicos, intensamente explotadas en el litoral chileno, incluso aquellas con potencial dispersivo más bajo como la lapa. Como consecuencia, resulta imperativo establecer una red de áreas marinas protegidas (totales y/o parciales).

- La región norte del área de estudio (Chile central), es donde se concentran las latitudes más importantes para la producción de propágulos dispersivos y también es la región en la que se encuentran las áreas de llegada y salida de larvas con mayor probabilidad de reclutamiento, en ambas especies. Estos resultados señalan la necesidad de establecer acciones de protección efectivas en esta región.

Bibliografía General

Afflerbach JC, Lester SE, Dougherty DT, Poon SE (2014) A global survey of “TURF-reserves”, Territorial Use Rights for Fisheries coupled with marine reserves. Glob Ecol Conserv 2:97–106

Aguirre C, Garreaud RD, Rutllant JA (2014) Surface ocean response to synoptic-scale variability in wind stress and heat fluxes off south-central Chile. Dyn Atmos Ocean 65:64–85

Aguirre C, Pizarro Ó, Strub PT, Garreaud R, Barth JA (2012) Seasonal dynamics of the near-surface alongshore flow off central Chile. J Geophys Res Ocean 117:1–17

Aiken CM, Castillo MI, Navarrete SA (2008) A simulation of the Chilean Coastal Current and associated topographic upwelling near Valparaíso, Chile. Cont Shelf Res 28:2371–2381

Aiken CM, Navarrete SA, Castillo MI, Castilla JC (2007) Along-shore larval dispersal kernels in a numerical ocean model of the central Chilean coast. Mar Ecol Prog Ser 339:13

Aiken CM, Navarrete SA, Pelegrí JL (2011) Potential changes in larval dispersal and alongshore connectivity on the central Chilean coast due to an altered wind climate. J Geophys Res Biogeosciences 116:1–14

Aldana M, García-Huidobro MR, Pulgar VM, Pulgar J (2017) Upwelling promotes earlier onset and increased rate of gonadal development of four coastal herbivores. Bull Mar Sci 93:000–000

Aldana M, Pulgar JM, Orellana N, Patricio Ojeda F, García-Huidobro MR (2014) Increased parasitism of limpets by a trematode metacercaria in fisheries management areas of central Chile: Effects on host growth and reproduction: Management areas and parasitism. Ecohealth 11:215–226

Almany GR, Berumen ML, Thorrold SR, Planes S, Jones GP (2007) Local Replenishment of Coral Reef Fish Populations in a Marine Reserve. Science (80-) 316:742–744

Aravena G, Broitman B, Stenseth NC (2014) Twelve years of change in coastal upwelling along the central-northern coast of Chile: spatially heterogeneous responses to climatic variability. PLoS One 9:e90276

Arrau L (1958) Desarrollo del erizo comestible de chile *Loxechinus albus* Mol. Rev Biol Mar VII:39–60

Auel H, Verheye HM (2007) Hypoxia tolerance in the copepod *Calanoides carinatus* and the effect of an intermediate oxygen minimum layer on copepod vertical distribution in the northern Benguela Current upwelling system and the Angola-Benguela Front. J Exp Mar Bio Ecol 352:234–243

Ayata S-D, Lazure P, Thiébaut É (2010) How does the connectivity between populations mediate range limits of marine invertebrates? A case study of larval dispersal between the Bay of Biscay and the English Channel (North-East Atlantic). Prog Oceanogr 87:18–36

Batchelder HP, Edwards CA, Powell TM (2002) Individual-based models of copepod populations in coastal upwelling regions: Implications of physiologically and environmentally influenced diel vertical migration on demographic success and nearshore retention. Prog Oceanogr 53:307–333

Beaugrand G, Brander KM, Lindley JA, Souissi S, Reid PC (2003) Plankton effect on cod recruitement in the North Sea. Nature 426:661–664

Berenshtein I, Kiflawi M, Shashar N, Wieler U, Agiv H, Paris CB (2014) Polarized light sensitivity and orientation in coral reef fish post-larvae. PLoS One 9

Berumen ML, Almany GR, Planes S, Jones GP, Saenz-Agudelo P, Thorrold SR (2012) Persistence of self-recruitment and patterns of larval connectivity in a marine protected area network. Ecol Evol 2:444–452

Botsford LW, Brumbaugh DR, Grimes C, Kellner JB, Largier J, O'Farrell MR, Ralston S, Soulanille E, Wespestad V (2009) Connectivity, sustainability, and yield: bridging the gap between conventional fisheries management and marine protected areas. Rev Fish Biol Fish 19:69–95

Botsford LW, Hastings A, Gaines SD (2001) Dependence of sustainability on the configuration of marine reserves and larval dispersal distance. Ecol Lett 4:144–150

Branch GM, Odendaal F (2003) The effects of marine protected areas on the population dynamics of a South African limpet, *Cymbula oculus*, relative to the influence of wave action. Biol Conserv 114:255–269

Brochier T, Colas F, Lett C, Echevin V, Cubillos LA, Tam J, Chlaida M, Mullon C, Fréon P (2009) Small pelagic fish reproductive strategies in upwelling systems: A natal homing evolutionary model to study environmental constraints. Prog Oceanogr 83:261–269

Brommer JE (2000) The evolution of fitness in life-history theory. Biol Rev 75:377–404

Brown G. DI, Gonzalez M, Lopez D, Duran L, Rivero R, Collado G, Betancourt C (1997) Informe Final Proyecto FIP-IT/94-33. Estudio de los ciclos vitales de las especies comerciales de lapas del genero *Fissurella sp*, en las regiones I a X. :196

Bustos E, Olave S, Troncoso R, Godoy C (1992) Investigación repoblamiento de recursos bentónicos Area Piloto IV Región.Etapa IV. 5. Investigaciones en erizo *Loxechinus albus* (Molina. 1782).

Butler IV MJ, Paris CB, Goldstein JS, Matsuda H, Cowen RK (2011) Behavior constrains the dispersal of long-lived spiny lobster larvae. Mar Ecol Prog Ser 422:223–237

Byrne M, Selvakumaraswamy P (2011) Sea urchin development in a global change hotspot, potential for southerly migration of thermotolerant propagules. Deep Res 58:712–719

Caffey HM (1985) Spatial and temporal variation in settlement and recruitment of intertidal barnacles. Ecol Monogr 55:313–332

Cárdenas L, Castilla JC, Viard F (2009) A phylogeographical analysis across three biogeographical provinces of the south-eastern Pacific: the case of the marine gastropod *Concholepas concholepas*. J Biogeogr 36:969–981

Cárdenas L, Castilla JC, Viard F (2016) Hierarchical analysis of the population genetic structure in *Concholepas concholepas* , a marine mollusk with a long-lived dispersive larva. Mar Ecol 37:359–369

Caro AU, Navarrete SA, Castilla JC (2010) Ecological convergence in a rocky intertidal shore metacommunity despite high spatial variability in recruitment regimes. PNAS 107:18528–18532

Carr SD, Capet XJ, McWilliams JC, Pennington JT, Chavez FP (2008) The influence of diel vertical migration on zooplankton transport and recruitment in an upwelling region: Estimates from a coupled behavioral-physical model. Fish Oceanogr 17:1–15

Castilla JC (1999) Coastal marine communities: trends and perspectives from human-exclusion experiments. Trends Ecol Evol 14:280–283

Castilla JC (2010) Fisheries in Chile: small pelagics, management, rights, and sea zoning. Bull Mar Sci 86:221–234

Castilla JC, Durán LR (1985) Human exclusion from the rocky intertidal zone of central Chile: the effects on *Concholepas concholepas* (Gastropoda). Oikos:391–399

Castilla J, Fernández M (1998) Small-Scale Benthic Fisheries in Chile : On Co-Management and Sustainable Use of Benthic Invertebrates. Ecol Appl 8:124–132

Chavez LHP (2004) FONDEF DOOI1141d. Innovaciones tecnológicas para repoblamiento y producción de lapas chilenas de explotación (*Fissurella latimarginata* y *Fissurella cumingi*) en áreas de manejo y centros de cultivo. :255

Contreras S, Castilla JC (1987) Feeding behaviuor and morphological adaptations in two sympatric sea urchin species in central Chile. Mar Ecol Prog Ser 38:217–224

Cowen R, Gawarkiewicz G, Pineda J, Thorrold S, FE W (2007) Population Connectivity in Marine Systems an overview. Oceanography 20:14–21

Cowen R, Lwiza K, Sponaugle S, Paris C (2000) Connectivity of marine populations: open or closed? Science (80-) 287:857–859

Cowen R, Sponaugle S (2009a) Larval dispersal and marine population connectivity. Ann Rev Mar Sci 1:443–466

Cowen RK, Sponaugle S (2009b) Larval Dispersal and Marine Population Connectivity. Ann Rev Mar Sci 1:443–466

Cresci A, Paris CB, Durif CMF, Shema S, Bjelland RM, Browman HI (2017) Glass eels (*Anguilla anguilla*) have a magnetic compasslinked to the tidal cycle. Sci Adv 3: e160200:1–9

Dayton P (1985) The Structure and Regulation of Some South American Kelp communities. Ecol Monogr 55:447–468

Defeo O, Castilla JC (2005) More than One Bag for the World Fishery Crisis and Keys for Co-management Successes in Selected Artisanal Latin American Shellfisheries. Rev Fish Biol Fish 15:265–283

Defeo O, Castrejón M, Pérez-Castañeda R, Castilla JC, Gutiérrez NL, Essington TE, Folke C (2016) Co-management in Latin American small-scale shellfisheries: Assessment from long-term case studies. Fish Fish 17:176–192

Denny CM, Willis TJ, Babcock RC (2004) Rapid recolonisation of snapper *Pagrus auratus*: Sparidae within an offshore island marine reserve after implementation of no-take status. Mar Ecol Prog Ser 272:183–190

Durán LR, Castilla JC, Oliva D (1987) Intensity of human predation on rocky shores at las cruces in central chile. Environ Conserv 14:143–149

Edgar GJ, Barrett NS (1999) Effects of the declaration of marine reserves on Tasmanian reef fishes, invertebrates and plants. J Exp Mar Bio Ecol 242:107–144

Fernández M, Blanco M, Ruano-chamorro C, Subida MD (2017) Reproductive output of two benthic resources (*Fissurella latimarginata* and *Loxechinus albus*) under different management regimes along the coast of central Chilea. Lat Am J Aquat Res 45:391–402

Fernández M, Castilla JC (2005) Marine Conservation in Chile: Historical Perspective, Lessons, and Challenges. Conserv Biol 19:1752–1762

Figueroa D, Moffat C (2000) On the influence of topography in the induction of coastal upwelling along the Chilean coast. Geophys Res Lett 27:3905–3908

Fincham JI, Rijnsdorp AD, Engelhard GH (2013) Shifts in the timing of spawning in sole linked to warming sea temperatures. J Sea Res 75:69–76

Fisher RA (1930) The Genetical Theory of Natural Selection. Genetics 154:272

Freire J, García-Allut A (2000) Socioeconomic and biological causes of management failures in European artisanal fisheries: The case of Galicia (NW Spain). Mar Policy 24:375–384

Gaines S, White C, Carr M, Palumbi S (2010) Designing marine reserve networks for both conservation and fisheries management. Proc Natl Acad Sci U S A 107:18286–93

Garavelli L, Colas F, Verley P, Yannicelli B, Lett C (2016) Influence of biological factors on connectivity patterns for *Concholepas concholepas* (loco) in Chile. PLoS One:209

Garcia-Huidobro MR, Águila JMP, Águila VMP, Aldana M (2015) The impact of predators and resource levels on physiological traits of *Fissurella crassa* (Archeogastropoda). Hidrobiológica 25:14–22

Gaymer CF, Palma AT, Vega JMA, Monaco CJ, Henríquez LA (2010) Effects of la Niña on recruitment and abundance of juveniles and adults of benthic community-structuring species in northern Chile. Mar Freshw Res 61:1185–1196

Gelcich S, Edwards-Jones G, Kaiser MJ, Watson E (2005) Using Discourses for Policy Evaluation: The Case of Marine Common Property Rights in Chile. Soc Nat Resour 18:377–391

Gelcich S, Fernández M, Godoy N, Canepa A, Prado L, Castilla JC (2012) Territorial user rights for fisheries as ancillary instruments for marine coastal conservation in Chile. Conserv Biol 26:1005–15

Gelcich S, Godoy N, Prado L, Castilla JC (2008) Add-on conservation benefits of marine territorial user rights fishery policies in central Chile. Ecol Appl 18:273–281

Gelcich S, Hughes TP, Olsson P, Folke C, Defeo O, Fernández M, Foale S, Gunderson LH, Rodríguez-Sickert C, Scheffer M, Steneck RS, Castilla JC (2010) Navigating transformations in governance of Chilean marine coastal resources. PNAS 107:16794–9

Gell FR, Roberts CM (2002) The fishery effects of marine reserves and fishery closures. 1250 24th Street, NW, Washington, DC 20037, USA.

Gell FR, Roberts CM (2003) Benefits beyond boundaries: the fishery effects of marine reserves. Trends Ecol Evol 18:448–455

Gillooly JF, Charnov EL, West GB, Savage VM, Brown JH (2002) Effects of size and temperature on developmental time. Nature 417:70–73

Glaser M, Baitoningsih W, Ferse SCA, Neil M, Deswandi R (2010) Whose sustainability? Top-down participation and emergent rules in marine protected area management in Indonesia. Mar Policy 34:1215–1225

Godoy N, Gelcich S, Vasquez JA, Castilla JC (2010) Spearfishing to depletion: Evidence from temperate reef fishes in Chile. Ecol Appl 20:1504–1511

González J, Stotz W, Garrido J, Orensanz JM, Parma AM, Tapia C, Zuleta A (2006) The Chilean turf system: How is it performing in the case of the loco fishery? Bull Mar Sci 78:499–527

Goñi R, Quetglas A, Reñones O (2006) Spillover of spiny lobsters *Palinurus elephas* from a marine reserve to an adjoining fishery. Mar Ecol Prog Ser 308:207–219

Graham WM, Largier JL (1997) Upwelling shadows as nearshore retention sites: The example of northern Monterey Bay. Cont Shelf Res 17:509–532

Grimm V (1999) Ten years of individual-based modelling in ecology: what have we learned and what could we learn in the future? Ecol Modell 115:129–148

Grimm V, Railsback SF (2005) Individual-based modeling and ecology. Princeton University Press

Guisado C, Arias E, Pérez E, Galleguillos F, Valdebenito M (1998) Estudio reproductivo del erizo en las regiones I a VIII. Informes técnicos FIP.FIP-IT/96-44. :233pp

Guisado C, Castilla J (1987) Historia de vida, reproducción y avances en el cultivo del erizo comestible chileno *Loxechinus albus* (Molina, 1782) (Echinoidea, Echinidae). In: Arana P (ed) Manejo y desarrollo pesquero. Escuela de Ciencias del Mar. Universidad Católica de Valparaiso, p 59–68

Halpern BS, Walbridge S, Selkoe KA, Kappel C., Micheli F, D'Agrosa C, Casey K, Ebert C, Fox H., Fujita R, Heinemann D, Lenihan H, P.Madin E, Perry M, Selig E., Spaldin M, Steneck R, Watson R (2008) A Global Map of Human Impact on Marine Ecosystems. Science (80-) 319:948–952

Halpern BS, Warner RR (2003) Matching marine reserve design to reserve objectives. Proc R Soc Lond B 270:1871–8

Harrison HB, Williamson DH, Evans RD, Almany GR, Thorrold SR, Russ GR, Feldheim KA, Herwerden L Van, Planes S, Srinivasan M, Berumen ML, Jones GP (2012) Larval export from marine reserves and the recruitment benefit for fish and fisheries. Curr Biol 22:1023–1028

Hart M, Scheibling RE (1988) Heat waves, baby booms, and the destruction of kelp beds by sea urchins. Mar Biol 99:167–176

Hays GC (2003) A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations. Hydrobiologia 503:163–170

Hedgecock D, Barber PH, Edmands S (2007) Genetic approaches to measuring connectivity. Oceanography 20:70–79

Hedgecock D, Pudovkin AI (2011) Sweepstakes reproductive success in highly fecund marine fish and shellfish: A review and commentary. Bull Mar Sci 87:971–1002

Hilborn R, Stokes K, Maguire J-J, Smith T, Botsford LW, Mangel M, Orensanz J, Parma A, Rice J, Bell J, Cochrane KL, Garcia S, Hall SJ, Kirkwood G, Sainsbury K, Stefansson G, Walters C (2004) When can marine reserves improve fisheries management? Ocean Coast Manag 47:197–205

Hoegh-Guldberg (1995) Temperature, Food Availability, and the Development of Marine Invertebrate Larvae. Am Zool 35:415–425

Hormazabal S, Combes V, Morales CE, Correa-Ramirez MA, Lorenzo E Di, Nuñez S (2013) Intrathermocline eddies in the coastal transition zone off central Chile (31-41°S). J Geophys Res Ocean 118:4811–4821

Houston AI, McNamara JM (1999) Models of Adaptive Behaviour. An Approach Based on State. Press, Cambridge University, Cambridge

Huret M, Petitgas P, Woillez M (2010) Dispersal kernels and their drivers captured with a hydrodynamic model and spatial indices: A case study on anchovy (*Engraulis encrasicolus*) early life stages in the Bay of Biscay. Prog Oceanogr 87:6–17

Irisson JO, Paris CB, Leis JM, Yerman MN (2015) With a little help from my friends: Group orientation by larvae of a coral reef fish. PLoS One 10:1–14

Jones GP, Milicich MJ, Emslie MJ, Lunow C (1999) Self-recruitment in a coral reef fish population. Nature 402:802–804

Jones GP, Planes S, Thorrold SR (2005) Coral reef fish larvae settle close to home. Curr Biol 15:1314–1318

Juan S de, Gelcich S, Ospina-Alvarez A, Perez-Matus A, Fernández M (2015) Applying an ecosystem service approach to unravel links between ecosystems and society in the coast of central Chile. Sci Total Environ 533:122–132

Kaiser MJ, Blyth-Skyrme RE, Hart PJB, Edwards-Jones G, Palmer D (2007) Evidence for greater reproductive output per unit area in areas protected from fishing. Can. J. Fish. aquat. Sci. 64: 1284-1289

Kaplan DM, Botsford LW, Farrell MRO, Gaines SD, Jorgensen S, Applications SE, Mar N, Otarrell R (2009) Model-Based Assessment of Persistence in Proposed Marine Protected Area Designs. Ecol Appl 19:433–448

Kaplan DM, Botsford LW, Jorgensen S (2006) Dispersal per recruit: An efficient method for assessing sustainability in marine reserve networks. Ecol Appl 16:2248–2263

Kelly S, Scott D, MacDiarmid AB, Babcock RC (2000) Spiny lobster, *Jasus edwardsii*, recovery in New Zealand marine reserves. Biol Conserv 92:359–369

Kido JS, Murray SN (2003) Variation in owl limpet *Lottia gigantea* population structures, growth rates, and gonadal production on southern California rocky shores. Mar Ecol Prog Ser 257:111–124

Kirincich AR, Barth JA (2009) Alongshelf Variability of Inner-Shelf Circulation along the Central Oregon Coast during Summer. J Phys Oceanogr 39:1380–1398

Kirincich AR, Barth JA, Grantham BA, Menge BA, Lubchenco J (2005) Wind-driven inner-shelf circulation off central Oregon during summer. J Geophys Res C Ocean 110:1–17

Kough AS, Paris CB, Staaterman E (2014) In situ swimming and orientation behavior of spiny lobster (*Panulirus argus*) postlarvae. Mar Ecol Prog Ser 504:207–219

Kritzer JP, Sale PF (2004) Metapopulation ecology in the sea: From Levins’ model to marine ecology and fisheries science. Fish Fish 5:131–140

Kritzer JP, Sale PF (2006) Marine metapopulation (JP Kritzer and PF Sale, Eds.), Elsavier a. Burlington, USA

Lacroix G, Barbut L, Volckaert FAM (2018) Complex effect of projected sea temperature and wind change on flatfish dispersal. Glob Chang Biol 24:85–100

Lagos NA, Castilla JC, Broitman BR (2008) Spatial environmental correlates of intertidal recruitment: A test using barnacles in northern chile. Ecol Monogr 78:245–261

Lagos NA, Navarrete SA, Véliz F, Masuero A, Castilla JC (2005) Meso-scale spatial variation on settlement and recruitmen of intertidal barnacles along the coast of central Chile. Mar Ecol Prog Ser 290:165–178

Larraín AP (1975) Los equinoideos regulares fósiles y recientes de Chile. Gayana Zool 35:1–188

Leis JM, Herwerden LV, Patterson HM (2011) Estimating connectivity in marine fish populations: what works best? Oceanogr Mar Biol 49:193–234

Leis J, Paris C, Irisson J, Yerman M, Siebeck U (2014) Orientation of fish larvae in situ is consistent among locations, years and methods, but varies with time of day. Mar Ecol Prog Ser 505:193–208

Leis J, Siebeck U, Hay A, Paris C, Chateau O, Wantiez L (2015) In situ orientation of fish larvae can vary among regions. Mar Ecol Prog Ser 537:191–203

Leiva GE, Castilla JC (2002) A review of the world marine gastropod fishery: evolution of catches, management and the Chilean experience. Rev Fish Biol Fish 11:283–300

Leslie HM (2005) A synthesis of marine conservation planning approaches. Conserv Biol 19:1701–1713

Lester SE, Halpern BS (2008) Biological responses in marine no-take reserves versus partially protected areas. Mar Ecol Prog Ser 367:49–56

Lester SE, Halpern B, Grorud-Colvert K, Lubchenco J, Ruttenberg BI, Gaines SD, Airamé S, Warner RR (2009) Biological effects within no-take marine reserves: a global synthesis. Mar Ecol Prog Ser 384:33–46

Letelier J, Pizarro O, Nuñez S (2009) Seasonal variability of coastal upwelling and the upwelling front off central Chile. J Geophys Res 114:C12009

Lett C, Ayata SD, Huret M, Irisson JO (2010) Biophysical modelling to investigate the effects of climate change on marine population dispersal and connectivity. Prog Oceanogr 87:106–113

Levin PS, Fogarty MJ, Murawski SA, Fluharty D (2009) Integrated Ecosystem Assessments: Developing the Scientific Basis for Ecosystem-Based Management of the Ocean. PLoS Biol 7:e1000014

Levitan DR (1991) Influence of Body Size and Population Density on Fertilization Success and Reproductive Output in a Free-Spawning Invertebrate. Biol Bull 181:261–268

Lo-Yat A, Meekan MG, Carleton JH, Galzin R (2006) Large-scale dispersal of the larvae of nearshore and pelagic fishes in the tropical oceanic waters of French Polynesia. Mar Ecol Prog Ser 325:195–203

Loot R, Aldana M, Navarrete SA (2005) Effects of human exclusion on parasitism in intertidal food webs of central Chile. 19:203–212

López-Duarte PC, Carson HS, Cook GS, Fodrie FJ, Becker BJ, Dibacco C, Levin LA (2012) What controls connectivity? An empirical, multi-species approach. Integr Comp Biol 52:511–524

Lowerre-barbieri S, Decelles G, Pepin P, Catalán IA, Muhling B, Erisman B, Cadrin SX, Alós J, et al. (2016) Reproductive resilience : a paradigm shift in understanding spawner-recruit systems in exploited marine fish. Fish Fish:1–28

Lozano J, Galera J, Lopez S, Turon X, Palacin C, Morera G (1995) Biological cycles and recruitment of *Paracentrotus lividus* (Echinodermata: Echinoidea) in two contrasting habitats. Mar Ecol Prog Ser 122:179–192

Madeira D, Costa PM, Vinagre C, Diniz MS (2016) When warming hits harder: survival, cellular stress and thermal limits of *Sparus aurata* larvae under global change. Mar Biol 163

Manríquez P, Galaz S, Opitz T, Hamilton S, Paradis G, Warner R, Castilla J, Labra F, Lagos N (2012) Geographic variation in trace-element signatures in the statoliths of near-hatch larvae and recruits of *Concholepas concholepas* (loco). Mar Ecol Prog Ser 448:105–118

Marta-Almeida M, Dubert J, Peliz Á, Queiroga H (2006) Influence of vertical migration pattern on retention of crab larvae in a seasonal upwelling system. Mar Ecol Prog Ser 307:1–19

McCulloch A, Shanks AL (2003) Topographically generated fronts, very nearshore oceanography and the distribution and settlement of mussel larvae and barnacle cyprids. J Plankton Res 25:1427–1439

McLeod I, McCormick M, Munday P, Clark T, Wenger A, Brooker R, Takahashi M, Jones G (2015) Latitudinal variation in larval development of coral reef fishes: implications of a warming ocean. Mar Ecol Prog Ser 521:129–141

Metaxas A, Saunders M (2009) Quantifying the “bio-” components in biophysical models of larval transport in marine benthic invertebrates: advances and pitfalls. BiolBull 216:257–72

Mileikovsky SA (1971) Types of larval development in marine bottom invertebrates, their distribution and ecological significance: a re-evaluation. Mar Biol 10:193–213

Molinet C, Herrera C, Gebauer P, Landaeta MF, Moreno CA (2010) Estados tempranos de Echinoidea en canal Lagreze, Islas Guaitecas, sur de Chile. Rev Biol Mar Oceanogr 45:19–33

Moreno CA (2001) Community patterns generated by human harvesting on Chilean shores: A review. Aquat Conserv Mar Freshw Ecosyst 11:19–30

Moreno CA., Molinet C, Díaz P, Díaz M, Codjambassis J, Arévalo A (2011) Bathymetric distribution of the Chilean red sea urchin (*Loxechinus albus*, Molina) in the inner seas of northwest Patagonia: Implications for management. Fish Res 110:305–311

Morgan SG (2014) Behaviorally Mediated Larval Transport in Upwelling Systems. Adv Oceanogr 2014:1–17

Morgan SG, Fisher JL, Largier JL (2011) Larval retention, entrainment, and accumulation in the lee of a small headland : Recruitment hot spots along windy coasts. Limnol Ocean 56:161–178

Morgan SG, Fisher JL, Miller SH, McAfee ST, Largier JL (2009) Nearshore larval retention in a region of strong upwelling and recruitment limitation. Ecology 90:3489–3502

Mullon C, Fréon P, Parada C, Lingen CD Van Der, Huggett J, Penven P (2003) Modelling the effect of buoyancy on the transport of anchovy (*Engraulis capensis*) eggs from spawning to nursery grounds in the southern Benguela: an IBM approach. Fish Oceanogr 12:170–184

Munguia-Vega A, Jackson A, Marinone SG, Erisman B, Moreno-Baez M, Girón-Nava A, Pfister T, Aburto-Oropeza O, Torre J (2014) Asymmetric connectivity of spawning aggregations of a commercially important marine fish using a multidisciplinary approach. PeerJ 2:e511

Myers RA, Worm B (2003) Rapid worldwide depletion of predatory fish communities. Nature 423:280–283

Narváez DA., Navarrete SA, Largier J, Vargas CA. (2006) Onshore advection of warm water, larval invertebrate settlement, and relaxation of upwelling off central Chile. Mar Ecol Prog Ser 309:159–173

Narváez DA, Poulin E, Leiva G, Hernández E, Castilla JC, Navarrete SA (2004) Seasonal and spatial variation of nearshore hydrographic conditions in central Chile. Cont Shelf Res 24:279–292

Navarrete SA, Broitman BR, Menge BA (2008) Interhemispheric Comparison of Recruitment To Intertidal Communities : Pattern Persistence and Scales of Variation. Ecology 89:1308–1322

Navarrete SA, Wieters EA, Broitman BR, Castilla JC (2005) Scales of benthic-pelagic coupling and the intensity of species interactions: from recruitment limitation to top-down control. Proc Natl Acad Sci USA 102:18046–18051

Nickols KJ, Gaylord B, Largier JL (2012) The coastal boundary layer: Predictable current structure decreases alongshore transport and alters scales of dispersal. Mar Ecol Prog Ser 464:17–35

Nielsen KJ, Navarrete SA (2004) Mesoscale regulation comes from the bottom-up: intertidal interactions between consumers and upwelling. Ecol Lett 7:31–41

O’Connor MI, Bruno JF, Gaines SD, Halpern BS, Lester SE, Kinlan BP, Weiss JM (2007) Temperature control of larval dispersal and the implications for marine ecology, evolution, and conservation. Proc Natl Acad Sci U S A 104:1266–71

Olguín A, Jerez G (2003) Chile especies bentónicas de importancia comercial. Serie-. ChileRecursos Pesq 1:30pp

Oliva D, Castilla JC (1992) Recognition guide and morphometry of ten species of genus *Fissurella* (Bruguire 1789) (Mollusca: Gastropoda) common in fishery and indigenous shellmidden from central southern Chile. Gayana Zool 56:77–108

Orensanz J (Lobo), Parma A, Jerez G, Barahona N, Montecinos M, Elias I (2005) What are the key elements for the sustainability of“ S-fisheries”? Insights from South America. Bull Mar Sci 76:527–556

Ospina-Álvarez A, Catalán I a, Bernal M, Roos D (2015) From egg production to recruits: connectivity and inter-annual variability in the recruitment patterns of European anchovy in the northwestern Mediterranean Running title: From acoustics to anchovy recruits. Prog Oceanogr 138:431–447

Ospina-Álvarez A, Palomera I, Parada C (2012) Changes in egg buoyancy during development and its effects on the vertical distribution of anchovy eggs. Fish Res 117–118:86–95

Ospina-Álvarez A, Palomera I, Parada C (2012) Changes in egg buoyancy during development and its effects on the vertical distribution of anchovy eggs. Fish Res 117–118:86–95

Ospina-Álvarez A, Parada CE, Palomera I (2012) Vertical migration effects on the dispersion and recruitment of European anchovy larvae: from spawning to nursery areas. Ecol Modell 231:65–79

Ouréns R, Freire J, Fernández L (2012) Definition of a new unbiased gonad index for aquatic invertebrates and fish: Its application to the sea urchin *Paracentrotus lividus*. Aquat Biol 17:145–152

Parada C, Mullon C, Roy C, Fréon P (2008) Does vertical migratory behaviour retain fish larvae onshore in upwelling ecosystems? A modelling study of anchovy in the southern Benguela. African J Mar Sci 30:437–45

Paris CB, Cowen RK (2004) Direct evidence of a biophysical retention mechanism for coral reef fish larvae. Limnol Oceanogr 59:1964–1979

Pauly D, Christensen V, Dalsgaard J, Froese R, Torres Jr. F (1998) Fishing down the food webs. Science (80-) 279:860–863

Pelc R, Baskett M, Tanci T, Gaines S, Warner R (2009) Quantifying larval export from South African marine reserves. Mar Ecol Prog Ser 394:65–78

Pelc RA, Warner RR, Gaines SD, Paris CB (2010) Detecting larval export from marine reserves. Proc Natl Acad Sci U S A 107:18266–71

Pérez-Matus A, Ospina-Álvarez A, Camus PA, Carrasco SA, Fernández M, Gelcich S, Godoy N, Ojeda FP, Pardo LM, Rozbascylo N, Subida MD, Thiel M, Wieters EA, Navarrete SA (2017) Temperate rocky subtidal reef community reveals human impacts across the entire food web. Mar Ecol Prog Ser 567:1–16

Pérez M. C, González ML, López D (2007) Breeding cycle and early development of the keyhole limpet *Fissurella nigra* (Lesson, 1831). J Shellfish Res 26:315–318

Peterson W (1998) Life cycle strategies of copepods in coastal upwelling zones. J Mar Syst 15:313–326

Pfaff MC, Branch GM, Wieters EA, Branch RA, Broitman BR (2011) Upwelling intensity and wave exposure determine recruitment of intertidal mussels and barnacles in the southern Benguela upwelling region. Mar Ecol Prog Ser 425:141–152

Pineda J, Hare JA, Sponaugle S (2007) Larval transport and dispersal in the coastal ocean and consequences for population connectivity. Oceanography 20:22–39

Poulin E, Palma AT, Leiva G, Narvaez D, Pacheco R, Navarrete SA, Castilla JC (2002) Avoiding offshore transport of competent larvae during upwelling events: The case of the gastropod *Concholepas concholepas* in central Chile. Limnol Oceanogr 47:1248–1255

Pulgar J, Aldana M, Alvarez M, Garcia-Huidobro R, Molina P, Morales JP, Pulgar VM (2013) Upwelling affects food availability, impacting the morphological and molecular conditions of the herviborous limpet *Fissurella crassa* (Mollusca: Archeogastropoda). J Mar Biol Assoc United Kingdom 93:1–6

Queiroga H, Cruz T, Santos A dos, Dubert J, González-Gordillo JI, Paula J, Peliz Á, Santos AMP (2007) Oceanographic and behavioural processes affecting invertebrate larval dispersal and supply in the western Iberia upwelling ecosystem. Prog Oceanogr 74:174–191

Reynoso-Granados T, Monsalvo-Spencer P, Serviere-Zaragoza E, Guzmán del Próo SA (2007) Larval and early juvenile development of the volcano keyhole limpet, *Fissurella volcano*. J Shellfish Res 26:65–70

Rochette S, Huret M, Rivot E, Pape O Le (2012) Coupling hydrodynamic and individual-based models to simulate long-term larval supply to coastal nursery areas. Fish Oceanogr 21:229–242

Rogers-Bennett L, Haaker PL, Karpov KA, Kushner DJ (2002) Using spatially areas explicit for data to marine protected abalone in California. Conserv Biol 16:1308–1317

Roughan M, Mace AJ, Largier JL, Morgan SG, Fisher JL, Carter ML (2005) Subsurface recirculation and larval retention in the lee of a small headland: A variation on the upwelling shadow theme. J Geophys Res C Ocean 110:1–18

Roughgarden J, Gaines S, Possingham H (1988) Recruitment dynamics in complex life cycles. Science (80-) 241:1460–1466

Roughgarden J, Iwasa Y, Blaxter C (1985) Demographic theory for an open population with space-limited recruitment. Ecology 66:54–67

Roughgarden J, Pennington JT, Stoner D, Alexander S, Miller K (1991) Collision of upwelling fronts with the intertidal zone: the cause of recruitment pulses in barnacles populations of central California. Acta Oecologica 12:35–51

Rudjakov JA (1970) The possible causes of diel vertical migrations of planktonic animals. Mar Biol 6:98–105

Rumrill S (1990) Natural mortality of marine invertebrate larvae. Ophelia 32:163–198

Rutllant JA, Rosenbluth B, Hormazabal S (2004) Intraseasonal variability of wind-forced coastal upwelling off central Chile (30°S). Cont Shelf Res 24:789–804

Sale PF, Kritzer JP (2003) Determining the extent and spatial scale of population connectivity: Decapods and coral reef fishes compared. Fish Res 65:153–172

Sanford E, Menge BA. (2001) Spatial and temporal variation in barnacle growth in a coastal upwelling system. Mar Ecol Prog Ser 209:143–157

Shama LNS (2015) Bet hedging in a warming ocean: Predictability of maternal environment shapes offspring size variation in marine sticklebacks. Glob Chang Biol 21:4387–4400

Shanks AL, Largier J, Brink L, Brubaker J, Hooff R (2000) Demonstration of the onshore transport of larval invertebrates by the shoreward movement of an upwelling front. Limnol Oceanogr 45:230–236

Shears NT, Grace RV, Usmar NR, Kerr V, Babcock RC (2006) Long-term trends in lobster populations in a partially protected vs. no-take Marine Park. Biol Conserv 132:222–231

Spicer JI, Gaston KJ (1999) Physiological diversity and its ecological implications. Oxford, UK.

Sponaugle S, Grorud-Colvert K (2006) Environmental variability, early life-history traits, and survival of new coral reef fish recruits. Integr Comp Biol 46:623–33

Staaterman E, Paris CB, Kough AS (2014) First evidence of fish larvae producing sounds. Biol Lett 10:1–5

Strub P, Mesías J, Montecino V, Rutlant J, Salinas S (1998) Coastal ocean circulation off western South America. In: In:, Robinson A, Brink K (eds) (eds) The sea, Vol 11. JWiley & Sons, New York, p 273–314

Szuwalski CS, Vert-Pre KA, Punt AE, Branch TA, Hilborn R (2015) Examining common assumptions about recruitment: A meta-analysis of recruitment dynamics for worldwide marine fisheries. Fish Fish 16:633–648

Talmage SC, Gobler CJ (2011) Effects of elevated temperature and carbon dioxide on the growth and survival of larvae and juveniles of three species of northwest Atlantic bivalves. PLoS One 6:e26941

Tapia FJ, Largier JL, Castillo M, Wieters EA, Navarrete SA (2014) Latitudinal Discontinuity in Thermal Conditions along the Nearshore of Central-Northern Chile. PLoS One 9:e110841

Tapia FJ, Navarrete SA, Castillo M, Menge BA, Castilla JC, Largier J, Wieters EA, Broitman BL, Barth JA. (2009) Thermal indices of upwelling effects on inner-shelf habitats. Prog Oceanogr 83:278–287

Thiel M, Macaya EC, Acuna E (2007) The Humboldt Current System of northern and central Chile: oceanographic processes, ecological interactions and socioeconomic feedback. Oceanogr Mar Biol 45:195–344

Thiel M, Macaya E, Acuña E, Arntz W, Bastias H, Brokordt K, Camus P, Castilla J, Castro L, Cortés M, Dumont C, Escribano R, Fernandez M, Gajardo J, Gaymer C, Gomez I, González a, González H, Haye P, Illanes J, Iriarte J, Lancellotti D, Luna-Jorquera G, Luxoro C, Manriquez P, Marín V, Muñoz P, Navarrete S, Pérez E, Pouline E, Sellanes J, Sepúlveda H, Stotz W, Tala F, Thomas a, Vargas C, Vásquez J, Vega J (2007) The Humboldt Current System Of Northern and Central Chile. Oceanogr Mar Biol An Annu Rev 45:195–344

Thomsen S, Kanzow T, Colas F, Echevin V, Krahmann G, Engel A (2016) Do submesoscale frontal processes ventilate the oxygen minimum zone off Peru? Geophys Res Lett 43:8133–8142

Thorrold SR, Jones GP, Planes S, Hare JA (2006) Transgenerational marking of embryonic otoliths in marine fishes using barium stable isotopes. Can J Fish Aquat Sci 63:1193–1197

Thorrold SR, Zacherl DC, Levin LA (2007) Population Connectivity and Larval Dispersal Using Geochemical Signatures in Calcified Structures. Oceanography 20:80–89

Thorson G (1950) Reproductive and larval ecology of marine bottom invertebrates. Biol Rev 25:1–45

Tognelli MF, Fernández M, Marquet PA (2009) Assessing the performance of the existing and proposed network of marine protected areas to conserve marine biodiversity in Chile. Biol Conserv 142:3147–3153

Treml EA, Halpin PN (2012) Marine population connectivity identifies ecological neighbors for conservation planning in the Coral Triangle. Conserv Lett 5:441–449

Watson JR, Siegel DA, Kendall BE, Mitarai S, Rassweiller A, Gaines SD (2011) PNAS Plus: Identifying critical regions in small-world marine metapopulations. Proc Natl Acad Sci 108:E907–E913

Weersing K, Toonen R (2009) Population genetics, larval dispersal, and connectivity in marine systems. Mar Ecol Prog Ser 393:1–12

Werner FE, Cowen RK, Paris CB (2007) Coupled Biological and Physical Models, Present Capabilities and Necessary Developments for Future Studies of Population Connectivity. Oceanography 20:54–69

White C, Costello C (2011) Matching spatial property rights fisheries with scales of fish dispersal. Ecol Appl 21:350–62

White JW, Rassweiler A, Samhouri JF, Stier AC, White C (2014) Ecologists should not use statistical significance tests to interpret simulation model results. Oikos 123:385–388

Wieters E (2005) Upwelling control of positive interactions over mesoscales: a new link between bottom-up and top-down processes on rocky shores. Mar Ecol Prog Ser 301:43–54

Wieters E, Kaplan D, Navarrete S, Sotomayor A, Largier J, Nielsen K, Véliz F (2003) Alongshore and temporal variability in chlorophyll a concentration in Chilean nearshore waters. Mar Ecol Prog Ser 249:93–105

Willis TJ, Millar RB, Babcock RC (2003) Protection of exploited fish in temperate regions: high density and biomass of snapper. J Appl Ecol 40:214–227

Wing SR, Botsford LW, Largier JL, Morgan LE (1995) Spatial structure of relaxation events and crab settlement in the northern California upwelling system. Mar Ecol Prog Ser 128:199–211

Wolanski E, Doherty P, Carleton J (1997) Directional swimming of fish larvae determines connectivity of fish populations on the great barrier reef. Naturwissenschaften 84:262–268

Wood CL, Micheli F, Fernández M, Gelcich S, Castilla JC, Carvajal J (2013) Marine protected areas facilitate parasite populations among four fished host species of central Chile. J Anim Ecol 82:1276–87

Woodson CB, McManus MA. (2007) Foraging behavior can influence dispersal of marine organisms. Limnol Oceanogr 52:2701–2709

Yáñez E (2003) Actividad pesquera y de acuicultura en Chile.

Zacherl D, Manríquez P, Paradis G, Day R, Castilla J, Warner R, Lea D, Gaines S (2003) Trace elemental fingerprinting of gastropod statoliths to study larval dispersal trajectories. Mar Ecol Prog Ser 248:297–303

Zamora S, Stotz W (1992) Ciclo reproductivo de *Loxechinus albus* (Molina 1782) (Echinodermata : Echinoidea) en Punta Lagunillas, IV Región, Coquimbo, Chile. Rev Chil Hist Nat 65:121–133

Apéndice

Apéndice I
Material Suplementario Capítulo 2

Table S1. Reproductive parameters of limpet and urchin used as fixed parameters in the potential egg production equation, (Eqs. 2 and 3). S indicates proportion of mature individuals and K proportion of *F. latimarginata*.

Fissurella latimarginata								*Loxechinus albus*				
Name	**Sampling year**	**S**			**K**			**Name**	**Sampling year**	**S**		
		Total sampled	Mature	(%) Mature	Total sampled	Num. *(F latimarginata)*	% *(F. latimarginata)*			Total sampled	Mature	(%) Mature
Chigualoco	2006	196	143	0.73	1449	196	0.14	Bonifacio sector A	2008	41	24	0.59
Chigualoco	2007	220	193	0.88	537	220	0.41	Bonifacio sector B	2007	103	79	0.77
El Quisco sector A	1999	372	217	0.58	756	372	0.49	Bonifacio sector B	2009	227	201	0.89
El Quisco sector A	2000	78	77	0.99	225	78	0.35	Chaihuin sector C	2003	42	32	0.76
El Quisco sector A	2003	45	45	1.00	236	45	0.19	Chan chan	2009	162	114	0.70
El Quisco sector A	2004	95	94	0.99	284	95	0.33	El Quisco sector A	2005	382	361	0.95
El Quisco sector A	2005	167	166	0.99	744	167	0.22	El Quisco sector A	2006	174	174	1.00
El Quisco sector A	2006	162	160	0.99	705	162	0.23	Farellones de Carelmapu	2003	193	119	0.62
El Quisco sector A	2009	117	116	0.99	713	117	0.16	Farellones de Carelmapu	2004	258	132	0.51
Huentelauquen	2006	33	29	0.88	440	33	0.08	Farellones de Carelmapu	2005	214	139	0.65
Laguna Verde sector C	2004	542	495	0.91	843	542	0.64	Farellones de Carelmapu	2007	184	77	0.42
Laguna Verde sector C	2005	298	275	0.92	669	298	0.45	Farellones de Carelmapu	2008	201	147	0.73
Laguna Verde sector C	2007	279	262	0.94	536	279	0.52	Horcon	2001	212	162	0.76
Los Vilos sector B	2000	489	428	0.88	978	489	0.50	Horcon	2002	680	608	0.89
Los Vilos sector B	2001	580	356	0.61	672	580	0.86	Horcon	2003	281	213	0.76
Los Vilos sector B	2002	333	271	0.81	690	333	0.48	Isla doña Sebastiana	2004	121	44	0.36
Los Vilos sector B	2003	428	314	0.73	751	428	0.57	Isla doña Sebastiana	2005	388	188	0.48
Los Vilos sector B	2004	607	518	0.85	1107	607	0.55	Isla doña Sebastiana	2006	756	381	0.50
Los Vilos sector B	2006	447	301	0.67	767	447	0.58	Isla doña Sebastiana	2007	453	153	0.34
Los Vilos sector B	2007	282	249	0.88	504	282	0.56	Isla doña Sebastiana	2008	440	293	0.67
Los Vilos sector B	2008	287	240	0.84	470	287	0.69	La Cachina	2008	299	216	0.72
Los Vilos sector B	2009	257	191	0.74	373	257	0.69	Laguna Verde sector C	2004	189	144	0.76
Los Vilos sector C	2003	143	74	0.52	574	143	0.25	Laguna Verde sector C	2005	486	298	0.61
Los Vilos sector C	2004	515	460	0.89	1193	515	0.43	Laguna Verde sector C	2007	301	232	0.77
Los Vilos sector C	2006	229	193	0.84	770	229	0.29	Los molinos sector A	2002	31	25	0.77
Mississipi	2002	348	289	0.83	457	348	0.76	Los Vilos sector B	2001	78	60	0.77
Papudo	2003	479	381	0.79	702	479	0.68	Los Vilos sector B	2002	251	135	0.34
Papudo	2004	348	289	0.83	848	348	0.41	Los Vilos sector B	2008	247	247	1.00
Papudo	2005	617	505	0.82	909	617	0.68	Los Vilos sector C	2004	492	263	0.53
Pichidangui	2006	26	23	0.88	288	26	0.09	Mehuin sector B	2003	637	539	0.85
Totoralillo Sur	2007	145	126	0.87	615	145	0.24	Mehuin sector B	2005	282	240	0.85
Totoralillo sur-Las Plaillas	2007	81	68	0.84	532	81	0.15	Mehuin sector B	2006	455	447	0.98
Mean				**0.84**			**0.43**	Mean				**0.69**

Apéndice II
Material Suplementario Capítulo 3

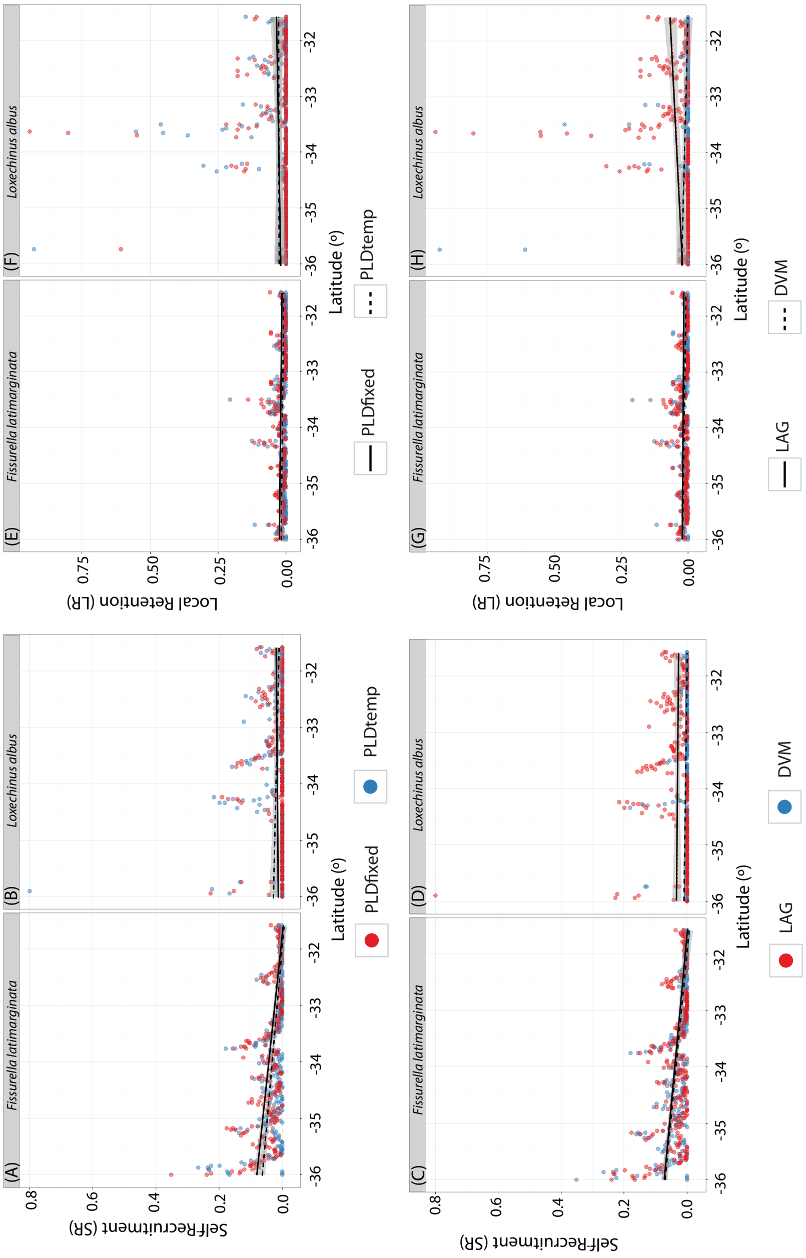


Fig. S1. Relationship between self-recruitment (SR) and latitudes for *Fissurella latimarginata* (A and C) and *Loxechinus albus* (B and D), and between Local Retention (LR) and latitudes for *F. latimarginata* (E and G) and *L. albus* (F and H). The upper plots show the comparison between the two PLD scenarios, PLD fixed (red dots and solid line) and temperature-dependent PLD (blue dots and dashed line). The bottom plots show the comparison between behavior scenarios, passive Lagrangian transport (LAG) (red dots and solid line) and Dial Vertical Migration (DVM) (blue dots and dashed line).

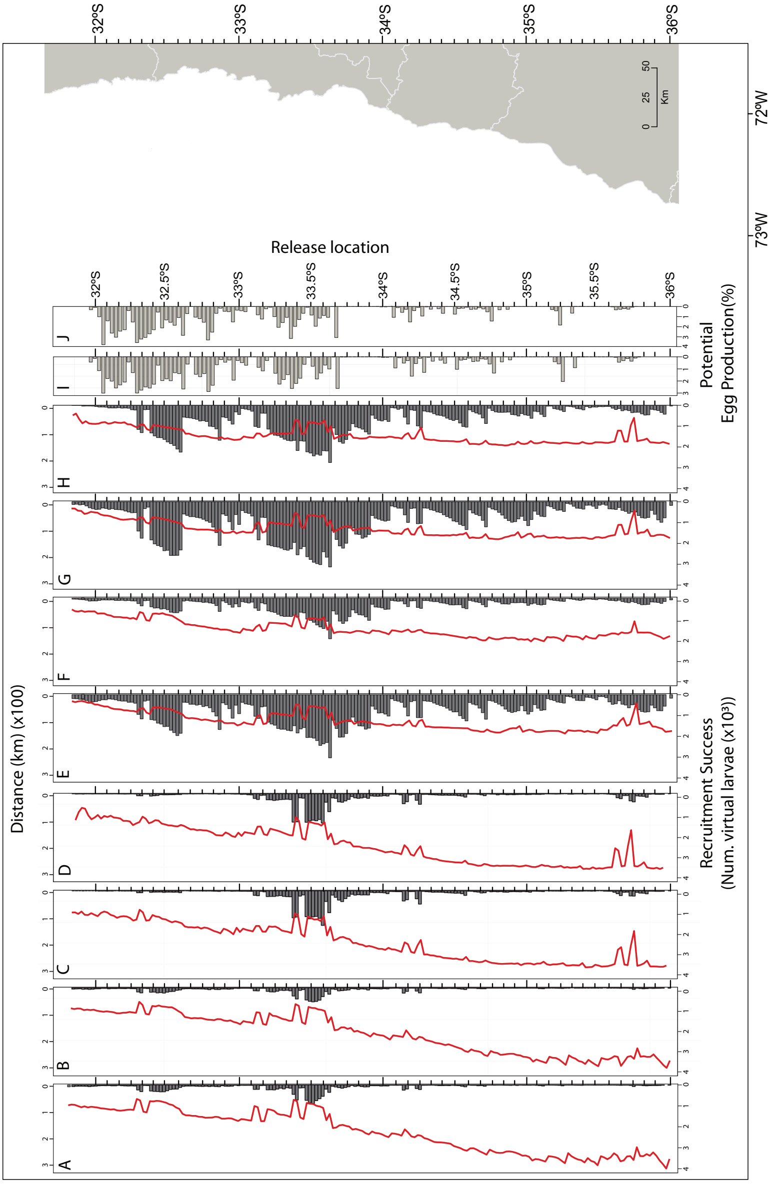


Fig. A1. Spatial variability on recruitment success and dispersal distance along the study region under different simulated scenarios. The map shows the study area where the release-recruitment locations are represented by nearshore latitudinal bands of 2 km (location). Black bars show mean recruitment success per latitudinal band and red lines indicate mean dispersal distance. The simulation scenarios, shown for *Loxechinus albus* and *Fissurella latimarginata* respectively, are: (A and F) passive Lagrangian transport and fixed Planktonic Larval Duration (PLD), (B and G) passive Lagrangian transport with a species-specific temperature-dependent PLD,, (C and H) particles with Diel Vertical Migration (DVM) behavior and fixed PLD, and (D and I) particles with DVM behavior and PLD based on temperature-dependent PLD. The contribution (percentage) of oocytes/m2 (potential egg production) of each location to the regional (study area) production is shown for *L. albus* (E) and *F. latimarginata* (J).

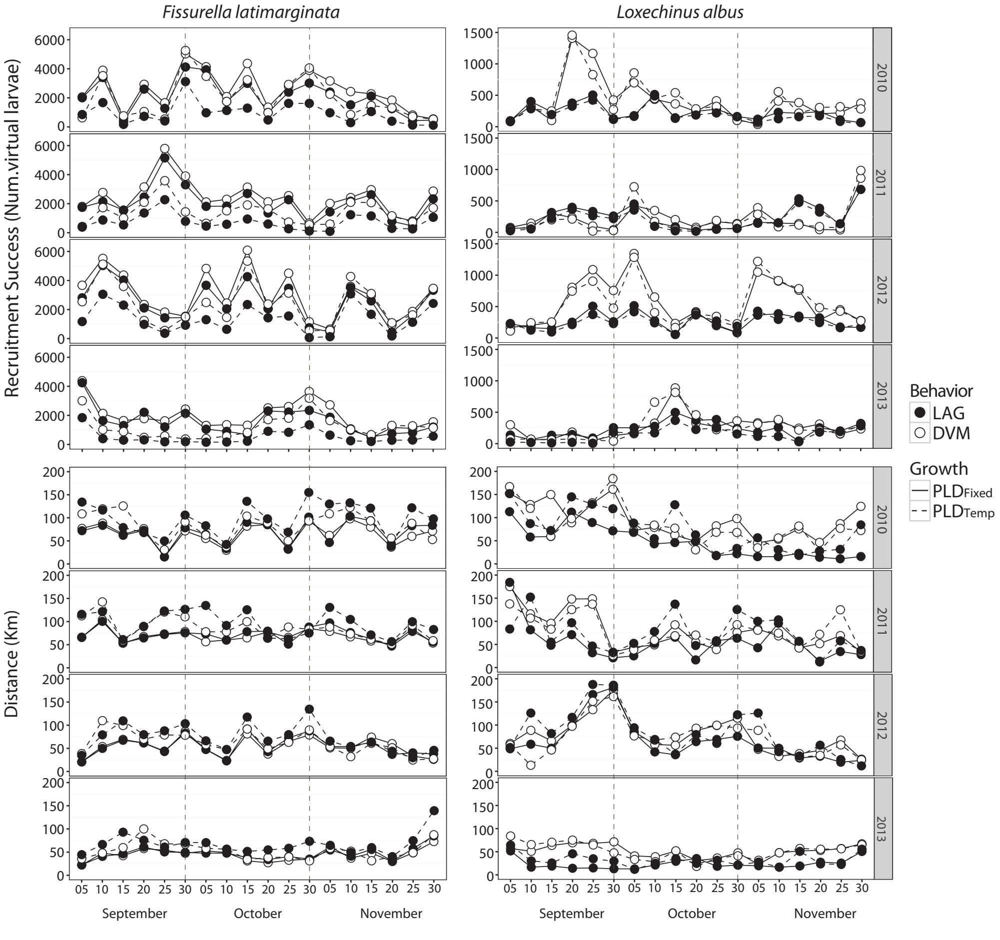


Fig. A2. Temporal variability on the number of particles recruited (upper plot panel) and on dispersal distance traveled by recruited particles (lower plot panel) under different simulated scenarios. Black circles show passive Lagrangian transport (LAG) and white circles Diel Vertical Migration (DVM) behavior. Solid lines show fixed Planktonic Larval Duration (PLDfixed), 5 days for *F. latimarginata* and 20 days for *L. albus* and dotted line)s temperature-dependent PLD (PLDTemp).

Apéndice III

Resumen de los artículos publicados y enviados para publicación

FERNANDEZ, M., BLANCO, M., RUANO-CHAMORRO, C., SUBIDA, M.D., 2017. REPRODUCTIVE OUTPUT OF TWO BENTHIC RESOURCES (*FISSURELLA LATIMARGINATA* AND *LOXECHINUS ALBUS*) UNDER DIFFERENT MANAGEMENT REGIMES ALONG THE COAST OF CENTRAL CHILE. LATIN AMERICAN JOURNAL OF AQUATIC RESEARCH, 45(2), 391-402.

Inversión reproductiva de dos recursos bentónicos (*Fissurella latimarginata* y *Loxechinus albus*) bajo diferentes regímenes de manejo a lo largo de la costa central de Chile.

Los beneficios biológicos y ecológicos de las áreas marinas total y parcialmente protegidas están bien documentados. Sin embargo, los beneficios que alcanzan las áreas más allá de los límites de las reservas aun están emergiendo a pesar de que son esenciales para la recuperación de los caladeros de pesca y para obtener apoyo para la protección del océano entre las partes interesadas. Analizamos la influencia de la protección en el índice gonadosomático y también en el peso seco del cuerpo de dos especies de gran importancia tanto ecológica como económica: la lapa ojo de cerradura, *Fissurella latimarginata* y el erizo rojo, *Loxechinus albus*, con el fin de determinar el potencial beneficio de las áreas protegidas en el aumento de la inversión reproductiva y, por lo tanto, en la potencial repoblación de las áreas explotadas. Comparamos dos niveles de protección en Chile central, determinados por el régimen de manejo pesquero (a su vez asociado a la presión pesquera): (a) áreas con restricciones de pesca (esfuerzo pesquero bajo o nulo; derechos territoriales de uso pesquero y áreas de no acceso) y (b) áreas de libre acceso (altas tasas de explotación). También evaluamos la influencia independiente del afloramiento en las dos variables. Los resultados mostraron para ambas especies que (a) el peso seco del cuerpo no está afectado por el régimen de manejo, (b) el régimen de manejo no mostró un impacto consistente en el índice gonadosomático y (c) el afloramiento no afectó ninguna de las variables respuesta. Nuestros hallazgos ayudan a desentrañar los principales factores determinantes de los patrones reproductivos bajo escenarios de impacto humano constantes, sugiriendo que la selección de sitios para establecer áreas marinas protegidas parece ser menos relevante que el control eficiente del esfuerzo pesquero y el tamaño mínimo legal para asegurar la repoblación natural.

BLANCO, M., OSPINA-ALVAREZ, A., GONZÁLEZ, C., FERNANDEZ, M., 2017. EGG PRODUCTION PATTERNS OF TWO INVERTEBRATE SPECIES IN ROCKY SUBTIDAL AREAS UNDER DIFFERENT FISHING REGIMES ALONG THE COAST OF CENTRAL CHILE. PLOS ONE, 12 (5), e0176758.

Patrones de producción de huevos de dos especies de invertebrados en áreas del submareal rocoso bajo distinto régimen pesquero a lo largo de la costa central de Chile.

La pesca es una de las principales fuentes de impacto humano, reduciendo la densidad y la talla de una amplia gama de especies explotadas en comparación con áreas que exhiben fuertes regulaciones (áreas en las que se prohíbe la captura y áreas parcialmente protegidas, incluyendo las áreas con derechos de uso territorial para la pesca, TURFs). Dado que el tamaño y la densidad pueden tener importantes consecuencias sobre la reproducción y, por lo tanto, la repoblación natural, monitoreamos el tamaño, la densidad y la fecundidad potencial de los adultos de la lapa (*Fissurella latimarginata*) y el erizo rojo (*Loxechinus albus*) en áreas bajo dos regímenes de pesca (TURFs y áreas de libre acceso, OAA). Al analizar la distribución de los hábitats adecuados, predecimos los patrones espaciales de la producción potencial de huevos, para identificar los puntos calientes para la reproducción a lo largo de la costa central de Chile. El sistema actual de TURFs en Chile central mostró una mayor producción potencial de huevos de F.latimarginata y *L. albus* que lo esperado en un escenario completo de libre acceso (67% y 52% respectivamente). La producción potencial de huevos fue más del doble cuando se comparó un escenario completo de TURF con la condición de completo libre acceso en ambas especies. El tamaño y la densidad individual explicaron entre el 60 y el 100% de la variabilidad en la producción potencial de huevos, lo que sugiere la importancia de la mejora de ambas variables biológicas en las TURFs en Chile. La producción potencial de huevos para ambas especies en la parte norte del dominio estudiado fue mayor debido al efecto combinado del (a) hábitat adecuado y (b) la concentración de TURFs. Nuestros resultados sugieren que las áreas parcialmente protegidas, como las TURFs, pueden mejorar significativamente la producción de propágulos que podrían repoblar áreas explotadas.

BLANCO, M., OSPINA-ALVAREZ, A., AIKEN, C.M., NAVARRETE, S.A., FERNANDEZ, M. (SUBMITTED). THE INFLUENCE OF LARVAL TRAITS ON DISPERSAL AND CONNECTIVITY PATTERNS OF TWO EXPLOITED MARINE INVERTEBRATES IN CENTRAL CHILE.

Influencia de los rasgos larvales en la dispersión y los patrones de conectividad de dos invertebrados marinos explotados en Chile central.

La interacción entre las variables ambientales y los rasgos biológicos larvales es relevante para identificar los procesos críticos que determinan la dinámica de las poblaciones marinas. Un mejor entendimiento de los patrones de conectividad de las poblaciones marinas, es fundamental para definir planes de manejo y conservación. A través de un modelo biofísico de dispersión larvaria basado en individuos se propone evaluar el efecto de la variabilidad oceanográfica y los rasgos biológicos (migración nictimeral de las larvas y desarrollo dependiente de la temperatura) en el éxito del reclutamiento, la distancia de dispersión y los patrones de conectividad larval. Se han seleccionado dos especies explotadas por la pesca artesanal en Chile, el erizo rojo (*Loxechinus albus*; 20 días de desarrollo planctotrófico) y la lapa (*Fissurella latimarginata*; 5 días de desarrollo lecitotrófico). Se observó que la variación geográfica y temporal de los procesos de circulación dominan el transporte y la dispersión efectiva de las larvas en la región, así la localización y fecha de desove son los principales determinantes del éxito del reclutamiento, la distancia de dispersión y los patrones de conectividad en ambas especies, independientemente de los rasgos biológicos larvales. La migración vertical de las dos especies de larvas de invertebrados marinos modifica la tasa de reclutamiento pero no siempre implica un incremento de la retención local. La mayoría del reclutamiento fue alóctono, con niveles bajos de auto-reclutamiento y retención local, incluso para la especie con un tiempo de vida planctónica corto. Los patrones geográficos de salida y llegada fueron similares para ambas especies, observándose una mayor importancia relativa de la región norte del dominio de estudio. Esta consistencia en los patrones entre especies es promisoria, ya que facilita el manejo multipespecífico. Nuestros resultados permiten identificar los principales determinantes del éxito del reclutamiento y la distancia de dispersión para dos especies de gran interés comercial en Chile, y se sugieren recomendaciones para el manejo y la conservación en una de las regiones costeras más productivas pero también más explotadas del mundo.

Apéndice IV
Artículos publicados en su formato original

Lat. Am. J. Aquat. Res., 45(2): 391-402, 2017
DOI: 10.3856/vol45-issue2-fulltext-14

Research Article

Reproductive output of two benthic resources (*Fissurella latimarginata* and *Loxechinus albus*) under different management regimes along the coast of central Chile

Miriam Fernández[1], Marta Blanco[1], Cristina Ruano-Chamorro[1] & Maria Dulce Subida[1]
[1]Núcleo Milenio Centro de Conservación Marina, Estación Costera de Investigaciones Marinas
Departamento de Ecología, Facultad de Ciencias Biológicas
Pontificia Universidad Católica de Chile, Santiago, Chile
Corresponding author: Miriam Fernandez (mfernandez@bio.puc.cl)

ABSTRACT. The biological and ecological benefits of fully and partially marine protected areas are well documented. However, the benefits reaching areas beyond the limits of the reserves are still emerging in spite the fact that they are essential for fishing grounds recovery and to gain support for the protection of the ocean among stakeholders. We analyzed the influence of protection on gonadosomatic index, and also body dry weight, of two economically and ecologically important species: the keyhole limpet, *Fissurella latimarginata* and the red sea urchin, *Loxechinus albus*, in order to determine the value of protected areas in directly enhancing reproduction, and therefore potential seeding on exploited areas. We compared two levels of protection in central Chile, determined by fisheries management regimes (in turn associated to fishing pressure): a) areas with fishing restrictions (low or none fishing effort; territorial use rights for fisheries and no-take areas) and b) open access areas (high exploitation rates). We also evaluated the independent influence of upwelling on both variables. Our results show for both species that a) body dry weight is not affected by management regime, b) management regime did not show a consistent impact on gonadosomatic index and c) upwelling did not affect the response variables. Our findings help disentangling the main factors determining reproductive patterns under contrasting human impact scenarios, suggesting that the selection of sites for establishing marine protected areas seems to be less relevant than efficient control of fishing effort and minimum legal size to assure natural seeding.

Keywords: *Fissurella latimarginata*, *Loxechinus albus***,** seeding, reproduction, marine protected areas, TURF, conservation, management, upwelling.

INTRODUCTION

Marine protected areas (MPA) have increased worldwide in response to increasing human impacts on the ocean (Halpern *et al*., 2008). The benefits of MPA, particularly for fished areas, have been widely reported (Roberts *et al*., 2001; Halpern, 2003; Lester *et al*., 2009). Most of the evidence focused on the benefits of protection inside the boundaries of protected areas, measured on a set of biological variables such as species richness as well as abundance, biomass, and/or adult size of exploited species (Jennings *et al*., 1996; Roberts *et al*., 2001; Halpern, 2003; Shears *et al*., 2006; Lester *et al*., 2009). It is clear that fully protected areas confer more benefits than partially protected areas on most of these biological variables (Lester & Halpern, 2008; Gelcich *et al*., 2012). However, it is also evident that establishing fully protected areas generates social resistance (West *et al*., 2006). Thus, there is a compromise between reaching higher benefits fully protecting smaller fractions of the ocean and achieving lower enhancement but partially protecting larger proportions of the world ocean. Territorial Use Rights for Fisheries (TURF), implemented for management purposes, can also provide ancillary benefits for marine conservation as partially protected areas, over large fractions of the ocean (Gelcich *et al*., 2012).

The performance of fully and partially MPAs beyond the limits of the reserve is essential for fishing grounds recovery and to gain support among stakeholders (Roberts *et al*., 2001; Gells & Roberts, 2003a; Halpern & Warner, 2003; Russ *et al*., 2004; Sale *et al*., 2005). Spillover of exploitable adult biomass from no-take reserves clearly benefits local fisheries outside the boundaries of protected areas (*e.g*., Roberts, 2001; Goñi *et al*., 2006). The benefits may reach even

---

Corresponding editor: Patricio Arana

larger distances through the export of dispersive propagules, which seem to be enhanced inside protected areas. The enhancement in egg and larval production has been associated to higher reproductive potential inside both fully protected areas due to the combined effect of increased adult size and higher density of exploited species (Roger-Bennett *et al*., 2002; Gells & Roberts, 2003a; Willis *et al*., 2003; Pelc *et al*., 2009). Empirical evidence shows increases in reproductive potential (egg or gonad production) ranging between 2 and 18 fold in protected areas with respect to fished areas (Roger-Bennett *et al*., 2002; Willis *et al*., 2003; Pelc *et al*., 2009). The benefits of partially protected areas could be lower than fully protected areas, as the increase in size and density, two critical variables affecting egg production, is higher in no-take areas than in partially protected areas (Lester *et al*., 2009; Gelcich *et al*., 2012). All the analyses, however, have focused on the indirect consequences of enhanced size and density, while the direct influence of protection on reproductive investment has rarely been assessed (Kaiser *et al.*, 2009).

Direct influence of protection on seeding is expected to be positive if sites selected for conservation or TURFs are particularly productive (an attribute often dominant in the selection of areas for TURFs). In fact, the 20 to 25% increases in gonad weight observed in the scallop *Pecten maximus* between protected and open access areas suggest that protection can directly affect reproductive investment (Kaiser *et al*., 2009). However, negative effects can also be expected under density-dependent feeding, or parasitism scenarios (Loot *et al*., 2005; Wood *et al*., 2013). For instance, infection rates of several invertebrate species, including the keyhole limpet *Fissurella crassa*, are significantly higher in marine protected areas (Loot *et al*., 2005; Wood *et al*., 2013). However, the higher abundance of parasites infecting the gonads of *Fissurella* spp. in partially protected areas (TURFs) seem to enhance the gonadosomatic index in TURFs, suggesting a potential positive direct effect of fishing restriction on the reproductive success of keyhole limpets (Aldana *et al.,* 2014). Further evidence on the direct influence of protection on reproductive output are needed to better understand the role of fully and partially protected areas on seeding beyond the boundaries of protection, the influence of site selection for conservation and management, and the relevance of individual reproductive potential for conservation planning and management.

The coast of central Chile provides a good model to analyze the direct effect of protection on reproduction (*e.g.*, gonad investment). First, this section of the coast is heavily impacted by artisanal fisheries (Fernández & Castilla, 2005). Second, there is a mosaic of human impact that includes fully and partially (TURFs; Gelcich *et al*., 2012) protected areas interspaced with open access fishing zones (Fernández & Castilla, 2005). Thus, levels of protection of the coastal ecosystem can be associated to fisheries management regimes. Third, the spatial variation in upwelling influence on coastal areas also allows assessing the effect of this environmental driver on reproduction. Finally, there is a need to advance in management and conservation plans of coastal areas, identifying the most relevant zones for propagules production (Tognelli *et al*., 2009). We compared two levels of protection, determined by fisheries management regimes (in turn associated to fishing pressure) on reproductive investment (gonadosomatic index) and body dry weight of two economically and ecologically important rocky reef species in central Chile: the keyhole limpet, *Fissurella latimarginata* and the red sea-urchin, *Loxechinus albus*. Both variables, body dry weight and gonadosomatic index, provide indication of the general physiological condition (*i.e.*, energy assigned to reserves) of the organisms. Additionally, we also evaluated the independent influence of upwelling on body dry weight and gonadosomatic index, in order to help interpreting the potential influence of environmental conditions on reproductive investment. Thus, our results have local and global relevance, as they allow defining specific management and conservation strategies for the study area but also they can help informing on the direct influence of protection on reproduction (and therefore on seeding) besides the indirect effect expected through enhanced size and density of reproductive individuals.

MATERIALS AND METHODS

The study system

Both model species are targeted by the artisanal fishery that operates along the coast of central Chile. This geographic area (30º-36ºS) is characterized by high human impact (particularly fishing), low number of fully marine protected areas (<0.001%), and large fractions of the coast under a co-management system based Territorial Use Rights for Fisheries, covering 30% of the coastal area (Fernández & Castilla, 2005). Therefore, the TURF system confers most of the protection to coastal marine ecosystems, contributing to sustainable exploitation and conservation goals (Gelcich *et al*., 2012). Since levels of protection are associated to fisheries management regimes (no-take, TURF and open access), the effect we actually evaluated, we used both terms indistinctly throughout the manuscript. The coastal landscape of the study area is also characterized by strong heterogeneity driven by spatially persistent differences in oceanographic conditions that affect temperature and determine the local supply of nutrients and hence, primary production (upwelling, Wieters *et al*., 2003; Navarrete *et al*., 2005; Wieters, 2005; Tapia *et al*., 2009, 2014). Temperature and food supply can affect energy budget of organisms, determining the energy assigned to body mass and gonads (Clarke, 1987; Leslie *et al*., 2005; Monaco *et al*., 2014). For this reason, the role of upwelling intensity in modifying reproductive investment needs to be considered in our assessment, despite the fact that we cannot simultaneously evaluate both factors (management regime and upwelling) at a given site (a site corresponds to one or the other: low or high upwelling influence).

Specifically, our study area was located on a small fraction of the coast of central Chile, between 32.6ºS and 33.5ºS. Within this ecoregion (Camus, 2001), we selected five sites (Maitencillo, Laguna Verde, Quintay, El Quisco and Las Cruces; Fig. 1). Laguna Verde and Quintay were classified as sites more strongly influenced by upwelling (see Wieters, 2005; Tapia *et al*., 2009, 2014) than the remaining three sites (low upwelling). The influence of protection was associated to the management regimes operating in this region, we sampled (a) areas with restricted access for fishing (RAA), and (b) open access areas (OAAs). In each site we sampled an OAA adjacent to a RAA (named here area or sampling area). Among the latter, we sampled one no-take area (Las Cruces) and four TURFs. Thus, altogether we sampled ten areas (Fig. 1).

In the analysis, we pooled no-take and TURFs, as in the sampling region there is only one no-take area. Otherwise we would have not been able to determine if potential differences were exclusively due to human impact or environmental variability. Previous evidence suggests that the no-take area of Las Cruces exhibits a similar response of traditional biological variables (size, density) than some TURFs for benthic resources (Gelcich *et al*., 2012).

Sampling and data analysis

At each sampling area between 13 and 46 reproductive individuals of the keyhole limpet *Fissurella latimarginata* and the red sea-urchin *Loxechinus albus* were collected during the reproductive peak reported for both species (Table 1; Guisado & Castilla, 1987; Brown *et al*., 1997). Individuals, larger than minimum size of reproduction (6 cm for limpets and 7 cm for urchins) were collected by professional divers in each site.

Sampling was repeated in 2012 and 2014. Since the same patterns in the response variables were observed between years, we pooled all the samples in order to increase sample size. In total, we sampled 295 individuals of *F. latimarginata* and 273 of *L. albus* following all bioethics protocols approved for this study (CBB-233/2012).

At the laboratory, body size of all specimens was measured using a caliper (±0.1 mm), considering peristomial length for limpets and diameter without spines for sea-urchins. After obtaining the wet weight of each individual (mg), animals were dissected and the gonads were extracted. The soft and hard (calcareous) body parts, in addition to the gonads, were placed first on towel paper for 10 min to eliminate the excess of water, and then separated on labeled containers. Subsequently, all parts were dried in a standard oven at 60ºC for 48 h. Finally, dry weights were obtained with a Sartorius BP211D digital balance to the nearest 0.01 mg. Body dry weight was considered as a proxy of body condition.

In order to compare reproductive output between fisheries management regimes, the proportion between gonad dry weight and soft body dry weight was obtained (Gonadosomatic Index; GSI). We also compared individual body dry weights between fisheries management regimes to further evaluate effect of protection levels (associated here to management regimes) on energy reserves that can be assigned either to body mass or gonads. Since body mass and gonadosomatic index are influenced by size, and size is affected by levels of protection, the first step was to assess the effect of fisheries management regime on mean individual size. A two-way analysis of variance (ANOVA) with a complete non-balanced block design without replication was used to assess the effect of fisheries management regime (two levels, fixed factor) blocked by site (five levels, random factor) on mean individual size. We used a complete block design in order to account for the spatial auto-correlation of the observations. Spatial autocorrelation might occur because observations from neighbor areas with different management regimes (within site observations) might be more similar to each other than to observations from other sites since environmental conditions might differ among sites not related to management regimes. Data are slightly unbalanced due to the slightly different number of individuals measured in each area (Table 1). Fligner-Killeen test was used to assess the homogeneity of variances and Shapiro-Wilk test was used to assess the normality of the error distributions. The ANOVA assumptions were met for *F. latimarginata* but not for *L. albus*. Thus, in this case a Generalized Linear Model (GLM) using "quasi-poisson" family error distribution was performed. The model fit was checked with chi-square test for deviance *vs* the degrees of freedom.

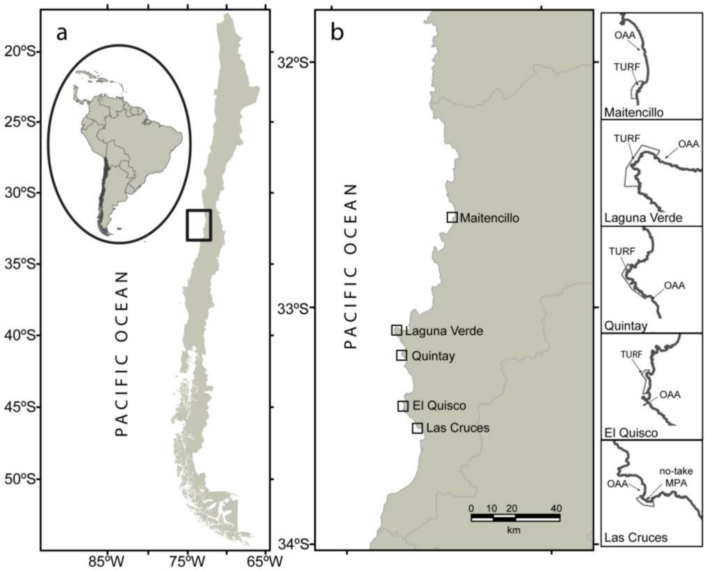


Figure 1. a) Maps of the general location of the study region showing sites, and b) specific areas where samples were collected in Fishing Restricted Access Areas (either no-take area or TURF) and adjacent Open Access Areas (OAAs).

Table 1. Sample size and body size ranges of reproductive individuals collected to estimate dry weight and gonadosomatic index for each species and fisheries management regime.

Species	Site	Fishing condition	Sample size	Body size range (cm)
F. latimarginata	Maitencillo	Restricted access	38	(6.42-10.77)
		Open access	46	(6.05-10.20)
	Laguna Verde	Restricted access	20	(8.03-9.48)
		Open access	37	(6.39-8.11)
	Quintay	Restricted access	37	(7.59-9.87)
		Open access	34	(7.17-9.86)
	El Quisco	Restricted access	15	(7.24-9.79)
		Open access	20	(7.07-9.61)
	Las Cruces	Restricted access	32	(6.60-11.41)
		Open access	16	(7.20-10.26)
L. albus	Maitencillo	Restricted access	38	(7.31-11.47)
		Open access	35	(7.03-10.90)
	Laguna Verde	Restricted access	40	(7.94-10.50)
		Open access	17	(7.02-9.34)
	Quintay	Restricted access	39	(8.60-10.80)
		Open access	38	(8.57-12.83)
	El Quisco	Restricted access	20	(7.65-11.32)
		Open access	10	(8.23-11.58)
	Las Cruces	Restricted access	23	(8.83-11.42)
		Open access	13	(7.21-9.84)

Since individual body dry weight (IDW) and the gonadosomatic index (GSI) were highly correlated with body size ($r > 0.45$ in all cases), we used body size as a covariate in our analyses to assess the effects of fisheries management regime and upwelling. Following the method of residuals analysis proposed by Ouréns *et al.* (2012), we first computed the individual linear regression model between each log-transformed response variable (IDW and GSI) and mean individual body size for each combination of levels of both factors. Then, for each significant linear model we removed the effect of the covariable (body size) on the response variable (IDW and GSI) extracting the residuals for each linear regression, and used the residuals as the new response variable in subsequent analyses. When no significant relationship was found between the log-transformed response variables and the log-transformed body size (only three models, all for *L. albus*), the new response variable were obtained by subtracting each observation from the mean. We assessed the effect of fisheries management regime on each new variable by using a 2-way ANOVA with the same non-balanced complete block design (by site) described above. Contrastingly, in order to test for the effect of upwelling (fixed factor) we used a 2-way ANOVA with a nested design (site nested within upwelling) due to environmentally driven site differences within levels of factor upwelling. Whenever ANOVA assumptions were not met, GLMs (family structure "quasi-Poisson") were used instead; again, the GLM model fit was checked with a chi-square test for deviance *vs* the degrees of freedom. Laguna Verde was excluded from the analysis of *F. latimarginata* because there was no overlap in size between the two management regimes of this site. Similarly, Laguna Verde and Las Cruces were also excluded for *L. albus*. All the statistical analyses were carried out using the free software R version 3.1.3 (R Development Core Team 2013).

RESULTS

Body size

We found a significant effect of fisheries management regime ($F_{1,289} = 56.22$, $P < 0.0001$) and site ($F_{4,289} = 12.32$, $P < 0.0001$) on body size of keyhole limpets. However, management regime did not have the same effect in all sites (Fig. 2a) in spite of a general trend towards larger body sizes in RAA. Laguna Verde and El Quisco showed the greater differences between RAA and OAA (largest individuals in RAA). Differences in body size between pairs of sites were not related to the distance (km) between them (Fig. 2a). Thus, differences in mean size of keyhole limpets were observed between El Quisco and Quintay (which are close together), but also between El Quisco and Maintencillo, or between Quintay and Maintencillo, which are further away (Fig. 1).

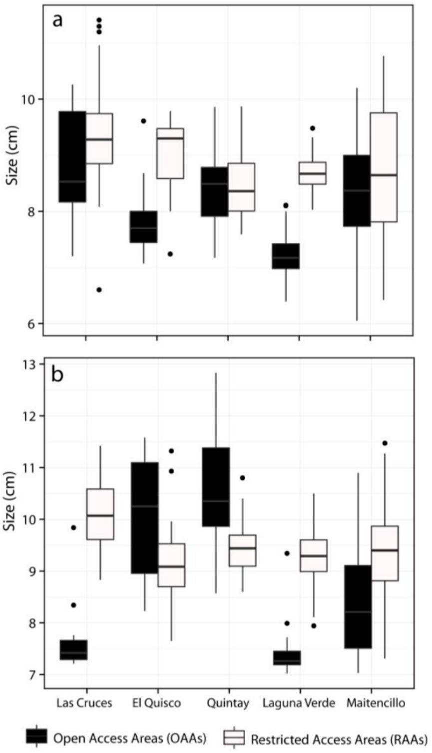


Figure 2. Boxplots showing individual body size for each sampling site in areas under different fishing management regimes. White bars represent areas with entry restriction to fishing named here Restricted Access Areas (RAAs, include one no-take area and four Territorial Use Rights for Fisheries; TURF). Black bars indicate areas with no access restrictions, called here Open Access Areas (OAAs). a) *Fissurella latimarginata* and b) *Loxechinus albus*.

We also found a significant effect of fisheries management regime ($F_{1,271} = 41.87$, $P < 0.001$) and site ($F_{4,267} = 33.99$, $P < 0.001$) on the body size of sea-urchins (Fig. 2b). Larger sea-urchins in RAA were observed in Las Cruces, Laguna Verde and Maitencillo, and the opposite trend in El Quisco and Quintay (Fig. 2b). As observed for keyhole limpets, mean differences

Table 2. Results of the relationship between body dry weight (log transformation) and size (log transformation) of the keyhole limpet *Fissurella latimarginata* and the red sea-urchin *Loxechinus albus* for the different sites and fisheries management regimes. RAA: Restricted Access Areas for fishing (which can be either no-take areas or Territorial use Rights for Fisheries; TURF), OAA: Open Access Areas.

Site	Fishing regime	*Fissurella latimarginata*			*Loxechinus albus*		
		Intercept	Slope	*P*-value	Intercept	Slope	*P*-value
Las Cruces	OAA	-5.68	3.71	<0.001	-1.63	2.73	<0.001
	RAA (no take)	-3.00	2.55	<0.001	-1.09	2.55	<0.001
Quisco	OAA	-5.02	3.29	<0.001	-1.58	2.74	<0.001
	RAA (TURF)	-5.99	3.97	<0.001	-2.29	3.05	<0.001
Quintay	OAA	-6.86	4.19	<0.001	0.15	1.99	<0.001
	RAA (TURF)	-3.28	2.49	<0.001	-1.76	2.79	<0.001
Laguna Verde	OAA	-1.03	1.44	0.02	-0.26	2.04	<0.001
	RAA (TURF)	-4.16	3.06	0.009	-1.95	2.88	<0.001
Maintencillo	OAA	-2.85	2.45	<0.001	-2.73	3.24	<0.001
	RAA (TURF)	-5.03	3.41	<0.001	-1.41	2.63	<0.001

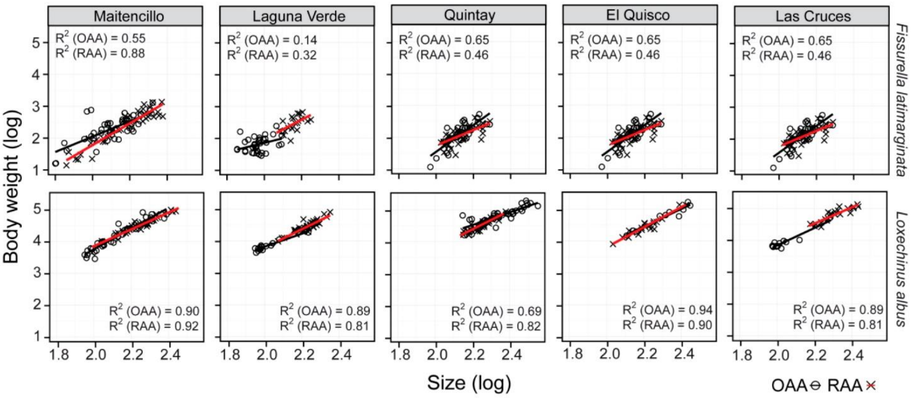


Figure 3. Relationship between body dry weight (log) and size (log; length [mm] in the keyhole limpet *F. latimarginata* and diameter [mm] in the sea-urchin *Loxechinus albus*) in the five study sites, considering one Open Access Area (OAA; circles and black line) and one Restricted Access Area (RAA: crosses and red line) per site. The regression coefficients (R^2) for each fishing regime and site are also shown. Table 2 includes the parameters of the regressions.

in body size between pairs of sites was not related to the distance between sites: differences were observed between both the closest sites (Laguna Verde and El Quisco) and the two farthest ones (Las Cruces and Maitencillo).

Since body size showed significant differences between fisheries management regimes and sites, it was treated as a covariable in the remaining analysis conducted to test for the influence of fisheries management regime and upwelling.

Body weight

Body dry weight was significantly correlated with body size in both species, regardless of the fisheries management regime or site (Table 2, Fig. 3).

After removing the influence of size on body weight (residual analysis), no influence of fisheries management regime on body dry weight of keyhole limpets ($F_{1,233}$ = 0.99, P = 0.32) and red sea-urchin ($F_{1,176}$ = 1.25, P = 0.26) were detected. Body dry weight also increased significantly with body size when sites were

Table 3. Results of the relationship between body dry weight (log transformation) and size (log transformation) for the keyhole limpet *Fissurella latimarginata* and the red sea-urchin *Loxechinus albus* for the different sites and upwelling conditions.

Site	Environmental condition	*Fissurella latimarginata*			*Loxechinus albus*		
		Intercept	Slope	*P*-value	Intercept	Slope	*P*-value
Las Cruces	Low upwelling	-4.31	3.12	<0.001	-2.19	3.02	<0.001
Quisco	Low upwelling	-8.58	5.08	<0.001	-2.04	2.90	<0.001
Quintay	High upwelling	-5.00	3.31	<0.001	-0.87	2.41	<0.001
Maintencillo	Low upwelling	-3.82	2.88	<0.001	-2.14	2.96	<0.001
Laguna Verde	High upwelling	-3.99	2.96	<0.001	-1.61	2.72	<0.001

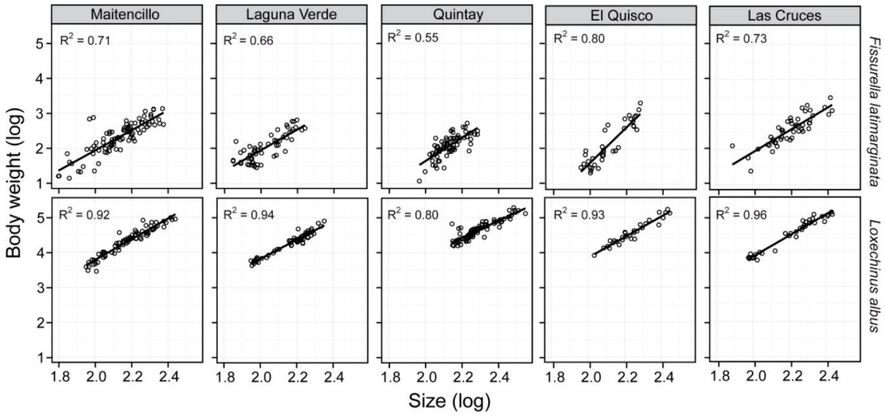


Figure 4. Relationship between body dry weight (log) and size (log: length in the keyhole limpet *F. latimarginata* [mm] and diameter [mm] in the red sea-urchin *Loxechinus albus*) in the five study sites. Two sites were labeled as high upwelling (Quintay and Laguna Verde) and the remaining as low upwelling. The regression coefficients (R^2) for each site are shown. Table 3 includes the parameters of the regressions.

analyzed considering the influence of upwelling, by pooling data from both management regimes for each site (Table 3, Fig. 4). The nested ANOVA performed on the residuals of the relationship between body dry weight and body size did not detect any influence of upwelling condition. The results were consistent between species (keyhole limpet: $F_{4,290} = 0.11$, $P = 0.97$; red sea-urchin: $F_{4,268} = 0.13$, $P = 0.97$).

Reproductive output

Gonadosomatic index was also significantly correlated with body size in both species for most sites and both fisheries management regimes, with some exceptions (see Table 4, Fig. 5). The residual analyses showed no effect of fisheries management regime ($F_{1,233} = 1.39$, $P = 0.24$) or site ($F_{3,233} = 0.13$, $P = 0.94$) on gonadosomatic index of the keyhole limpet after removing the effect of size (residuals). Although data from the site that was excluded from the analysis (Laguna Verde) cannot be statistically compared because of lack of overlap in size, the slopes between both fishing regimes showed similar trends (Fig. 5). In the case of the red sea-urchin, no differences in gonadosomatic index after removing the effect of size were found among sites ($P > 0.9$ in all cases). Although fisheries management regime showed significant effects on the residuals of the regressions between gonadosomatic index and size, no consistent pattern was detected across sites.

The gonadosomatic index significantly increased with size in both species only at the sites characterized by low upwelling influence (Table 5, Fig. 6). Nevertheless, the residual analysis of the relationships between gonadosomatic index and size did not show significant differences between upwelling conditions neither for the keyhole limpet ($F_{4,290} = 0.03$, $P = 0.99$) nor for the red sea-urchin ($F_{4,268} = 0.4$, $P = 0.81$).

Table 4. Results of the relationship between gonadosomatic index (log transformation) and size (log transformation) of the keyhole limpet *Fissurella latimarginata* and the red sea-urchin *Loxechinus albus* for the different sites and fisheries management regimes. RAA: Restricted Access Areas for fishing (which can be either no-take areas or territorial use rights for fisheries; TURF), OAA: Open Access Areas.

Site	Fishing regime	*Fissurella latimarginata*			*Loxechinus albus*		
		Intercept	Slope	*P*-value	Intercept	Slope	*P*-value
Las Cruces	OAA	-12.81	5.17	0.011	-2.33	-0.10	0.922
	RAA (no take)	-4.34	1.31	0.11	-5.01	1.25	0.021
Quisco	OAA	-11.54	4.50	0.018	-2.69	0.21	0.766
	RAA (TURF)	-7.79	2.95	0.012	-9.88	3.21	0.003
Quintay	OAA	-7.72	2.71	0.034	-3.94	0.61	0.309
	RAA (TURF)	2.97	-2.37	0.11	-1.28	-0.61	0.495
Laguna Verde	OAA	-7.23	2.65	<0.001	-4.92	1.11	0.045
	RAA (TURF)	-8.51	3.08	<0.001	-5.99	1.52	0.009
Maintencillo	OAA	0.18	-0.99	0.60	-1.96	-0.34	0.773
	RAA (TURF)	-2.85	0.65	0.58	-11.39	3.91	0.001

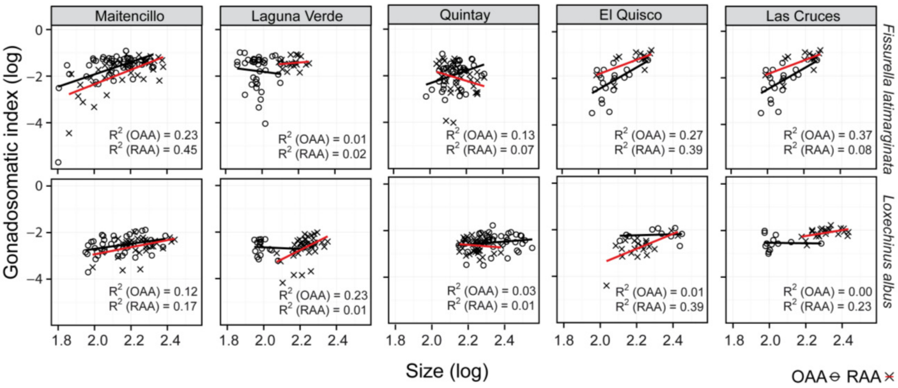


Figure 5. Relationship between gonadosomatic index (log) and size (log; length [mm] in the keyhole limpet *F. latimarginata* and diameter [mm] in the case of the red sea-urchin *Loxechinus albus*) in the five study sites, considering one Open Access Area (OAA: identified by circles and black line) and one Restricted Access Area (RAA: identified by crosses and red line) per site. The regression coefficients (R^2) for each fishing regime and site are shown. Table 4 includes the parameters of the regressions.

DISCUSSION

The main conclusions of our study are the consistent patterns evidenced by a) the lack of effect of fisheries management regime (related to protection level) on the individual body dry weight in both species, b) the poor influence of fisheries management regime on reproductive investment (*i.e.*, gonadosomatic index), suggesting that the selection of sites for sitting of marine protected areas or TURFs seems to be less relevant for seeding than efficient control of fishing effort and minimum legal size, as these two variables are major indirect determinants of egg production (Roger-Bennett *et al*., 2002; Willis *et al*., 2003; Pelc *et al*., 2009), and (c) the lack of effect of upwelling on body condition (body dry weight) and reproductive investment (gonadosomatic index). Although in general we found no effects of the study variables, the results are of local and global interest. First, because we clearly show that at the spatial scale of our analysis, the main driver of coastal dynamics in the study area (upwelling; see Wieters *et al*., 2003; Navarrete *et al*., 2005; Wieters, 2005; Tapia *et al*., 2009, 2014) does not influence critical indicators of general physiological conditions and reproductive investment in two herbivore species. And second, because our results help di-

Table 5. Results of the relationship between gonadosomatic index (log transformation) and size (log transformation) of the keyhole limpet *Fissurella latimarginata* and the red sea-urchin *Loxechinus albus* for the different sites and upwelling conditions.

Site	Enviromental condition	*Fissurella latimarginata*			*Loxechinus albus*		
		Intercept	Slope	*P*-value	Intercept	Slope	*P*-value
Las Cruces	Low upwelling	-7.43	2.69	0.001	-5.24	1.35	<0.001
Quisco	Low upwelling	-12.68	5.11	<0.001	-8.11	2.46	0.001
Quintay	High upwelling	-2.18	0.07	0.941	-4.02	0.63	0.113
Maintencillo	Low upwelling	-7.47	2.69	<0.001	-4.72	0.99	0.004
Laguna Verde	High upwelling	-4.01	1.15	0.130	-3.97	0.60	0.224

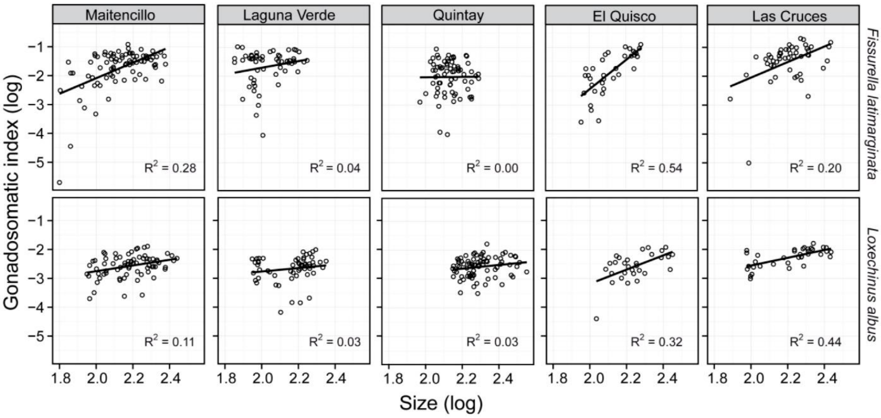


Figure 6. Relationship between gonadosomatic index (log) and size (log; length [mm] in the keyhole limpet *F. latimarginata* and diameter [mm] in the case of the red sea-urchin *Loxechinus albus*) in the five study sites. Two sites are classified as high upwelling (Quintay and Laguna Verde) and the remaining as low upwelling intensity. The regression coefficients (R^2) per site are shown. Table 5 includes the parameters of the regressions.

sentangling the main determinants of reproductive patterns observed in protected areas, which is critical for decision making (*e.g.*, site selection for conservation and management, spatial planning).

In line with existing evidence, our results show the benefits of protection for enhancing size of exploited species inside the boundaries of protected areas (Lester *et al.*, 2009; Gelcich *et al.*, 2012). However, a) in some sites significant larger sizes in the RAA with respect to OAA were not found, in spite the suggestive general trend towards size enhancement and b) in El Quisco and Quintay mean size of the red sea-urchin exhibited the opposite pattern (larger sizes in open access areas). A plausible explanation is that most of our RAA are only partially protected from fishing. Across all sites we observed, on average, 17 and 28% increase in body size with protection in the keyhole limpet and in the red sea-urchin, respectively. A larger average increase in size (30%) has been reported in global analyses comparing individual size between no-take and open access areas (Lester *et al.*, 2009). However, smaller changes, comparable with our results (~17%), have been observed in global comparisons between partially protected and open access areas, including an broad range of species (Lester & Halpern, 2008), suggesting the higher benefits of full protection within the limits of the reserves. Nevertheless, our findings reinforce and highlight the benefits of partially protected areas, particularly in regions where excluding human activities does not seem a viable option (Tognelli *et al.*, 2009). Our results suggest the need of further exploration of the influence of fishing effort on mean size of exploited species (*e.g.*, comparing TURFs across a gradient of fishing level) since exploitation seems to be the major determinant of differences in body size. Another suggestion that fishing, rather than environmental factors, determines local mean body size, is that variability in mean body size across sites was not consistent between the two grazer species, and did not show a regional effect, as differences occurred among the closest or the farthest sites. Therefore, it seems relevant to determine the level of human impact that affects body size, and as a consequence influences the variables related to reproductive investment, critical for management and conservation, such as egg production.

Enhanced size in protected areas can amplify the benefits of protection outside the boundaries of protected zones by increasing individual production of dispersive propagules (Gell & Roberts, 2003b). Empirical evidence predicts between 2 to 5 times increase in abalone egg production in protected areas with respect to fished areas, associated to 30% increase of size of adults (Rogers-Bennett *et al*., 2002). The contribution of partially protected areas to potential egg production may be less significant than no-take areas since smaller changes in size, as those observed in this study, can have tremendous impact on potential fecundity (*e.g.*, Espinosa *et al.*, 2006) However, not only size, but also density is enhanced in partially and fully protected areas (Lester & Halpern, 2008). The relative importance of increased size and abundance in protected areas on reproductive potential is yet poorly understood. Most studies report increases in egg production within protected areas due to the combined influence of size and density (Roger-Bennett *et al*., 2002; Willis *et al*., 2003; Pelc *et al*., 2009). Another element contributing to local reproductive potential is the direct influence of fishing regime on reproductive investment; however this is even less understood (Kaiser *et al*., 2009) and our results help filling this important gap. Density-dependent reproduction or parasite load can be potential mechanisms behind direct effect of protection on reproductive investment.

Our evaluation on the direct influence of protection on both reproductive investment and general condition of keyhole limpets and red sea-urchins showed a consistent lack of effect of protection on body dry weight and gonadosomatic index. This finding contrast with the results of similar comparison in the scallops *Pecten maximum*, showing that gonad weight per unit of body size increased between 19 and 24% in the areas protected from fishing, associated to a 8-fold increase in density (Kaiser *et al*., 2009). Our results showing persistent patterns in the comparison of fishing management regimes are solid as they are based on comparisons among five sites and two species. Moreover, fishing management regime consistently showed no effect regardless of upwelling condition. Contrasting results on the direct influence of protection on reproductive investment (*e.g.*, Kaiser *et al.* 2009, this study) suggest the need to advance our understanding of the mechanisms behind. Clearly, density-dependent effects (*e.g.*, feeding, parasitism, behavior such as territorialism) might influence individual energy budgets and determine differential investment in gonads in protected areas (Kaiser *et al*., 2009; Aldana *et al*., 2014). However, the potential factors appear to be complex. For instance, parasitic biomass in gonads seems to generate contrasting patterns on gonad investment (Loot *et al*., 2005; Aldana *et al*., 2014). External factors may also play a role. In our particular case, we expected that partially protected areas (TURFs) would exhibit larger effects on both response variables than no-take or open access areas, as fishers might select the most productive areas for TURFs. However, we cannot conclude that fishers' selection for productive sites, or density dependent factors determine the patterns found in this study. The lack of direct effect of protection on reproductive investment drives our main conclusion that the selection of particular areas for sitting marine protected areas seems to be less relevant than effective enforcement, which promotes enhancement of size and density (Halpern, 2003; Lester & Halpern, 2008; Lester *et al*., 2009).

It is also remarkable that the upwelling gradient analyzed here, including the influence of a major upwelling center (Curaumilla), did not influence reproductive output or body size condition. A five-fold increase in planktonic chlorophyll-*a* produces a 3-fold increase in larval production of the filter feeding barnacle *Balanus glandula* (Leslie *et al*., 2005). Despite macroalgal growth seems to be higher in areas under high upwelling influence (Wieters *et al*., 2003), this effect does not seem to be transmitted to herbivores in the form of body dry weight or gonadosomatic index (but see Pulgar *et al.*, 2013). Our results again highlight that this environmental factor, at least at the scale of variability of our study sites, does not seem to be a major determinant for body condition of the main herbivores exploited in central Chile.

Our results strongly suggest that at the local level (Chile), major fishing regulations such as minimum legal size and quotas, need to be enforced, in order to control size and density of reproductive individuals. Recent studies have shown that illegal fishing of benthic resources can generate catch levels similar to the legally reported landing (González *et al*., 2006), clearly suggest poor enforcement. Our results show that maintaining larger individuals in protected areas is critical for seeding. Therefore, special incentives should be created to maintain the Chilean TURF system, because of its contribution to egg production by enhancing size and density of exploited benthic species. Our analysis also allowed to extrapolate the value of fully and partially protected areas (including TURFs) on less studied variables, such as reproductive output and egg production.

ACKNOWLEDGMENTS

This work was funded by Iniciativa Científica Milenio (Project CCM RC 1300004) from Ministerio de Economía, Fomento y Turismo de Chile, and Fondecyt (Projects: 1130976 to MFB, and 11130580 to MDS). The authors thank B. Bularz, S. López, R. Calderón, M. Figueroa, M. Saldías and M. Andreu for their help in data collection and processing samples in the laboratory. We are also very grateful to fishermen of Maitencillo, Laguna Verde, Quintay, and El Quisco. We appreciate the comments of two anonymous reviewers to help improving the manuscript.

REFERENCES

Aldana, M., J.M. Pulgar, N. Orellana, F.P. Ojeda & M.R. García-Huidobro. 2014. Increased parasitism of limpets by a *Trematode metacercaria* in fisheries management areas of Central Chile: effects on host growth and reproduction. Ecol. Health, 11: 215-226.

Brown, G., M. González, D. López, L. Durán, R. Rivero, G. Collado & C. Betancourt. 1997. Estudio de los ciclos vitales de las especies comerciales de lapas del genero *Fissurella* spp. en las Regiones I a X. Informe Final Proyecto FIP-IT/94-33: 196 pp.

Clarke, A. 1987. Temperature, latitude and reproductive effort. Mar. Ecol. Prog. Ser., 38: 89-99.

Camus, P. 2001. Biogeografía marina de Chile continental. Rev. Chil. Hist. Nat., 74: 587-617.

Espinosa, F., J.M. Guerra-Garcia, F. Daren & J.C. Garcia-Gomez. 2006. Aspects of reproduction and their implications for the conservation of the endangered limpet, *Patella ferruginea*. Invert. Rep. Dev., 49(1-2): 85-92.

Fernández, M. & J.C. Castilla. 2005. Marine conservation in Chile: historical perspective, lessons, and challenges. Conserv. Biol., 19: 1752-1762.

Gelcich, S., M. Fernández, N. Godoy, A. Canepa, L. Prado & J.C. Castilla. 2012. Territorial user rights for fisheries as ancillary instruments for marine coastal conservation in Chile. Conserv. Biol., 26: 1005-1015.

Gell, F.R. & C.M. Roberts. 2003a. The fishery effects of marine reserves and fishery closures. World Wildlife Foundation, Washington DC, 90 pp.

Gell, F.R. & C.M. Roberts. 2003b. Benefits beyond boundaries: the fishery effects of marine reserves. Trends Ecol. Evol., 18: 448-455.

González, J., W. Stotz, J. Garrido, J.M. Orensanz, A.M. Parma, C. Tapia & A. Zuleta. 2006. The Chilean turf system: how is it performing in the case of the loco fishery? Bull. Mar. Sci., 78: 499-527. doi:10.1080/089 41920590915279.

Goñi, R., A. Quetglas & O. Reñones. 2006. Spillover of spiny lobsters *Palinurus elephas* from a marine reserve to an adjoining fishery. Mar. Ecol. Prog. Ser., 308: 207-219.

Guisado, C. & J.C. Castilla. 1987. Historia de vida, reproducción y avances en el cultivo del erizo comestible chileno *Loxechinus albus* (Molina, 1782) (Echinoidea, Echinidae). In: P. Arana (ed.). Manejo y desarrollo pesquero. Escuela de Ciencias del Mar, Universidad Católica de Valparaíso, Valparaíso, pp. 59-68.

Halpern, B.S. 2003. The impact of marine reserves: do reserves work and does reserve size matter? Ecol. Appl., 13: S117-S137.

Halpern, B.S. & R.R. Warner. 2003. Matching marine reserve design to reserve objectives. Proc. Biol. Sci., 270: 1871-1878.

Halpern, B.S., S. Walbridge, K. Selkoe, C. Kappel, F. Micheli, C. D´Agrosa, J. Bruno, K. Casey, C. Ebert, H. Fox, R. Fujita, D. Heinemann, H. Lenihan, E. Madin, M. Perry, E. Selig, M. Spalding, R. Steneck & R. Watson. 2008. A global map of human impact on marine ecosyst. Science, 319: 948-952.

Jennings, S., S.S. Marshall & N.V.C. Polunin. 1996. Seychelles marine protected areas: comparative structure and status of reef fish communities. Biol. Conserv., 75: 201-209.

Kaiser, M.J., R.E. Blyth-Skyrme, P.J.B. Hart, G. Edwards-Jones & D. Palmer. 2009. Evidence for greater reproductive output per unit area in areas protected from fishing. Can. J. Fish. Aquat. Sci., 64(9): 1284-1289.

Leslie, H.M., E.N Breck, F. Chan, J. Lubchenco & B. Menge. 2005. Barnacle reproductive hotspots linked to nearshore ocean conditions. Proc. Natl. Acad. Sci. USA, 102: 10534-10539.

Lester, S. & B. Halpern. 2008. Biological responses in marine no-take reserves versus partially protected areas. Mar. Ecol. Prog. Ser., 367: 49-56.

Lester, S., B. Halpern, K. Grorud-Colvert, J. Lubchenco, B. Ruttenberg, S. Gaines, S. Airamé & R. Warner. 2009. Biological effects within no-take marine reserves: a global synthesis. Mar. Ecol. Prog. Ser., 384: 33-46.

Loot, G., M. Aldana & S. Navarrete. 2005. Effects of human exclusion on parasitism in intertidal food webs of central Chile. Conserv. Biol., 19: 203-212.

Monaco, C.J., D.S. Wethey & B. Helmuth. 2014. A dynamic energy budget (DEB) model for the keystone predator *Pisaster ochraceus*. PLoS ONE 9(8): e104658. doi:10.1371/journal.pone. 0104658.

Navarrete, S.A., E. Wieters, B. Broitman & J.C. Castilla. 2005. Scales of benthic-pelagic coupling and the intensity of species interactions: from recruitment limitation to top down control. Proc. Natl. Acad. Sci. USA, 102: 18046-18051.

Ouréns, R., J. Freire & L. Fernández. 2012. Definition of a new unbiased gonad index for aquatic invertebrates and fish: Its application to the sea urchin *Paracentrotus lividus*. Aquat. Biol., 17: 145-152. doi: 10.3354/ab00476.

Pelc, R., M. Baskett, T. Tanci, S. Gaines & R. Warner. 2009. Quantifying larval export from South African marine reserves. Mar. Ecol. Prog. Ser., 394: 65-78.

Pulgar, J., M. Aldana, M. Alvarez, R. Garcia-Huidobro, P. Molina, J.P. Morales & V.M. 2013. Upwelling affects food availability, impacting the morphological and molecular conditions of the herviborous limpet *Fissurella crassa* (Mollusca: Archeogastropoda). J. Mar. Biol. Assoc. UK, 93: 797-802.

R Core Team. 2013. R: a language and environment for statistical computing. Foundation for statistical computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/.

Roberts, C.M., J.A. Bohnsack, F. Gell, J.P. Hawkins & R. Goodridge. 2001. Effects of marine reserves on adjacent fisheries. Science, 294: 1920-1923.

Rogers-Bennett, A.L., P.L. Haaker, K.A. Karpov, D.J. Kushner, L. Rogers-Bennett & L. Haaker. 2002. Using spatially areas explicit for data to marine protected abalone in California. Conserv. Biol., 16: 1308-1317.

Russ, G.R., A.C. Alcala, A.P. Maypa, H.P. Calumpong & A.T. White. 2004. Marine reserve benefits local fisheries. Ecol. Appl., 14: 597-606.

Sale, P.F, R.K. Cowen, B.S. Danilowicz, G.P. Jones, J.P. Kritzer, K.C. Lindeman, S. Planes, N.V.C. Polunin, G.R. Russ, Y.J. Sadovy & R.S. Steneck. 2005. Critical science gaps impede use of no-take fishery reserves. Trends Ecol. Evol., 20: 74-80.

Received: 9 March 2016; Accepted: 23 January 2017

Shears, N.T., R.V. Grace, N.R. Usmar, V. Kerr & R.C. Babcock. 2006. Long-term trends in lobster populations in a partially protected *vs* no-take Marine Park. Biol. Conserv., 132: 222-231.

Tapia, F.J., J.L. Largier, M. Castillo, E.A. Wieters & S.A. Navarrete. 2014. Latitudinal discontinuity in thermal conditions along the nearshore of central-northern Chile. PLoS ONE, 9: e110841-110811.

Tapia, F., S.A. Navarrete, M. Castillo, B.A. Menge, J.C. Castilla, J. Largier, E.A. Wieters & B.L. Broitman. 2009. Thermal indices of upwelling effects on inner-shelf habitats. Prog. Oceanogr., 83: 278-287.

Tognelli, M.F., M. Fernández & P. Marquet. 2009. Assessing the performance of the existing and proposed network of marine protected areas to conserve marine biodiversity in Chile. Biol. Conserv., 142: 3147-3153.

West, P., I. James & D. Brockington. 2006. Parks and peoples: the social impact of protected areas. Ann. Rev. Anthropol., 35: 251-277.

Wieters, E. 2005. Upwelling control of positive interactions over mesoscales: a new link between bottom-up and top-down processes on rocky shores. Mar. Ecol. Prog. Ser., 301: 43-54.

Wieters, E.A., D.M. Kaplan, S.A. Navarrete, A. Sotomayor, J. Largier, K.J. Nielsen & F. Veliz. 2003. Alongshore and temporal variability in chlorophyll-*a* concentration in Chilean nearshore waters. Mar. Ecol. Prog. Ser., 249: 93-105.

Willis, T.J., R.B. Millar & R.C. Babcock. 2003. Protection of exploited fish in temperate regions: high density and biomass of snapper. J. Appl. Ecol., 40(2): 214-227.

Wood, C., F. Micheli, M. Fernández, S. Gelcich, J.C. Castilla & J. Carvajal. 2013. Marine protected areas facilitate parasite populations among four fished host species of central Chile. J. Anim. Ecol., 82: 1276-1287.

PLOS | ONE

RESEARCH ARTICLE

Egg production patterns of two invertebrate species in rocky subtidal areas under different fishing regimes along the coast of central Chile

Marta Blanco*, **Andres Ospina-Álvarez**, **Catherine González**, **Miriam Fernández**¤

Núcleo Milenio - Centro de Conservación Marina CCM, Estación Costera de Investigaciones Marinas ECIM, Departamento de Ecología, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Santiago, Chile

¤ Current address: Departamento de Ecología, Pontificia Universidad Católica de Chile, Santiago, Chile
* marblasa@gmail.com

Abstract

Fishing is a major source of human impact, reducing density and size of a wide range of exploited species in comparison to areas exhibiting strong regulations (no-take and partially protected areas, including Territorial Use Rights for Fisheries, TURFs). Since size and density might have important consequences on reproduction, and therefore natural re-seeding, we monitored adult size, density and potential fecundity of the keyhole limpet (*Fissurella latimarginata*) and the red sea urchin (*Loxechinus albus*) in areas under two fishing regimes (TURFs and Open Access Areas, OAAs). Analyzing the distribution of suitable habitats, we predict spatial patterns of potential egg production, to identify reproductive hotspots along the central coast of Chile. The current system of TURFs in central Chile showed higher potential egg production of *F. latimarginata* and of *L. albus* than expected under a complete OAAs scenario (67 and 52% respectively). Potential egg production showed more than a twofold reduction when the complete TURFs scenario was compared against complete OAAs condition in both species. Individual size and density explained between 60% and 100% of the variability in potential egg production, suggesting the importance of the enhancement of both biological variables in TURFs in Chile. Potential egg production for both species in the northern part of the studied domain was higher due to the combined effect of (a) suitable habitat and (b) concentration of TURFs. Our results suggest that partially protected areas, such as TURFs can significantly enhance the production of propagules that could seed exploited areas.

Citation: Blanco M, Ospina-Álvarez A, González C, Fernández M (2017) Egg production patterns of two invertebrate species in rocky subtidal areas under different fishing regimes along the coast of central Chile. PLoS ONE 12(5): e0176758. https://doi.org/10.1371/journal.pone.0176758

Editor: James P. Meador, Northwest Fisheries Science Center, UNITED STATES

Received: March 15, 2016

Accepted: April 14, 2017

Published: May 8, 2017

Data Availability Statement: All relevant data are within the paper and its Supporting Information files.

Funding: We thank Fundación Mutua Madrileña (MB), Fondecyt 3150425 (AO), Fondecyt 1130976 (MF) and the Iniciativa Científica Milenio CCM RC 1300004 from the Ministerio de Economía, Fomento y Turismo de Chile.

Competing interests: The authors have declared that no competing interests exist.

Introduction

Coastal zones are among the most impacted ecosystems of the world [1]. Overfishing in particular is one of the most pervasive sources of human impact, that can reduce abundance of target species and propagate effects to the whole community [2–4]. In fact, 63% of assessed stocks and 82% of unassessed stocks currently require rebuilding [5,6]. This situation is of major concern in fisheries that are critically important for diversity and food security, such as artisanal fisheries, which currently concentrate approximately 50% of the world catch and 90% of the fishers worldwide [7]. Therefore, there is an urgent need to improve fisheries management in general and artisanal coastal fisheries in particular. The tools to advance in management of artisanal fisheries range from new ecosystem approaches, total allowable catches as well as spatial management including limited-entry areas (e.g., Territorial Use Rights for Fisheries; TURFs) and permanent fishing bans (e.g., Marine Reserves) [8–10].

The benefits of the permanent fishing bans established in no-take areas have been widely reported, showing higher abundance [11–13], larger adult size of exploited species [14,15]; and also higher species richness [16] in comparison with background areas [17–19]. Partially marine protected areas, including limited-entry TURFs, show in many cases similar patterns than no-take areas in these relevant biological variables (species richness, abundance and adult size of target species) [20, 21], conferring clear benefits over open access or background areas. These results are critically important because very often the implementation of no-take areas generates social resistance [21,22]. Thus, although no-take areas cannot be completely replaced by partially marine protected areas [21], the latter can offer the opportunity of protection enhancing stakeholders' compromise and secondarily improving our understanding on ecosystems functioning [23–25].

Understanding the performance of fully or partially protected marine areas (no-take areas, TURFs) beyond the limits of the reserve is essential to really show the benefits for fishing grounds recovery and sustainable use of marine resources [19,26–28]. Spill over of exploitable biomass from no-take reserves clearly benefits fisheries [29], and may help gain support for protected areas among stakeholders [30]. Additionally, larger sizes and increased abundances of exploited species inside both fully [18,26] and partially [20] protected areas suggest that either process can enhance reproductive potential in protected areas in general. In fact, empirical evidence predicts between 2 to 5 times higher egg production in protected areas with respect to fished areas, based on a 30% larger commercial size abalone [31]. For snapper (*Pagrus auratus*) relative egg production was estimated to be 18 times higher in no-take reserves than in adjacent fished areas [32]. A 3-times greater gonad production per unit of area was also estimated in mussels inside marine reserves in South Africa, based on the combined effects of increased density and larger size individuals [33]. However, in sites exhibiting larger size individuals inside protected areas, but where density was not amplified, gonad production per unit of area was not higher, suggesting the importance of enhanced density on egg production. Egg production is also expected to change depending on the time elapsed since protection was established, allowing increase in size and abundance of exploited species. In fact, empirical evidence show an annual increase in egg production of lobster (*Jasus edwarsii*) after protection ranging between 4.8% and 9.1% in no-take reserves in New Zealand [34]. However, all these evidences do not account for the direct influence of protection on reproductive investment, as the analyses do not separate the relative importance of the indirect effect of enhancement of size and abundance of adult individuals on reproduction, from the direct influence of protection on gonad investment [35]. Direct estimates of gonad weight in scallops (*Pecten maximus*) suggest that there can be an additional benefit of protection, directly on gonad investment, with gonad weight ranging between 20% and 25% higher in protected areas [36]. Therefore, it is important to assess the relative importance of protection on adult size, density and gonad investment in enhancing reproductive potential of protected areas, since it is essential to understand (a) the influence of fishing effort on reproduction of exploited species, and (b) prospective spillover effects on background areas and networks of marine protected areas. It is also relevant to advance our understanding of the contribution of partially protected areas, such as TURFs that are growing globally, on biological variables beyond diversity, size or abundance.

The coast of central Chile is a good model to examine the influence of relevant, but poorly addressed biological variables, such as egg production, and also the most important variables influenced by human impact (size and density) in determining egg production. First, because the coast of Chile is one of the most productive coastal ecosystems of the world, yet, it is heavily impacted by artisanal fisheries, targeting a large number of fish, invertebrates and algae in rocky shores [37]. Second, because there is a mosaic of human impact, or fishing regimes, that includes few fully protected areas and a system of partially protected areas by fishers (TURFs), interspaced with unregulated fishing zones. Finally, because there is a need to advance in management and conservation plans for coastal areas, identifying the most relevant zones for propagules production [38], and the main determinants. Therefore, the main goal of this study was to develop a spatial model to predict potential egg production along the coast of central Chile, to analyze (a) the influence of human impacts on propagules production; and also (b) the most critical determinant of potential egg production. We chose two economically and ecologically valuable rocky reef species as a model, the keyhole limpet, *Fissurella latimarginata*, and the red sea urchin, *Loxechinus albus* both targeted by artisanal fishers. Thus, our results can have local relevance, but globally can also inform about the most important variables explaining egg production, and the potential losses in reseeding as a consequence of fishing.

Material and methods

The study system

The artisanal benthic fishery operating in Chile is characterized by a TURF system that was experimentally established in the early 90s, and formally implemented in the late 90s [37]. Under this TURF system, the fishers are organized within unions that administer a TURF and are obligated to conduct regular stock assessments. Fishers administering a TURF maintain a surveillance system and have exclusive fishing access to that TURF. Each year the fisher unions independently decide on the best local strategy to harvest their assigned quotas, following other nationwide regulations (such as minimum legal size, reproductive bans). However, the majority of the traditional fishing grounds is not under a TURF system and operates as traditional open access areas [20]. In open access areas (OAAs), fishers holding a fishing license can extract benthic resources following national regulations (e.g., minimum legal size, reproductive bans). The fishing licenses restrict fishing activities to regional levels (at the scale of hundreds of kilometers). Minimum legal size and reproductive bans also regulate exploitation of benthic resources in OAAs, but enforcement is poor. Several species are targeted by the artisanal benthic fisheries in central Chile. However, the primary target resources include locos (*Concholepas concholepas*), keyhole limpets (a set of *Fissurella* species) and sea urchins (*Loxechinus albus*) [37].

In spite of the increase in the fraction of the ocean protected in Chile, the coast of central Chile is exhibiting high influence of human impact, and low number (and surface area) of protected areas [37]. For this reason, the co-management system based on Territorial Use Rights for Fisheries (TURF) is seen as critical for management and conservation [39]. First, abundance of benthic resources is higher inside TURFs than in background exploited areas [20]. There is also evidence of larger sized individuals of exploited species inside TURFs [20, 40,41,42]. Moreover, TURFs in central Chile show similar patterns of abundance and adult size of exploited species than no-take areas [20]. Second, social resistance to TURFs is not comparable with no-take areas. In fact, there are only 4 marine protected areas along more than 1000 km of coastline in the most populated region of Chile (from 30˚S to 36˚S); less than

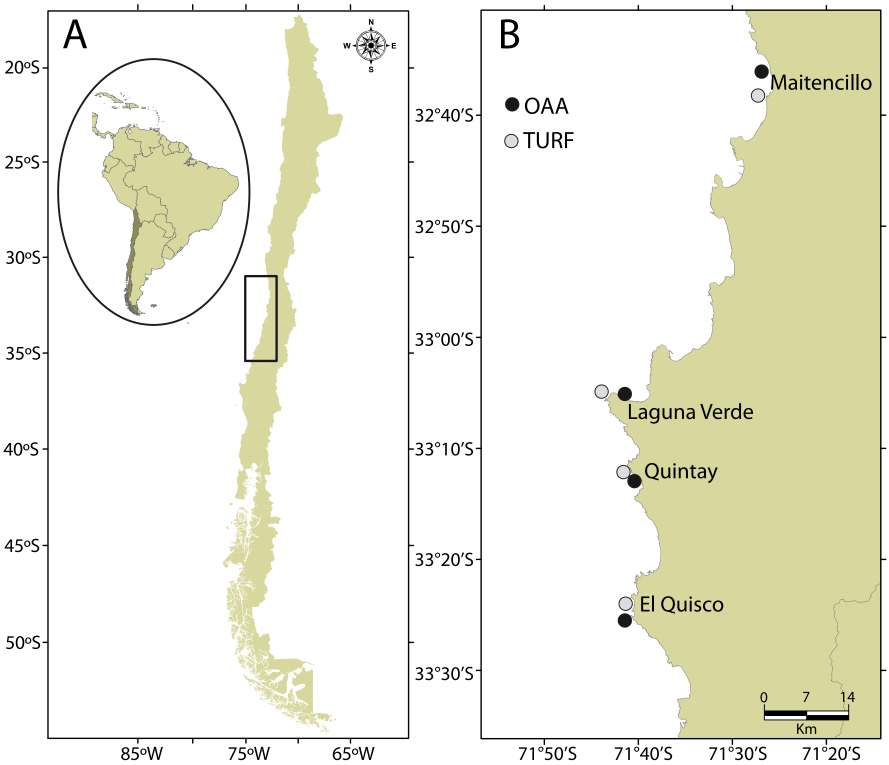


Fig 1. Map of the study area. Maps of Chilean coast showing (A) the study region and (B) the sampling sites where direct collection of organisms was conducted. Fishing regimes are indicated in black circles (Open Access Areas; OAAs) and gray circles (Territorial Use Rights for Fisheries; TURFs).

https://doi.org/10.1371/journal.pone.0176758.g001

0.001% protection of the coastal area. In contrast, in the same region there are 97 operative TURFs, covering 30% of the coastal area. Therefore, the TURF's system confers the opportunity to generate a network of partially protected areas that can serve both, together with other fully protected areas, to sustainable exploitation and to meet conservation goals [20]. For this reason, it becomes important to assess the value of TURFs beyond their limits (e.g., potential egg production) and also, to evaluate what variable enhanced in protected areas (size, abundance, gonad investment) is the most critical determinants of potential egg production.

The predictions of our study cover the coast of central Chile, specifically between 31.57˚S and 36.00˚S (Fig 1A). In this region there are 75 operative TURFs, covering 31% of coastal area. Along this 795 km of coastline, we selected four sites concentrated between 32.61˚S and 33.50˚S, were samples were conducted to assess adult size, density and gonad investment. At each site, we selected areas with different fishing regimes: areas limiting fishing access and catches (TURFs) and areas where fishers are not restricted to enter and fish (OAAs). We sampled eight sites, four TURFs and four adjacent OAAs (Fig 1B). At each site, we measured size and density (individuals/m^2) of both species by direct sampling, during 2012, and estimated potential fecundity (oocytes/female). Using this information, we estimated potential egg production, based on potential fecundity per unit of area per fishing regime.

Ethics statement

The Chilean Navy and the Undersecretary of Fishing granted all necessary permission and permits to conduct the described fieldwork. Non-destructive manipulation of endangered or protected species was required.

Estimates of potential fecundity

Potential fecundity, defined as the number of oocytes in the ovary (per female) [41], was estimated. Individuals were collected at the beginning of the reproductive seasons (August—September) reported for *F. latimarginata* [42] and for *L. albus* [43]. A total of 88 females of keyhole limpets and 75 females of sea urchins, larger than minimum size of reproduction (6 cm and 7 cm, respectively), were collected by professional divers. Specimens were frozen immediately and, later, length and wet gonad weight were recorded for each female. A small weighed fragment (0.2 ± 0.09 mg; mean = 0.119 mg) of the gonad was taken from the ovaries of each female, and preserved in 70% alcohol. Oocytes from each fragment were separated from the ovarian membrane through a washing process [44]. We used a 55 um mesh sieve to collect oocytes, which were then transferred to 100 ml vessel. A minimum of 3 aliquots of 3 ml were used to count the oocytes under the microscope. The number of oocytes was then expressed as the number of oocytes per mg of ovary. Oocytes per female were then calculated extrapolating the count to the total ovary weight. Thus, we were able to estimate potential fecundity, associated to the size distribution of each fishing regime, using the extracted model coefficients (α, intercept) and (β, slope) for the potential fecundity-size relationship described by the following regression model (Eq 1).

$$F = \alpha * e^{L * \beta} \tag{1}$$

Where F is the potential fecundity (oocytes/female) and L is the size of each individual. Size was measured as peristomial length for keyhole limpets and diameter without spines for sea urchins. Mean potential fecundity per fishing regime was estimated as the average potential fecundity from all individuals of the sample characterizing each fishing regime, for each site.

To estimate potential egg production between fishing regimes, defined as the potential of a given site to produce eggs (oocytes) taking into account density and individual potential fecundity, densities of keyhole limpets and sea urchins were estimated using a visual census. We sampled four 50 m transects per site, positioned perpendicular to the coastline from 3 to 15 m depth, separated 30 m apart from each other. All individuals of both species were counted on a 2 m width strip along transect. We used existing data to determine the fraction of *F. latimarginata* from the remaining *Fissurella* species in the sample (see below). To estimate densities per square meter, counts per transect was summed across all stations. Finally, density per square meter was estimated.

In order to characterize size in each fishing regime professional divers took a sample ranging from 29 to 39 keyhole limpets per site (252 keyhole limpets total for fishing regime), and between 17 and 20 sea urchins per site (144 sea urchins total for fishing regime). An exception was El Quisco OAA were only 10 urchins were collected. Total length was measured. Using this sampling we estimated the proportion of females (R) sexing individuals at the laboratory by a dissecting procedure (N = 196 keyhole limpets and N = 144 urchins). We relied on a large sampling conducted in 11 sites in our study region, between 1999 and 2009, to estimate (a) the proportion of *F. latimarginata* (K) and (b) the proportion of mature individuals (S). We considered mature individuals those that have reached the minimum size of reproduction (6 cm for *F. latimarginata* and 7 cm for *L. albus*). Based on size frequency distribution obtained from 9,245 individuals of *F. latimarginata* and 9,643 individuals of *L. albus*, we obtained the fraction of mature individuals. Based on a sample of 22,456 individuals, we estimated the fraction of *F. latimarginata*.

Using Eq 1, we obtained the mean potential fecundity in each site. Density, size, potential fecundity and mean potential egg production were compared between fishing regimes. We considered fishing regime as a fixed factor with two levels TURFs and OAAs. These comparisons were conducted using a Generalized Linear Model (GLM) analysis. For the variable density, we used quasipoisson family error distribution. For the variable potential fecundity and potential egg production we used inverse gaussian and for size we used gaussian family error distribution. The choice of the most appropriate link function and error distribution was made based on residual analyses. We tested the goodness of fitted model with a Chi-Squared test based on residual deviance and degrees of freedom (significance level 0.05). All the statistical analysis were done using R software, version (3.1.3) [45].

Potential egg production

To determine the spatial variability in potential egg production in relation to fishing regimes, we used the following equations:

$$P_{F.latimarginata} = F * D * R * S * K \tag{2}$$

$$P_{L.albus} = F * D * R * S \tag{3}$$

Where P is the potential egg production (oocytes/m^2), F is the potential fecundity (oocytes/female) from Eq 1, D is the density (individuals/m^2), R is the proportion of females, S is the proportion of mature individuals and K (parameter used for *F. latimarginata* in Eq 2), is the proportion of *F. latimarginata* in the sample of keyhole limpets. Parameters R, S and K were assumed fixed while potential fecundity (F) and density (D) varied spatially depending on available rocky shore habitat and fishing regime. Spatial variability in F and D of Eqs 2 and 3, derive from Eqs 4 to 6.

Spatial data

In order to account for spatial variability of rocky habitat and fishing regimes (TURFs and OAAs) along the coast of central Chile, we developed an indicator of the condition of small fractions of the coast (grids of 2 latitudinal kilometers). Condition was determined based on availability of suitable habitat and fishing regime. First, the coastline was obtained from digitalized Chilean Military Geographic Institute (IGM) charts 1:250,000. Then, we characterized the habitat type using high-resolution satellite photography. Second, we characterized the fishing regime (TURFs and OAAs) based on the presence or absence of TURFs in each coast fragment, using data available from SUBPESCA. All digitalization was conducted with the software ArcGis 9.3. The results were expressed as a percentage of total coast length containing suitable habitat and TURFs in a grid of two latitudinal kilometers. Third, a scaling factor between fishing regime (Ratio TURF/OAA) was estimated to account for differences in density (D) and potential fecundity (F) between fishing regimes (TURFs and OAAs). The factor was calculated for each parameter (D and F) for each species. Finally, we created an indicator to associate the scale of increase in density or potential fecundity (Ratio TURF/OAA) to the percentage of suitable habitat (rocky shores) associated to restricted areas (pTURF). This indicator of spatial variability (Spatial Var) was calculated considering the Ratio TURF/OAA for density (D) and potential fecundity (F), for 134 coastal units (2 latitudinal km grid) along the study area (Eq 4).

$$Spatial\ Var = (pTURF * Ratio\ (TURF/OAA)) + (pR - pTURF) \tag{4}$$

Where pR is the percentage of coastline with rocky shore habitat. In order to obtain the indicator of spatial variability (Spatial Var) for each coastal unit, a linear regression between the indicator (Spatial Var) and the variables of interest (potential fecundity and density) was estimated for the 8 grids containing the areas sampled in our study. Then, we used these relationships to predict potential fecundity (F) and density (D) for the 134 units of our regional domain.

$$D = Spatial\ Var * \beta_D \tag{5}$$

$$F = Spatial\ Var * \beta_F \tag{6}$$

Where *Spatial Var* is the value obtained by Eq 4, β_D is the slope of the regression between density (D) and Spatial Var, and β_F is the slope of the regression between potential fecundity (F) and Spatial Var. When Spatial Var is 0, the value of density, and therefore potential fecundity, is always 0 (not suitable rocky habitat). Using all these estimates, we were able to calculate potential egg production (P) for the study area:

$$P_{F.latimarginata} = (Spatial\ Var * \beta_F) * (Spatial\ Var * \beta_D) * R * S * K \tag{7}$$

$$P_{L.albus} = (Spatial\ Var * \beta_F) * (Spatial\ Var * \beta_D) * R * S \tag{8}$$

In order to determine the influence of available rocky habitat and fishing regime on predicted potential egg production, we compared the predicted potential egg production (dependent variable), in 134 coastal units, across the values of percentage of coastline with rocky habitat (pR) and the percentage of coastline with rocky habitat associated to TURFs areas (pTURF) (both as independent variables). These comparisons were conducted using a GLM analysis with a quasipoisson family error distribution. Furthermore, to evaluate the influence of human impacts on propagules production we compared two scenarios: (a) a full restricted access scenario against a full open access and (b) the current system of TURFs against a full open access scenario.

In order to define the most critical determinant of potential egg production, we compared the mean egg production per site (dependent variable), across mean density and mean size (independent variables) obtained in each site using an ANCOVA analysis.

Results

Density and potential fecundity

The relationship between potential fecundity (F) and total length (L) was described by an exponential model function for both species, showing the expected increase of potential fecundity with size. Estimated potential fecundity was F = 548,500 (258,100) $e^{L*0.31\ (\pm 0.05)}$ (df = 87, p-value < 0.01) for keyhole limpet and F = 1,745 (1,338) $e^{L*0.74\ (\pm 0.08)}$ (df = 75, p-value < 0.01) for sea urchin.

Table 1. Generalized linear models. Statistical results of the generalized linear models (GLM) applied to density, individual size, potential fecundity and potential egg production, across two fishing regime: TURFs (Territorial Use Rights for Fisheries) and OAAs (Open Access Areas).

A. *Fissurella Latimarginata*					
Model: glm (Density ~ Fishing Regime, family = quasipoisson)					
Deviance Explained: 18.47%					
	Df	Deviance	Resid. Df	Resid. Dev.	Pr (>Chi)
NULL			31	0.95	
Fishing Regime	1	0.20	30	0.75	0.01
Model: glm (Size ~ Fishing Regime, family = gaussian)					
Deviance Explained: 14.20%					
	Df	Deviance	Resid. Df	Resid. Dev.	Pr (>Chi)
NULL			251	440.99	
Fishing Regime	1	62.64	250	378.36	$1.25*10^{-10}$
Model: glm (Potential Fecundity ~ Fishing Regime, family = inverse.gaussian)					
Deviance Explained: 4.82%					
	Df	Deviance	Resid. Df	Resid. Dev.	Pr (>Chi)
NULL			251	$2.87*10^{-4}$	
Fishing Regime	1	$1.84*10^{-5}$	250	$2.73*10^{-4}$	$7.90*10^{-5}$
Model: glm (Potential Egg Production ~ Fishing Regime, family = inverse.gaussian)					
Deviance Explained: 57.71%					
	Df	Deviance	Resid. Df	Resid. Dev.	Pr (>Chi)
NULL			7	$9.43*10^{-4}$	
Fishing Regime	1	$5.44*10^{-4}$	6	$3.98*10^{-4}$	0.005
B. *Loxechinus albus*					
Model: glm (Density ~ Fishing Regime, family = quasipoisson)					
Deviance Explained: 6.93%					
	Df	Deviance	Resid. Df	Resid. Dev.	Pr (>Chi)
NULL			15	1.99	
Fishing Regime	1	0.13	14	1.86	0.31
Model: glm (Size ~ Fishing Regime, family = gaussian)					
Deviance Explained: 1.47%					
	Df	Deviance	Resid. Df	Resid. Dev.	Pr (>Chi)
NULL			143	214.90	
Fishing Regime	1	3.17	142	211.73	0.14
Model: glm (Potential Fecundity ~ Fishing Regime, family = inverse.gaussian)					
Deviance Explained: 0.17%					
	Df	Deviance	Resid. Df	Resid. Dev.	Pr (>Chi)
NULL			143	$2.22*10^{-6}$	
Fishing Regime	1	$3.64*10^{-9}$	142	$6.21*10^{-6}$	0.63
Model: glm (Potential Egg Production ~ Fishing Regime, family = inverse.gaussian)					
Deviance Explained: 13.87%					
	Df	Deviance	Resid. Df	Resid. Dev.	Pr (>Chi)
NULL			3	$2.13*10^{-5}$	
Fishing Regime	1	$2.96*10^{-6}$	2	$1.83*10^{-5}$	0.43

https://doi.org/10.1371/journal.pone.0176758.t001

Fishing regime showed a significant effect on mean size (L), density (D), potential fecundity (F) and potential egg production (P) of *F. latimarginata* (p-value always < 0.05) (Table 1A). On average, density of keyhole limpets was 65% higher in TURFs compared with OAAs (Fig 2A). Size was also significantly different between fishing regimes, although the change was

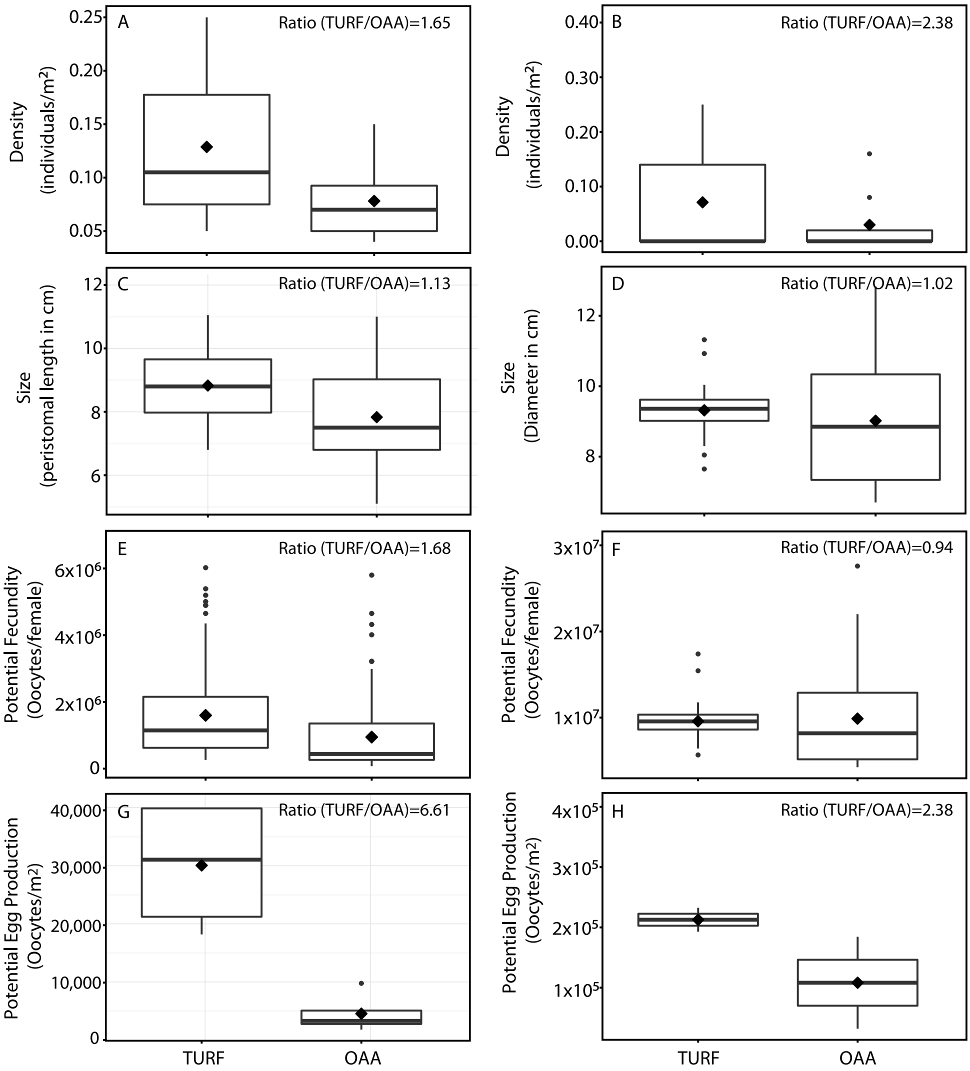


Fig 2. Biological variables between fishing regimes. Box plots showing density, size, potential fecundity and potential egg production in areas under different fishing regimes: Territorial Use Rights for Fisheries (TURF) and Open Access Areas (OAAs; not limiting the entry of fishers). The number in the right corner in each plot indicates the ratio between fishing regimes (TURF/OAA) for each variable. Black diamonds' indicate mean: (A) *Fissurella latimarginata* density; (B) *Loxechinus albus* density; (C) *F. latimarginata* size; (D) *L. albus* size; (E) *F. latimarginata* potential fecundity; (F) *L. albus* potential fecundity; (G) *F. latimarginata* potential egg production; and (H) *L. albus* potential egg production.

https://doi.org/10.1371/journal.pone.0176758.g002

smaller (13%; Fig 2C). Potential fecundity was also 68% greater in TURFs in comparison to OAAs. Similarly, potential egg production was six-fold higher in TURFs than in OAAs (Fig 2E and 2G, Table 1). In contrast, no significant effect of fishing regime on density, size, potential fecundity and potential egg production was observed for *L. albus* (Table 1B). Although density of sea urchins in TURFs appeared to be two-fold higher than in OAAs, the large variability observed among sites in this species did not yield statistical differences (Fig 2B). Sea urchin size was not significantly different between fishing regimes (Fig 2D, Table 1B). No difference in potential fecundity and high variability were also observed between TURFs and OAAs (Fig 2F, Table 1). Similarly, the influence of fishing regime on potential egg production was not significant despite an apparent two-fold larger potential egg production in TURFs (Fig 2H, Table 1).

Spatial variability in potential egg production

The spawning fraction (R) for *F. latimarginata* was 0.48 and for *L. albus* was 0.44. The fraction of mature individuals (S) was 0.84 for *F. latimarginata* and 0.69 for *L. albus*. The fraction of *F. latimarginata* in the keyhole limpet samples (K) was 0.43 (S1 Table). These estimates were used as constants in Eqs 2 and 3. The linear models selected to describe the relationship between density (D) and potential fecundity (F) against the indicator Spatial Var were statistically significant (Table 2).

Using the coefficients estimated by the linear regressions in the study sites, P (potential egg production) was predicted for the 134 units in the regional domain of our study as follows:

$$P_{F.latimarginata} = (Spatial\ Var * 11,977) * (Spatial\ Var * 0.00108) * 0.48 * 0.84 * 0.43 \qquad (9)$$

$$P_{L.albus} = (Spatial\ Var * 123,780) * (Spatial\ Var * 0.00035) * 0.44 * 0.69 \qquad (10)$$

In the study zone, 379 of 795 km of coastline (47.7%) between 31.57˚S and 36.00˚S showed rocky habitat suitable for each species under study. We estimated that 21.27% (169 km) of

Table 2. Linear regressions. Linear models relating density and potential fecundity, both dependent variables and Indicator (Spatial Var; independent variable). Linear regressions were used to obtain the relationship between the indicator (Spatial Var) and the variables studied (potential fecundity and density).

A. Fissurella latimarginata				
Model: lm (Density ~ Spatial Var- 1)				
$R^2 = 0.86$				
	Estimate	Std. Error	T value	Pr (>| t |)
Slope (β_D)	$1.08*10^{-3}$	$1.52*10^{-4}$	7.17	$1.8*10^{-4}$
Model: lm (Potential Fecundity ~ Spatial Var—1)				
$R^2 = 0.56$				
	Estimate	Std. Error	T value	Pr (>| t |)
Slope (β_F)	11977	3592	3.33	0.01
B. Loxechinus albus				
Model: lm (Density ~ Spatial Var—1)				
$R^2 = 0.87$				
	Estimate	Std. Error	T value	Pr (>| t |)
Slope (β_D)	$3.52*10^{-4}$	$6.53*10^{-5}$	5.39	0.01
Model: lm (Potential Fecundity ~ Spatial Var—1)				
$R^2 = 0.88$				
	Estimate	Std. Error	T value	Pr (>| t |)
Slope (β_F)	123780	15395	8.04	$8.83*10^{-5}$

https://doi.org/10.1371/journal.pone.0176758.t002

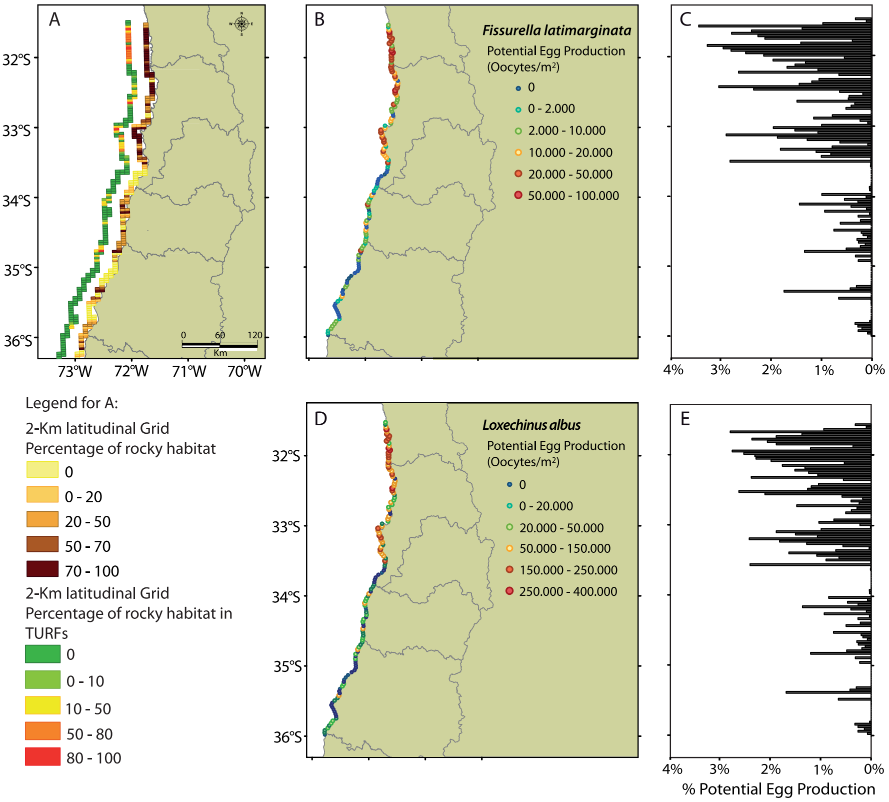


Fig 3. Spatial distribution of habitat, restricted access areas and potential egg production. Spatial maps showing (A) percentage of coastline with rocky habitat and restricted access (Territorial Use Rights for Fisheries, TURFs) and (B, D) predicted potential egg production (oocytes/m^2) along a latitudinal gradient with a 2-km grid resolution. Plots C and E show the contribution (percentage) of oocytes/m^2 (potential egg production) of each grid to the regional (study area) production.

https://doi.org/10.1371/journal.pone.0176758.g003

coastline exhibited restricted access, distributed in 75 operative TURFs. The highest percentage of rocky habitat under TURF was found between 31.57˚S and 33.50˚S (49.94% of the coastline), while in the southern section of the study region (33.50˚S to 36.00˚S) fewer TURFs associated to suitable rocky habitat were present (27.79% of the coastline; Fig 3A).

The spatial distribution of potential egg production predicted by the model showed similar patterns for both species, driven by the distribution of suitable habitat. Suitable habitat explained 91.57% (F = 2652.60, df = 1, p<0.001) and 94.78% (F = 2788.02, df = 1, p<0.001) of total variability in potential egg production of keyhole limpets and sea urchins, respectively. The highest percentage of potential egg production occurred in the north region of studied

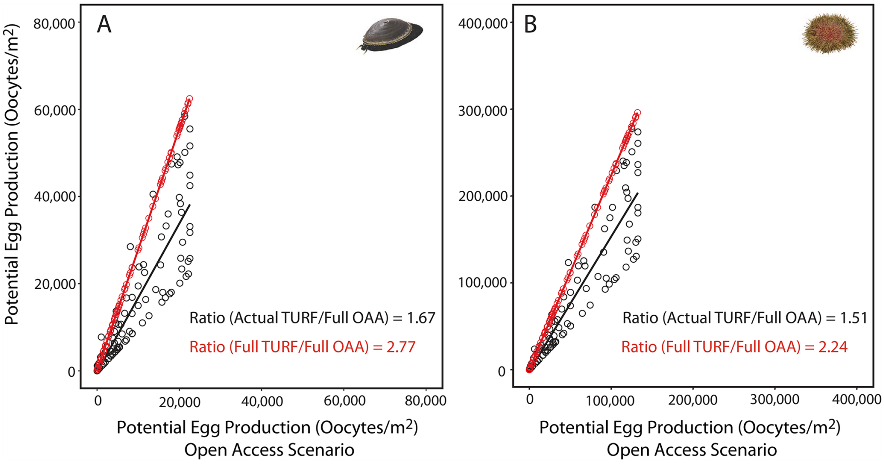


Fig 4. Influence of fishing on potential egg production. Comparison of potential egg production between the open access areas (OAAs) scenario against (a) current scenario (existing Territorial Use Rights for Fisheries, TURFs; black line and symbols) and (b) full protection (all TURFs; red line and symbols) for (A) *Fissurella latimarginata* and (B) *Loxechinus albus*. The numbers in the lower right corner in each plot show the ratio in potential egg production from the two scenarios.

https://doi.org/10.1371/journal.pone.0176758.g004

domain, where about 80% of potential egg production of both species were concentrated between 31.57˚S and 33.50˚S (Fig 3). In the southern region of the studied domain (33.50˚S to 36.00˚S), where suitable rocky habitat is present only along 24% of the coastline, egg production was lower. However, fishing regime influenced potential egg production in suitable habitats. The system of TURFs in our study region increased potential egg production of *F. latimarginata* by 67% against the predicted production under a complete OAAs scenario (Fig 4A). The increase was smaller for *L. albus* (52%; Fig 4B). Our predictions also showed the enormous influence of fishing in reducing potential egg production of both species. Potential egg production showed more than a twofold reduction when the complete TURFs scenario was compared against complete OAAs condition in both species (Fig 4A and 4B).

Size explained a similar proportion of the variability in potential egg production in both species (keyhole limpet: 23.09%, sea urchin: 20.22%; Table 3). However, the contribution of density to explain the variability in egg production potential was different between both species. Density explained 37.26% of the total variability in potential egg production in keyhole limpets and 79.77% in sea urchins (Table 3).

Discussion

In a global context, our main results show the influences of TURFs in enhancing size and density of exploited species and the direct consequences of enhanced size and density on potential egg production, thereby suggesting an important role of partially protected areas in producing propagules to seed exploited areas. Our results show further influences of management regime, as potential egg production was up to 200% lower in open access areas. Finally, although we did not find consistent results for both species we were able to determine enhanced potential

Table 3. Influence of size and density on potential egg production. Statistical results of the effect of density and size on potential egg production.

A. *Fissurella latimarginata*

Model: ANCOVA (Potential Egg Production ~ Density + Size)

	Df	Sum Sq	Mean Sq	Pr (>| F |)	Exp Var (%)
Density	1	$6.62*10^{8}$	$6.62*10^{8}$	0.08	37.26
Size	1	$4.10*10^{8}$	$4.10*10^{8}$	0.15	23.09
Residuals	5	$7.04*10^{8}$	$1.42*10^{8}$		

B. ***Loxechinus albus***

Model: ANCOVA (Potential Egg Production ~ Density + Size)

	Df	Sum Sq	Mean Sq	Pr (>| F |)	Exp Var (%)
Density	1	$1.86*10^{10}$	$1.86*10^{10}$	$1.47*10^{-3}$	79.77
Size	1	$4.72*10^{9}$	$4.72*10^{9}$	$2.92*10^{-3}$	20.22
Residuals	1	$9.92*10^{4}$	$9.92*10^{4}$		

https://doi.org/10.1371/journal.pone.0176758.t003

egg production. Locally, our results are relevant for identifying the main regions along the coast of central Chile that exhibit higher potential for egg production in two important, exploited resources, the keyhole limpet (*F. latimarginata*) and the red sea urchin (*L. albus*).

In accordance with published evidence, our results show the general benefits of protection enhancing relevant biological variables, such as abundance and/or adult size inside TURFs boundaries [20,21]. Although fully protected areas offer greater benefits than partially protected areas (74% greater density and 30% larger sizes, [21]), partially protected areas, such as TURFs, also generally showed significant effects in these two biological variables. Our results comparing TURFs and OAAs show similar patterns in density and size of exploited resources as expected from a synthesis of empirical studies comparing these biological variables in partially protected and background areas across a range of geographic locations worldwide (on average, 36% higher density, and 10% larger sizes in protected areas than in background areas [21]). We found that sizes were between 2% and 13% larger, and density between 65% and 238% higher (although non-significant for sea urchin) in TURFs than in open access areas. The large variability in density of sea urchins both in TURFs and open access areas may have precluded us from identifying a clear and significant pattern of higher density in TURFs for both species. Previous studies have also reported a lower impact of protection on *L. albus*, and larger variability in abundance, probably related to the patchy distribution of suitable microhabitats [20]. *L. albus* is predominantly associated with highly wave exposed zones, where they are frequently found forming aggregations.

Our results also suggest that the enhanced biological variables can potentially amplify the benefits of protection outside the boundaries of protected areas by increasing individual production of dispersive propagules [17–19]. First, the models we used to analyze potential fecundity showed an exponential increase in fecundity with size in both species. Second, the 13% differences in keyhole limpets' size in TURFs compared to OAAs produced a 68% greater potential fecundity of females. The size increase between TURFs and OAA is smaller than the average 30% increase in size reported in a worldwide analysis comparing individual size between no-take and open access areas [18]. Since small changes in size can have tremendous impact on potential fecundity, even the contribution of partially protected areas (10% larger sizes) to potential egg production through size enhancement of reproductive individuals might be substantial [18]. Worldwide evidence shows that on average, the greater sizes in no-take areas, up to 200% larger than in partially protected areas [18], can disproportionally influence dependent variables such as potential egg production. Therefore, it is important to further explore the relevance of enhanced size on potential fecundity in fully and partially protected areas. We recognize that effective larval spillover requires a broader approach, including other factors not considered in this study, from fertilization success to processes affecting planktonic larval phases and local adaptation of early recruits [46,47]. However, enhanced fertilization success can also be predicted in areas of higher population density [48] such as TURFs or no-take areas. It is also important to keep in mind the variability among species. Our analysis also suggests that differences in mean size of 2% between TURFs and OAAs of sea urchins do not produce significant differences in average potential fecundity.

The relevance of density in determining gonad production per unit of area has been clearly shown in the literature [32–34]. However, the interplay between the combined effects of density and size is less clear and our results did not yield clear conclusions in this direction. In the case of keyhole limpets, for which density and size were enhanced in TURFs areas, a significant difference in potential egg production was recorded. The comparison between the two species showed that potential egg production of *F. latimarginata* increased by protection 277% more than *L. albus* due to the combined influence of larger size and higher densities in TURFs. In spite of the fact that we did not find significant differences in sea urchin density and size associated to fishing regime, the spatial variability in potential egg production of sea urchin is mainly explained by density (80%) and secondly by size (20%). Size differences ranging between 2 and 13% between open access and TURFs areas seem to explain about 20% of the variability in potential egg production. Thus, our results suggest that density might have a larger influence on variability in potential egg production than individual size. However, a third factor to consider is the direct influence of protection on reproductive investment, and therefore egg production. So far, most evidence is insufficient for determining the relative importance of protection indirectly on adult size and density, and directly on gonad investment in enhancing reproductive potential in protected areas. Direct estimates of gonad weight in scallops (*Pecten maximus*) suggest that there can be an additional benefit of protection directly on gonad investment, with differences of gonad weight ranging between 20 and 25% in protected areas [36]. Therefore, it is important to increase the available information in general, to assess the direct influence of protection on gonad production. Further explorations, however, are needed to understand the most relevant determinants of egg production in protected areas, and to advance in strategies to enhance the benefits of protection outside the boundaries of protected areas (e.g., placing protected areas in sites assuring spill over, based on circulation patterns).

Our results show that the system of TURFs areas in our study region enhanced potential egg production of *F. latimarginata* by 67% in comparison to a complete open access scenario. In the case of sea urchins, a 52% greater potential egg production was estimated. Although a similar trend towards increasing potential egg production has been observed in other invertebrate species [31,33,34], the magnitude of the change is substantially different. Empirical evidence predicts between 2 to 5 times greater egg production in pink abalone (*Haliotis corrugata*) [31]. A 10% increase in egg production of lobster (*Jasus edwarsii*) per year after closure was estimated, suggesting a 4 fold increase over 15 years (average age of the partially protected areas studied here). We relate the smaller changes in the two species studied here to the fact that the protected areas used in this study are also fishing areas (partially protected). Consistently, the comparison of our results of egg production against studies conducted with invertebrates in no-take areas in other regions show that fully protected areas can provide higher benefits than partially protected areas, such as TURFs. However, partial protection may be the only possible form of protection in highly populated regions [38], and can still have significant positive influence in potential seeding. In our case, the influence of fishing is so high, that a 277% greater potential egg production of *F. latimarginata* can be expected between a complete OAAs scenario in comparison with a TURFs scenario. This hypothetical comparison against a no-take scenario is more similar to the studies comparing no-take areas in other invertebrate species [31,33,34]. In the case of *L. albus* a 224% increase can be expected. In our study region, we did not have enough no-take areas to include a set to compare the three levels of human impact (fishing regime) to really evaluate the influence of a gradient in fishing effort on potential egg production. However, our results suggest that the intermediate effect of TURFs can still contribute substantially to enhancing egg production in the study area and potentially contribute to seeding exploited areas.

Our results also provide insights for management and conservation at the local level. The highest percentage of potential egg production was estimated in the north region of studied domain for both species, following the distribution of suitable habitat. More than 80% of potential egg production of *F. latimarginata* and *L. albus* were produced between 31.57˚S and 33.50˚S. It is worth noticing that the northern part of our study area also concentrates more than 90% of landings of both species (SERNAPESCA 2013). This pattern may be driven not only by abundance of resources (and habitat), but also by differences in fishing pressure among sites [49]. The map of potential egg production, combined with other processes, such as coastal circulation patterns, can be a key element to design a network of partially and fully protected areas in one of the most productive, yet exploited coastal regions of the world. Our results show the relevance of focusing conservation efforts in the most important area for potential egg production, the northern domain of our study area, although it may imply restricting fishing effort. However, the potential distribution of propagules needs to be coupled with hydrodynamic and biological models would allow to improve our understanding of larval supply to different areas of the coast, by identifying source and sink populations [50].

Supporting information

S1 Table. Reproductive parameters of keyhole limpet and urchin used as fixed parameters in the potential egg production equation, (Eqs 2 and 3). S indicates proportion of mature individuals and K proportion of *F. latimarginata.*
(DOCX)

S2 Table. Keyhole limpet sex ratio data.
(CSV)

S3 Table. Urchin sex ratio data.
(CSV)

S4 Table. Data of density of individuals per transect.
(CSV)

S5 Table. Keyhole limpet potential fecundity data.
(CSV)

S6 Table. Urchin potential fecundity data.
(CSV)

S7 Table. Spatial information on a 2-km latitudinal grid.
(CSV)

S8 Table. Keyhole limpet model result.
(CSV)

S9 Table. Urchin model result.
(CSV)

S10 Table. Raw data information.
(CSV)

Acknowledgments

We thank B. Bularz, S. López, R. Calderón, M. Figueroa, C. Ruano and M. Andreu for their help in data collection and processing samples in the laboratory. S. Tapia and N. Godoy also helped conducting subtidal surveys to assess density. We also thank G.R. Finke for final revision of the manuscript and C. Styan and two anonymous reviewers for their helpful comments.

Author Contributions

Conceptualization: MB AOA MF.

Data curation: MB AOA.

Formal analysis: MB AOA.

Funding acquisition: MB AOA MF.

Investigation: MB AOA CG.

Methodology: MB AOA.

Project administration: MB AOA MF.

Resources: MB AOA MF.

Software: MB AOA.

Supervision: MB AOA MF.

Validation: MB AOA MF.

Visualization: MB AOA MF.

Writing – original draft: MB AOA MF.

Writing – review & editing: MB AOA CG MF.

References

1. Halpern BS, Walbridge S, Selkoe KA, Kappel C., Micheli F, D'Agrosa C, et al. A Global Map of Human Impact on Marine Ecosystems. Science (80-). 2008; 319: 948–952.
2. Pauly D, Christensen V, Dalsgaard J, Froese R, Torres F Jr.. Fishing down the food webs. Science. 1998. pp. 860–863. PMID: 9452385
3. Castilla JC. Coastal marine communities: trends and perspectives from human-exclusion experiments. Trends Ecol Evol. 1999; 14: 280–283. Available: http://www.ncbi.nlm.nih.gov/pubmed/10370266 PMID: 10370266
4. Myers RA, Worm B. Rapid worldwide depletion of predatory fish communities. Nature. 2003; 423: 280–283. https://doi.org/10.1038/nature01610 PMID: 12748640
5. Costello C, Ovando D, Hilborn R, Gaines SD, Deschenes O, Lester SE. Status and solutions for the world's unassessed fisheries. Science (80-). 2013; 517.
6. Worm B, Hilborn R, Baum JK, Branch TA, Collie JS, Costello C, et al. Rebuilding Global Fisheries. Science (80-). 2009; 325: 578–585.
7. FAO. Countries recognize vital role of small-scale fishers [Internet]. Rome; 2014. http://www.fao.org/news/story/es/item/234297/icode/

8. Afflerbach JC, Lester SE, Dougherty DT, Poon SE. A global survey of "TURF-reserves", Territorial Use Rights for Fisheries coupled with marine reserves. Glob Ecol Conserv. Elsevier B.V.; 2014;
9. Levin PS, Fogarty MJ, Murawski SA, Fluharty D. Integrated Ecosystem Assessments: Developing the Scientific Basis for Ecosystem-Based Management of the Ocean. PLoS Biol. 2009; 7: e1000014.
10. Freire J, García-Allut A. Socioeconomic and biological causes of management failures in European artisanal fisheries: The case of Galicia (NW Spain). Mar Policy. 2000; 24: 375–384.
11. Shears NT, Grace RV, Usmar NR, Kerr V, Babcock RC. Long-term trends in lobster populations in a partially protected vs. no-take Marine Park. Biol Conserv. 2006; 132: 222–231.
12. Denny CM, Willis TJ, Babcock RC. Rapid recolonisation of snapper Pagrus auratus: Sparidae within an offshore island marine reserve after implementation of no-take status. Mar Ecol Prog Ser. 2004; 272: 183–190.
13. Aburto-Oropeza O, Erisman B, Galland GR, Mascareñas-Osorio I, Sala E, Ezcurra E. Large Recovery of Fish Biomass in a No-Take Marine Reserve. Browman H, editor. PLoS One. 2011; 6: e23601. https://doi.org/10.1371/journal.pone.0023601 PMID: 21858183
14. Castilla JC, Durán LR. Human exclusion from the rocky intertidal zone of central Chile: the effects on Concholepas concholepas (Gastropoda). Oikos. 1985; 391–399. Available: http://www.jstor.org/discover/10.2307/3565575?uid=3737784&uid=2&uid=4&sid=21103324382993
15. Edgar GJ, Barrett NS. Effects of the declaration of marine reserves on Tasmanian reef fishes, invertebrates and plants. J Exp Mar Bio Ecol. 1999; 242: 107–144.
16. Jennings S, Marshall SS, Polunin NV C.. Seychelles marine protected areas: comparative structure and status of reef fish communities. Biol Conserv. 1996; 75: 201–209.
17. Halpern BS. The impact of marine reserves: Do reserves work and does reserve size matter? Ecol Appl. 2003; 13: S117–S137.
18. Lester SE, Halpern B., Grorud-Colvert K, Lubchenco J, Ruttenberg BI, Gaines SD, et al. Biological effects within no-take marine reserves: a global synthesis. Mar Ecol Prog Ser. 2009; 384: 33–46.
19. Roberts CM, Bohnsack JA, Gell F, Hawkins JP, Goodridge R. Effects of marine reserves on adjacent fisheries. Science (80-). 2001; 294: 1920–1923.
20. Gelcich S, Fernández M, Godoy N, Canepa A, Prado L, Castilla JC. Territorial user rights for fisheries as ancillary instruments for marine coastal conservation in Chile. Conserv Biol. 2012; 26: 1005–15. https://doi.org/10.1111/j.1523-1739.2012.01928.x PMID: 22971114
21. Lester SE, Halpern BS. Biological responses in marine no-take reserves versus partially protected areas. Mar Ecol Prog Ser. 2008; 367: 49–56.
22. Murray SN, Ambrose RF, Bohnsack JA, Botsford LW, Carr MH, Davis GE, et al. No-take Reserve Networks: Sustaining Fishery Populations and Marine Ecosystems. Fisheries. 1999; 24: 11–25.
23. Wood CL, Micheli F, Fernández M, Gelcich S, Castilla JC, Carvajal J. Marine protected areas facilitate parasite populations among four fished host species of central Chile. J Anim Ecol. 2013; 82: 1276–87. https://doi.org/10.1111/1365-2656.12104 PMID: 23855822
24. Walters CJ, Hilborn R, Parrish R. An equilibrium model for predicting the efficacy of marine protected areas in coastal environments. Can J Fish Aquat Sci. 2007; 64: 1009–1018.
25. Castilla JC. Roles of experimental marine ecology in coastal management and conservation. J Exp Mar Bio Ecol. 2000; 250: 3–21. Available: http://www.ncbi.nlm.nih.gov/pubmed/10969161 PMID: 10969161
26. Gell FR, Roberts CM. Benefits beyond boundaries: the fishery effects of marine reserves. Trends Ecol Evol. 2003; 18: 448–455.
27. Halpern BS, Warner RR. Matching marine reserve design to reserve objectives. Proc R Soc Lond B. 2003; 270: 1871–8.
28. Sale PF, Cowen RK, Danilowicz B., Jones GP, Kritzer JP, Lindeman KC, et al. Critical science gaps impede use of no-take fishery reserves. Trends Ecol Evol. 2005; 20: 74–80. https://doi.org/10.1016/j.tree.2004.11.007 PMID: 16701346
29. Goñi R, Quetglas A, Reñones O. Spillover of spiny lobsters Palinurus elephas from a marine reserve to an adjoining fishery. Mar Ecol Prog Ser. 2006; 308: 207–219.
30. Russ GR, Alcala AC, Maypa AP, Calumpong HP, White AT. Marine reserve benefits local fisheries. Ecol Appl. 2004; 14: 597–606. http://dx.doi.org/10.1890/03-5076
31. Rogers-Bennett L, Haaker PL, Karpov KA, Kushner DJ. Using Spatially Areas Explicit for Data to Marine Protected Abalone in California. Conserv Biol. 2002; 16: 1308–1317.
32. Willis TJ, Millar RB, Babcock RC. Protection of exploited fish in temperate regions: high density and biomass of snapper. J Appl Ecol. 2003; 40: 214–227.

33. Pelc R, Baskett M, Tanci T, Gaines S, Warner R. Quantifying larval export from South African marine reserves. Mar Ecol Prog Ser. 2009; 394: 65–78.

34. Kelly S, Scott D, MacDiarmid AB, Babcock RC. Spiny lobster, Jasus edwardsii, recovery in New Zealand marine reserves. Biol Conserv. 2000; 92: 359–369.

35. Manríquez PH, Castilla JC. Significance of marine protected areas in central Chile as seeding grounds for the gastropod Concholepas concholepas. Mar Ecol Prog Ser. 2001; 215: 201–211.

36. Kaiser MJ, Blyth-Skyrme RE, Hart PJB, Edwards-Jones G, Palmer D. Evidence for greater reproductive output per unit area in areas protected from fishing. 2009;

37. Fernández M, Castilla JC. Marine Conservation in Chile: Historical Perspective, Lessons, and Challenges. Conserv Biol. 2005; 19: 1752–1762.

38. Tognelli MF, Fernández M, Marquet PA. Assessing the performance of the existing and proposed network of marine protected areas to conserve marine biodiversity in Chile. Biol Conserv. Elsevier Ltd; 2009; 142: 3147–3153.

39. Gelcich S, Hughes TP, Olsson P, Folke C, Defeo O, Fernández M, et al. Navigating transformations in governance of Chilean marine coastal resources. PNAS. 2010; 107: 16794–9. https://doi.org/10.1073/pnas.1012021107 PMID: 20837530

40. Castilla J, Fernandez M. Small-scale benthic fisheries in Chile: on co-management and sustainable use of benthic invertebrates. Ecol Appl. 1998; 8: S124.

41. Anger K, Moreira GS. Morphometric and Reproductive Traits of Tropical Caridean Shrimps. J Crustac Biol. 1998; 18: 823–838.

42. Brown G. DI, Gonzalez M, Lopez D, Duran L, Rivero R, Collado G, et al. Informe Final Proyecto FIP-IT/94-33. Estudio de los ciclos vitales de las especies comerciales de lapas del genero Fissurella sp, en las regiones I a X. Universidad de Valparaiso; 1997. p. 196.

43. González L, Castilla J, Guisado C. Effects of larval diet and rearing temperature on metamorphosis and juvenile survival of the sea urchin Loxechinus albus (Molina, 1782) (Echinodermata: Echinoidea). J Shellfish Res. 1987; 6: 109–115.

44. Lowerre-Barbieri SK, Barbieri LR. A new method of oocyte separation and preservation for fish reproduction studies. Fish Bull. 1993; 91: 165–170.

45. R DCT. R: A Language and Environment for Statistical Computing [Internet]. Vienna, Austria: R Foundation for Statistical Computing; 2013. http://www.r-project.org/

46. Fogarty MJ, Botsford LW. Population connectivity and spatial management of marine fisheries. Oceanography. 2007; 20: 112–123.

47. Prado P, Romero J, Alcoverro T. Welcome mats? The role of seagrass meadow structure in controlling post-settlement survival in a keystone sea-urchin species. Estuar Coast Shelf Sci. Elsevier Ltd; 2009; 85: 472–478.

48. Levitan DR. Influence of Body Size and Population Density on Fertilization Success and Reproductive Output in a Free-Spawning Invertebrate. Biol Bull. 1991; 181: 261–268.

49. de Juan S, Gelcich S, Ospina-Alvarez A, Perez-Matus A, Fernandez M. Applying an ecosystem service approach to unravel links between ecosystems and society in the coast of central Chile. Sci Total Environ. 2015; 533: 122–132. https://doi.org/10.1016/j.scitotenv.2015.06.094 PMID: 26151656

50. Metaxas A, Saunders M. Quantifying the "bio-" components in biophysical models of larval transport in marine benthic invertebrates: advances and pitfalls. BiolBull. 2009; 216: 257–72. Available: http://www.ncbi.nlm.nih.gov/pubmed/19556593