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Renovables

**Patrones espaciales en el bentos submareal y su relación  
con regímenes de variabilidad en condiciones  
oceanográficas en la costa de Chile central**

Tesis para optar al grado de Doctor en Ciencias mención Manejo de Recursos  
Acuáticos Renovables

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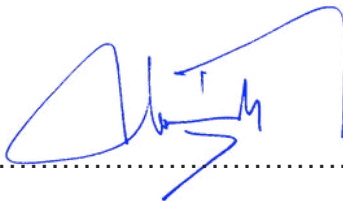
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*A mi hermosa familia*



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## RESUMEN

Las zonas costeras son ecosistemas de alta productividad biológica y de gran importancia socioeconómica a nivel mundial. La compleja geomorfología costera, la ocurrencia de procesos oceanográficos de diversa escala y los efectos antropogénicos constituyen elementos que influyen directamente sobre las especies que las habitan.

En el caso de las especies bentónicas, la estructura y funcionamiento de las comunidades marinas varía en estrecha relación con los cambios en el entorno físico, los que influyen sobre procesos poblacionales clave, tales como los patrones de dispersión larval y el asentamiento, afectando la dinámica poblacional y la composición comunitaria. El efecto de las características topográficas costeras y regímenes oceanográficos sobre la estructura espacial de las comunidades bentónicas ha sido abordado en el caso de comunidades del intermareal, pero se sabe menos sobre el submareal costero, principalmente por la falta de información con suficiente cobertura espacial y métodos de observación adecuados.

A nivel nacional, las Áreas de Manejo y Explotación de Recursos Bentónicos (AMERB) entregan derechos de uso sobre la explotación de especies bentónicas a comunidades costeras, bajo el amparo de un Plan de Manejo, en el marco del cual se deben conducir evaluaciones submareales periódicas de las especies comerciales explotadas y la comunidad bentónica asociada. Numerosos estudios centrados en esta medida han abordado aspectos asociados con sus impactos sobre la biodiversidad bentónica en comparación con áreas libres, así como análisis de la gobernanza y del comportamiento de las organizaciones de pescadores beneficiarias, además de modelación ecotrófica y evaluaciones de indicadores con enfoques holísticos. Sin embargo, a la fecha no se han realizado investigaciones que utilicen la información levantada en las evaluaciones de AMERB con el propósito de analizar cómo la variabilidad ambiental puede explicar la estructura de las comunidades bentónicas y en qué medida la consideración de esta variabilidad ambiental puede mejorar el manejo de las especies comerciales explotadas.

Con base en estos antecedentes, esta Tesis Doctoral se focaliza en el análisis de las comunidades y poblaciones presentes en AMERB y plantea como hipótesis que la variabilidad en las condiciones oceanográficas interactúa con la geomorfología costera para determinar de manera predecible la estructura de las comunidades del bentos submareal y sus variaciones espaciales. A escala interanual, esta variabilidad afecta el éxito del reclutamiento, con efectos significativos sobre la abundancia y estructura de tamaños poblacional adulta.

Para determinar el efecto de la variabilidad en las condiciones oceanográficas de la zona costera sobre la estructura de las comunidades del bentos submareal, se evaluó la composición de especies de 30 AMERB ubicadas en la zona central de Chile, cubriendo cerca de 300 km de costa, utilizando datos de evaluaciones directas realizadas durante la misma temporada primavera-verano. Durante estas evaluaciones se identificó un total de 100 taxa, los que fueron agrupados en 10 grupos funcionales.

Se evaluó la influencia y la importancia relativa de los factores ambientales sobre las asociaciones bentónicas mediante escalamiento multidimensional no métrico (NMDS) y análisis de ruta (*path analysis*), considerando tres categorías principales de factores externos: características topográficas (e.g., exposición de la costa), condiciones oceánicas superficiales (e.g., temperatura superficial) y variables relacionadas con la pesca (e.g., desembarques). El NMDS reveló una fuerte asociación entre la estructura de la comunidad bentónica y las condiciones tanto del terreno como de la superficie del océano (42% de la varianza explicada mediante PERMANOVA), y la ausencia de efectos significativos por parte de las variables relacionadas con la pesca. El modelo de análisis de ruta para las comunidades de fondos duros alcanzó un 49% de bondad de ajuste, con la presencia de filtradores, herbívoros, depredadores y carroñeros correlacionada significativamente con la presencia de las algas foliosas y corticadas, las que a su vez se correlacionaron con el porcentaje de sustrato rocoso en el AMERB y con el grado de exposición al oleaje de la línea de costa. El modelo para las comunidades de fondos blandos alcanzó una bondad de ajuste del 52%, con la presencia de filtradores de la infauna y detritívoros epifaunales dependiendo directamente de la temperatura superficial

y la clorofila-a. Las variables asociadas con la actividad pesquera no tuvieron un efecto aparente sobre la estructura de las comunidades submareales analizadas.

Para profundizar en el rol de la variabilidad ambiental a escala local como factor en la estructuración de comunidades submareales, se combinó el análisis de registros continuos de temperatura y oxígeno disuelto en el agua de fondo con el análisis comunitario del bentos en 6 AMERB distribuidas a lo largo de 180 km de costa en la Región del Biobío. La estructura de la comunidad bentónica fue evaluada mediante una ordenación NMDS basada en la presencia y abundancia relativa de 29 especies, utilizando PERMANOVA para probar el poder explicativo del tipo de sustrato y de nueve índices de variabilidad ambiental derivados de los registros *in situ*. Tres de estos nueve índices explicaron por sí solos un porcentaje de la varianza total similar a lo explicado por el tipo de sustrato (ca. 30%). Estos índices fueron: (a) la variabilidad de alta frecuencia de la temperatura de fondo; (b) el percentil 95 de la temperatura; y (c) la duración media de los eventos de hipoxia registrados durante el periodo de estudio. Cuando estos tres factores se combinaron con el tipo de sustrato en un solo análisis PERMANOVA, fue posible explicar el 84% de la varianza total en la ordenación NMDS. El resultado sugiere que las especies de fondo blando como el bivalvo *Ensis macha*, el gastrópodo *Chorus giganteus* y la jaiba *Cancer setosus*, podrían ser fisiológicamente más tolerantes a condiciones más rigurosas en términos de calentamiento más intenso y eventos de hipoxia más prolongados. Especies de fondo duro como los gastrópodos *Concholepas concholepas* y *Fissurella* sp., y el cirripedio *Austromegabalanus psittacus* estarían mejor adaptados a ambientes donde la temperatura es más baja en promedio, aunque altamente variable, y donde las condiciones de hipoxia son intensas pero más intermitentes. Estos hallazgos destacan el papel estructurador de la variabilidad y la ocurrencia de condiciones extremas, en lugar de los niveles medios en las propiedades del agua del fondo, como la temperatura y el oxígeno disuelto. Estas dos propiedades están estrechamente entrelazadas tanto en ésta como en otras regiones costeras de surgencia y son susceptibles de sufrir cambios en escenarios climáticos futuros.


A nivel de poblaciones, la variabilidad en las condiciones ambientales tiene efectos directos en el éxito de los procesos de asentamiento y reclutamiento, traspasando esta variabilidad a la dinámica poblacional y a la biomasa adulta, especialmente en el caso de especies con ciclos de vida cortos, como es el caso de la macha (*Mesodesma donacium*). Para analizar el efecto de la variabilidad en el reclutamiento de macha sobre la abundancia y vulnerabilidad a la sobrexplotación, se evaluó la dinámica poblacional de *M. donacium* en el AMERB Cucao, Región de Los Lagos (42° 38' S; 74° 07' W). La historia de las evaluaciones directas de la especie ha mostrado alta variabilidad en el reclutamiento al stock, la que no ha sido incorporada correctamente al proceso de determinación de cuotas de captura en el AMERB. Para el análisis se utilizó como información de entrada los resultados de las evaluaciones directas, y el reclutamiento se estimó considerando una secuencia de éxitos y fracasos que siguen una distribución de cadena de Markov. Los resultados mostraron que, bajo una condición de reclutamiento variable similar al observado en la historia del AMERB, la tasa de explotación que se aplica actualmente a *M. donacium* (25% del stock) implica un 80% de probabilidad de colapso futuro, mientras que una tasa de captura del 15% o inferior permitiría garantizar la sostenibilidad de la actividad extractiva frente a fallas en el reclutamiento. Estos resultados destacan la necesidad de revisar los supuestos y criterios sobre los cuales se basa el manejo de especies comerciales en AMERB, y revelan la necesidad de implementar modelos integrados de evaluación de stock, que permitan establecer puntos de referencia biológicos para determinar cuotas de captura bajo incertidumbre ambiental.

Finalmente, los resultados obtenidos dan sustento a la hipótesis central de esta Tesis, habiéndose demostrado que la variabilidad en las condiciones oceanográficas y la geomorfología costera determinan la estructura de las comunidades del bentos submareal en AMERB, de manera predecible. En el caso de *Mesodesma donacium*, esta variabilidad ambiental explica la existencia de fallas en el reclutamiento, con efectos sobre su estructura poblacional y vulnerabilidad a la sobrexplotación.

## **ABSTRACT**

Coastal ecosystems are highly productive and of great socio-economic importance worldwide. The complexity of coastal geomorphology, oceanographic variability over a wide range of scales, and local-scale anthropogenic disturbances strongly influence coastal habitats and the species inhabiting them.

The structure and functioning of benthic communities are strongly influenced by changes in the physical environment, which influence the physiology and behavior of adult stages, as well as key population processes such as the dispersal and settlement of planktonic larvae. Many published studies focus on the effect of coastal topographic features and oceanographic variability on the spatial structure of intertidal benthic communities. However, less is known as to the effects of such factors on subtidal communities, which is partly explained by a paucity of data with both sufficient spatial coverage and adequate observation methods.



In Chile, the Areas for the Management and Exploitation of Benthic Resources (AMEBR) grant artisanal fishers the right to harvest benthic species as long as there is a Management Plan in place and surveys of subtidal benthos are conducted periodically. To date, most studies on Chilean AMEBR have focused on aspects of governance and their impacts on benthic biodiversity compared with free-access areas. However, there have been no attempts to use the information collected from AMEBR benthic surveys to assess if and to what extent environmental variability may explain the structure of benthic communities, and whether considering this environmental variability can improve the management of commercially exploited species.

This Doctoral Dissertation focuses on the analysis of the communities and populations present in AMEBR, and hypothesizes that variability in oceanographic conditions interacts with coastal geomorphology to shape the community structure of subtidal benthos, and its spatial variation, in a predictable fashion. At the interannual scale, this variability is expected to affect recruitment success, with substantial effects on the abundance and size structure of the adult population.

To assess the effect of coastal oceanographic variability on the structure of subtidal benthic communities, the species composition at 30 AMERB spanning ca. 300 km of the central Chile coast was evaluated using data from stock-assessment surveys conducted during the same spring-summer season. A total of 100 taxa were identified and grouped into 10 functional groups. The influence and relative importance of environmental factors on benthic associations was evaluated with non-metric multidimensional scaling (NMDS) and path analysis. Three main categories of external factors were considered: topographic features (e.g., coastal exposure), surface ocean conditions (e.g., temperature), and fishing-related variables (e.g., landings). The NMDS showed a strong association between the structure of benthic communities and both the terrain and the ocean surface conditions (42% of the variance explained by PERMANOVA), and the absence of significant effects by fishing-related variables. The path-analysis model for hard bottom communities reached 49% goodness of fit, with the presence of filter feeders, herbivores, predators and scavengers significantly correlated with the presence of foliose and corticated algae, which in turn are correlated with the percentage of rocky substrate in the AMEBR and with the degree of wave exposure of the coastline. The model for soft bottom communities reached a goodness of fit of 52%, with the presence of infauna filter feeders and epifaunal detritivores depending directly on surface temperature and chlorophyll-a. The variables associated with fishing activity did not have an apparent effect on the structure of the analyzed subtidal communities.

To delve into the role of environmental variability at a local scale as a factor in the structuring of subtidal communities, the analysis of continuous records of temperature and dissolved oxygen in the bottom water was combined with the community analysis of macro?mega?benthos at 6 AMERB distributed along 180 km of coastline in the Biobío Region of central Chile. We evaluated benthic community structure through an NMDS ordination based on the presence and relative abundance of 29 species. To test the explanatory power of the type of substrate and nine indices of environmental variability derived from *in situ* records we used PERMANOVA. Three of these nine indices explained, by themselves, a percentage of the total variance similar to that explained by

the type of substrate (ca. 30%). These indices were: (a) high-frequency variability of the background temperature; (b) 95th percentile of the temperature; and (c) mean duration of the hypoxic events. When these three factors were combined with substrate type in a single PERMANOVA analysis, the total variance explained by the NMDS rose to 84%. These results suggest that soft-bottom species such as the bivalve *Ensis macha*, the gastropod *Chorus giganteus*, and the crab *Cancer setosus*, could exhibit higher tolerance to more rigorous conditions in terms of near-bottom heating and hypoxia. Hard bottom species such as the gastropods *Concholepas concholepas*, and *Fissurella* sp., and the barnacle *Austromegabalanus psittacus* would be better adapted to environments where the temperature is lower on average, although highly variable, and where hypoxic conditions are intense but more intermittent. These findings highlight the structuring role of variability and the occurrence of extreme conditions, rather than average levels, in bottom water properties, such as temperature and dissolved oxygen. These two properties are closely related in both this and other coastal upwelling regions, and are susceptible to changes in future climate scenarios.

At the population level, oceanographic variability has direct effects on the success of planktonic larval development and their subsequent recruitment, thus transferring this variability to population structure and adult biomass, especially in the case of species with short life cycles. This is the case of the surfclam *Mesodesma donacium*. To assess the impact of inter-annual variability in surfclam recruitment on their abundance and vulnerability to overexploitation, we studied the population dynamics of *M. donacium* in the AMEBR Cucao, Los Lagos Region (42° 38 'S; 74° 07' W). The history of direct evaluations of the species has shown high variability in recruitment to the stock, which has not been correctly incorporated into the process of determining catch quotas for this AMEBR. We based our analysis on the results of direct stock assessments, and estimated recruitment as a sequence of successes and failures following a Markov chain distribution. The results showed that, under a variable recruitment condition similar to that observed in the AMEBR's history, the exploitation rate currently applied to *M. donacium* (25% of the stock) implies an 80% probability of future collapse. A catch rate of 15% or less would ensure the sustainability of harvesting in the face of recruitment failures. These results



highlight the need to review the assumptions and criteria used to manage the harvesting of commercial species in AMERB, and reveal the need to implement integrated stock-assessment models that allow establishing biological reference points to adjust catch quotas under environmental uncertainty.

Finally, the results obtained support the central hypothesis of this dissertation, showing that variability in oceanographic conditions and coastal geomorphology determines in a predictable fashion the structure of subtidal benthos communities in AMEBR. As for the surfclam *Mesodesma donacium*, this environmental variability explains the occurrence of recruitment failures, with effects on its population structure and vulnerability to overexploitation.



# 1 INTRODUCCIÓN

## 1.1 Ecosistemas costeros

Los ecosistemas marinos costeros, en especial los de borde oriental, son sistemas altamente dinámicos donde ocurre una variedad de procesos físicos, ecológicos y biológicos que los hacen especialmente complejos y altamente productivos (Polis & Hurd, 1996; Cury et al., 2004; Castelao & Barth, 2005; Thiel et al., 2007). Los sistemas costeros constituyen el 8% de la superficie del océano, dan cuenta de más del 30% de su productividad primaria (Holt et al., 2009; Malone et al., 2017) y proporcionan una amplia gama de servicios ecosistémicos (Palumbi et al., 2009; Luisetti et al., 2014), incluyendo el mantenimiento de los sistemas básicos de soporte de la vida a nivel global, provisión de alimentos, protección natural contra tormentas e inundaciones, mantención de la calidad del agua, turismo y variados beneficios culturales y espirituales (UNEP, 2006).

En estos ambientes la topografía y geomorfología son importantes moduladores de la circulación (Castelao & Barth, 2005) y, por lo tanto, de las condiciones hidrográficas y físico-químicas dominantes en estos ambientes (Tapia et al., 2009; 2014). Adicionalmente, la presencia de desembocaduras de ríos aporta nutrientes (Dagg et al., 2004), carbono orgánico e inorgánico (Cole et al., 2007), metales traza y contaminantes (Carey et al., 2002; Sánchez et al., 2008). Tales condiciones influyen sobre la dinámica y patrones de distribución de especies costeras, sobre todo de aquellas cuya fase adulta es sésil o sedentaria (Barry & Dayton, 1991). Adicionalmente, la presencia histórica de asentamientos humanos ha contribuido significativamente a su alteración, generando pérdida de hábitats a través de la contaminación e incremento en la presencia de especies invasoras, además de la remoción por pesca de una gran proporción de la biomasa de especies comerciales a escala global (Castilla, 1999; O'Neill, 2001; MEA, 2003; Smith, 2003; UNEP, 2006).

## 1.2 Zona de estudio

Esta tesis se enfoca en la zona costera de las regiones del Biobío y de Los Lagos (**Figura 1**). Esta sección de la costa de Chile se encuentra bajo la influencia del Sistema de Corrientes de Humboldt (SCH), que se extiende desde aproximadamente los 45°S hasta el ecuador (Montecino & Lange, 2009) y que genera uno de los ecosistemas de surgencia más productivos a nivel global (Bakun et al., 2015). Las condiciones oceanográficas en esta zona se caracterizan por un flujo predominante de aguas superficiales de origen subantártico hacia el norte, y por el flujo hacia el sur y afloramiento costero de aguas subsuperficiales de origen ecuatorial (AESS), ricas en nutrientes y pobres en oxígeno (Thiel et al., 2007; Quiñones et al., 2010). La inyección de nutrientes en las aguas superficiales a través de eventos de surgencia resulta en una alta producción primaria, que sustenta niveles tróficos superiores (Wieters et al., 2003; Iriarte & González, 2004). Al sur de 36°S, los eventos de surgencia se intensifican durante primavera y verano producto del incremento en la intensidad del viento costero meridional (Figueroa, 2002), produciendo ciclos de surgencia y relajación de 3 a 10 días de duración (Strub et al., 1998; Figueroa & Moffat, 2000; Sobarzo et al., 2007; Strub et al., 2019). Durante el invierno, la descarga de aguas continentales provocada por el incremento en las lluvias, aporta nutrientes, materia orgánica y sólidos en suspensión a la plataforma continental adyacente (Saldías et al., 2012, 2016; Vargas et al., 2013). Ambos procesos, surgencia y descarga fluvial, constituyen factores relevantes en la generación de estratificación y variabilidad de la columna de agua (Sobarzo et al., 2007), lo que influye sobre un amplio rango de procesos costeros, cuyas escalas temporales van desde horas a estaciones del año (Sobarzo, 2020).

Debido a su estrecha conexión con el límite oriental de las corrientes ecuatoriales, el sistema de corrientes Perú-Chile se ve afectado por la variabilidad interanual a gran escala causada por eventos El Niño (Brainard & McLain, 1987; Carr et al., 2002; Karstensen & Ulloa, 2009). Durante la fase El Niño, el flujo de agua hacia el ecuador en la Corriente de Humboldt disminuye, o incluso se invierte, debido a la presencia de aguas ecuatoriales cálidas, con bajas concentraciones de nutrientes y ricas en oxígeno (Thiel et al. 2007), profundizando la termoclina, disminuyendo de la intensidad de la surgencia y

la producción primaria (Kampf & Chapman, 2016). Por otra parte, durante La Niña, la termoclina se hace menos profunda y se intensifican los efectos de la surgencia, con aguas superficiales más frías y ricas en nutrientes (Pennington et al. 2006; Thiel et al. 2007). Adicionalmente, la alternancia entre condiciones El Niño y La Niña está asociada a las variaciones interanuales en las descargas de agua dulce a la costa, con incrementos en los caudales durante la fase El Niño y disminuciones durante La Niña (Waylen & Poveda, 1992; Masotti et al., 2018).

En la zona centro sur (36°S a 42°S), la plataforma continental se extiende desde 40 a 70 km de ancho (Strub et al., 1998; Figueroa, 2002). Una fracción importante de la productividad primaria costera se hunde en la columna de agua y se remineraliza (Farías et al., 2015), consumiendo el oxígeno y contribuyendo a generar y mantener una de las Zonas de Mínimo Oxígeno (ZMO) más importantes a nivel global (Levin, 2003; Kampf & Chapman, 2016), la que cubre un rango de profundidades que varía entre 25 y 300 m (Helly & Levin, 2004; Sobarzo et al., 2007; Fuenzalida et al., 2009). En la costa de Chile central, la presencia e intrusión estacional de la ZMO sobre la plataforma continental (ver Pizarro et al. 2016) afecta la distribución batimétrica de las comunidades submareales de fondos blandos (Gallardo, 1985), caracterizadas por una baja diversidad (Gallardo et al., 2004; Veas et al., 2012) y dominadas por organismos adaptados a vivir en ambientes hipóxicos (González y Quiñones, 2000). Ocasionalmente, durante condiciones de surgencia intensa, la ZMO entra en zonas costeras, generando condiciones hipóxicas (Hernández-Miranda et al., 2010) con efectos sobre las comunidades bentónicas (Hernández-Miranda et al., 2012).

Adicionalmente, fenómenos de mayor escala, tales como la reciente “mega-sequía” observada a partir del 2010 en la zona central de Chile, que ha producido déficits de lluvia cercanos al 30% (Garreaud et al., 2017) y su relación con el cambio climático (Boisier et al., 2016), cuyos efectos proyectados en zonas costeras incluyen el aumento en la salinidad superficial (Jacob et al., 2018), una disminución en la temperatura del mar (Schneider et al., 2017), disminución en la concentración de oxígeno (Breitburg et al.,

2018), acidificación (Doney. 2009, Vargas et al., 2017), variaciones en el nivel del mar (Carson et al. 2016) e incrementos en oleaje (Winckler-Grez et al., 2020).

Esta breve síntesis de antecedentes ilustra la alta complejidad de los diversos procesos que ocurren al interior de la zona de estudio, lo que hace particularmente desafiante identificar las variables pueden contribuir a explicar la estructura y funcionamiento de las comunidades que aquí habitan.

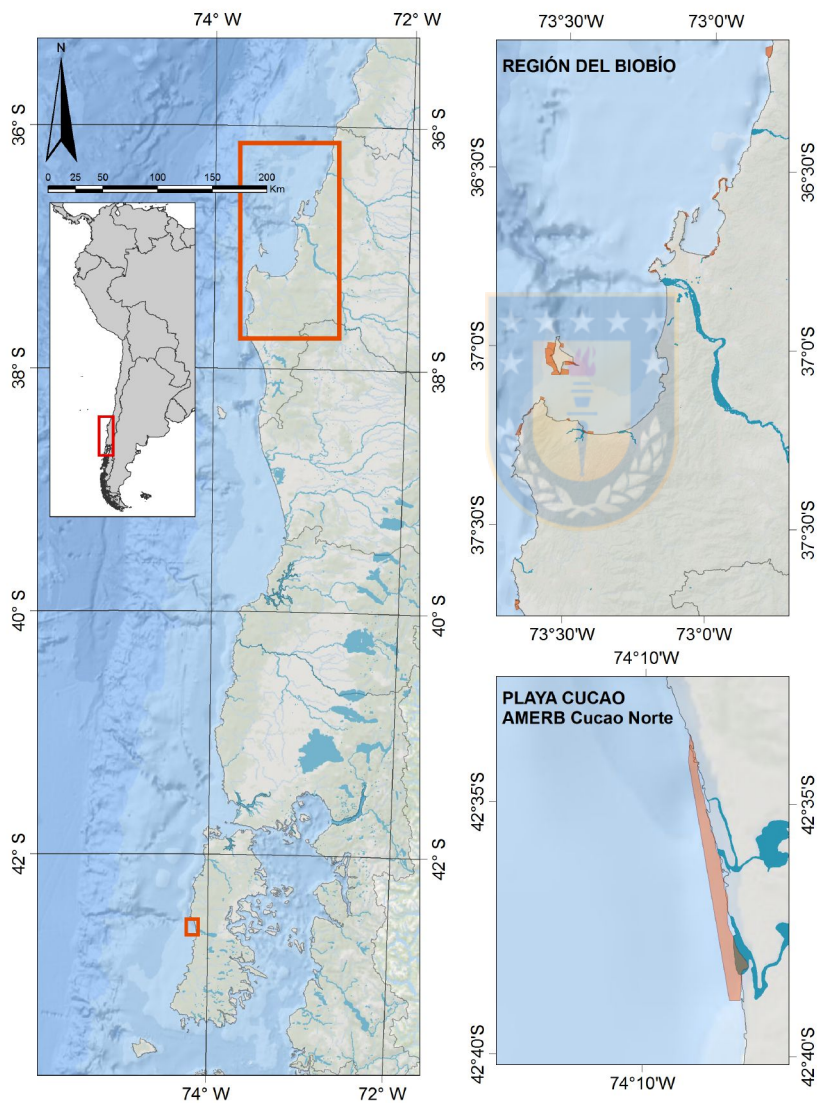


Figura 1. Zonas de estudio. En los recuadros se destacan las áreas correspondientes a la Región del Biobío y a playa Cucao, Región de Los Lagos.

### 1.3 Comunidades bentónicas

El estudio de patrones en la distribución de especies y los mecanismos que los generan ha sido una de las principales áreas de investigación en ecología y biología evolutiva (Pianka, 1966; Rohde, 1992; Gaston, 2000; Vasallo et al., 2020). La comprensión de los forzantes que modulan la variación espacial y temporal de la composición, abundancia y diversidad de las comunidades marinas es relevante para el diseño e implementación de medidas de conservación, así como para el manejo de hábitats costeros a escalas apropiadas (Reiss et al., 2009; Carr et al., 2017).

La estructura y funcionamiento de las comunidades bentónicas varía en estrecha relación con los cambios en su entorno físico (Grantham et al., 2003). La topografía y geomorfología, y su interacción con los vientos costeros, modulan la circulación y ejercen una fuerte influencia sobre las propiedades de la columna de agua (e.g. Tapia et al., 2014) y sobre los patrones de dispersión larval y asentamiento de invertebrados bentónicos (e.g. Navarrete et al., 2005; Barth et al., 2007), lo que a su vez influye sobre su distribución espacial y dinámica poblacional (Barshis et al., 2011). El tipo de sustrato es un factor de primer orden que, en zonas costeras, depende en gran medida de la exposición de la costa, de la batimetría, de la acción de las olas y de la influencia de las plumas de los ríos (Forrest et al., 2010; Burrows, 2012) y es crítico para el asentamiento larval en especies bentónicas, en las que la selección del sustrato antes del asentamiento tiene una fuerte base evolutiva (Morse, 1990).

La interacción entre factores climáticos, meteorológicos y oceanográficos a través de una gama de escalas espacio-temporales genera patrones de circulación costera, que a su vez determinan el suministro de alimentos, nutrientes y propágulos a las comunidades bentónicas (Gaines et al., 1985; Roughgarden et al., 1988; Blanchette et al., 2009; Menge & Menge, 2013; Largier, 2019). Los cambios en el régimen de oleaje costero parecen tener un fuerte efecto en las interacciones de las especies, en las tasas de reclutamiento y en el suministro de alimento a hábitats intermareales rocosos (Menge & Menge, 2013), a través del efecto de las olas en el transporte larval a los sitios de asentamiento (Navarrete et al., 2015; Morgan et al., 2018), así como sobre la supervivencia post-

asentamiento (Pineda et al., 2010). Adicionalmente, las condiciones físico-químicas del ambiente contribuyen a la estructuración espacial del bentos a través de su efecto sobre el comportamiento, fisiología y supervivencia de diferentes especies (Bremner et al., 2006).

Los procesos reproductivos influyen significativamente sobre la distribución y abundancia de especies bentónicas con ciclos de vida complejos (Roughgarden et al. 1988). La dinámica costera local, tanto en términos advectivos como ambientales, determina la duración del periodo de vida planctónica y el patrón de dispersión larval (e.g., O'Connor et al., 2007), lo cual afecta el asentamiento y estado de las poblaciones adultas (Bhaud, 1993; Giangrande et al., 1994; Grantham et al., 2003; Ospina-Alvarez et al., 2020). En zonas de surgencia, la intrusión recurrente de aguas frías y bajas en oxígeno en hábitats cercanos a la costa genera desafíos fisiológicos para los organismos que allí habitan, especialmente para especies sésiles (González & Quiñones, 2000; Grantham et al., 2004; Thiel et al., 2007; Hernández-Miranda et al., 2012). En la zona centro-sur de Chile, la surgencia interactúa con la topografía costera para producir una matriz o "mosaico" de regímenes ambientales locales (Tapia et al., 2009; Chan et al., 2017) los que en última instancia modulan la estructura de las comunidades (Broitman et al., 2001; Wieters et al., 2009).

Aunque la relación entre la estructura comunitaria y los factores ambientales es compleja (Anderson et al., 2008), es habitual que un número limitado de variables ambientales pueda explicar una fracción sustancial de la variabilidad en la estructura comunitaria (Legendre et al., 2005). En la última década, diversos estudios han abordado el efecto de las características topográficas costeras y regímenes oceanográficos sobre la estructuración espacial de las comunidades bentónicas intermareales (e.g. Wieters et al., 2009; Broitman et al., 2011). Sin embargo, el grado de conocimiento que existe sobre los factores que estructuran las comunidades bentónicas en el submareal costero es menor.

En un contexto de cambio climático, resulta pertinente determinar el potencial de las especies para adaptarse a las condiciones ambientales cambiantes y los efectos de esta

variabilidad sobre la dinámica de las comunidades costeras, la biodiversidad y el funcionamiento de los ecosistemas (Kordas et al., 2011; Doney et al., 2012).

#### **1.4 Poblaciones bentónicas explotadas**

La biomasa poblacional adulta de especies bentónicas depende del éxito reproductivo, de la dispersión y sobrevivencia larval en el plancton, del asentamiento larval y de la supervivencia post-asentamiento, bajo condiciones ambientales variables que, además, pueden verse afectadas por efectos antropogénicos (Defeo, 1996; Hunt & Scheibling, 1997; Ouréns et al., 2014). Estos factores interactúan a diferentes escalas, induciendo altos niveles de variabilidad espacial y temporal en procesos poblacionales clave, tales como el reclutamiento (Pineda, 2000; Botsford, 2001; Pineda et al., 2009). En zonas costeras, los cambios en la geomorfología y los regímenes oceanográficos costeros afectan a la pérdida advectiva de larvas de las zonas de asentamiento y, en consecuencia, al éxito de reclutamiento (Morgan et al., 2000; Lagos et al., 2008; Ebert, 2010). La circulación costera puede afectar la distribución de estados tempranos cerca de la costa (Tapia & Pineda, 2007; Shanks & Shearman, 2009), los patrones de asentamiento (Pineda, 1994; Ladah et al., 2005) y la mortalidad post-asentamiento (Hunt & Scheibling, 1997).

Parte de los enfoques tradicionales en evaluación poblacional de especies comerciales consideran como base la asociación entre el tamaño de la población adulta y la producción de reclutas (Ricker, 1954; Beverton & Holt, 1957; Deriso, 1980), la que no necesariamente incorpora la variabilidad ambiental como un factor relevante para las estimaciones de cuotas de captura (Kuraparinen et al., 2014). La abundancia poblacional en especies con ciclos de vida cortos y alta fecundidad, muestra normalmente una alta variabilidad, especialmente en respuesta a la variación en el reclutamiento (Hughes & Tanner, 2000). En efecto, las fallas en el reclutamiento y su variabilidad son características en muchas especies de ciclo de vida corto y pueden estar vinculadas a elevadas tasas de mortalidad natural y variabilidad en las tasas de crecimiento (Defeo, 1996; Pineda & Caswell, 1997; Bjørkvoll et al., 2012).



La falta de evaluaciones poblacionales adecuadas en pesquerías de pequeña escala es un problema importante a nivel mundial (Costello et al., 2012). Pese a que normalmente estas pesquerías artesanales poseen un rol relevante para la biodiversidad y la seguridad alimentaria (Berkes, 2003), se caracterizan por ser deficientes en datos (*data-poor fisheries*) y con un manejo basado en el análisis de indicadores empíricos y no modelo-basados (Dowling et al., 2015). Esto es debido a que ante la falta de información no es posible aplicar métodos cuantitativos de evaluación de la dinámica poblacional (Smith et al., 2009), lo que genera incertidumbre en cuanto a las medidas de manejo requeridas para asegurar su sustentabilidad (Punt et al., 2011).

### **1.5 Áreas de Manejo**

Las Áreas de Manejo y Explotación de Recursos Bentónicos (AMERB), son una medida de administración pesquera que otorga derechos territoriales a organizaciones de pescadores artesanales legalmente constituidas. Estos derechos están asociados con el uso y explotación sustentable de especies bentónicas comerciales bajo la figura de un Plan de Manejo (González, 1996; Castilla & Fernández, 1998; Gelcich et al., 2006; Castilla, 2010). Los pescadores beneficiarios o titulares de AMERB deben desarrollar un plan de administración para la captura sostenible de las especies objeto de explotación (especies principales), el que debe estar basado en los resultados de evaluaciones directas anuales o bienales de las comunidades bentónicas. Tales evaluaciones son realizadas por consultores privados contratados por los propios pescadores titulares de las AMERB. Los datos de estos estudios bentónicos, junto con estimaciones de abundancia para las especies de interés comercial, se presentan a la Subsecretaría de Pesca y Acuicultura (SUBPESCA, Ministerio de Economía), que autoriza una cuota de cosecha establecida bajo el objetivo de salvaguardar la recuperación natural del ecosistema (Stotz, 1997; Castilla & Fernández, 1998; Aburto et al., 2013; Gelcich et al., 2010; González et al., 2006; Marín & Gelcich, 2012).

Para la mayoría de las AMERB, el ciclo de manejo consiste en: a) una evaluación de la densidad de las especies objetivo, estructura de tamaño y relación longitud-peso, desde la que se obtienen estimaciones de biomasa y composición de tamaños; b) determinación de una propuesta de cuotas anuales basadas en la biomasa explotable y; c) una revisión de los resultados obtenidos en a) y b) por parte de SUBPESCA, que puede autorizar o modificar la cuota propuesta, permitiendo una tasa máxima de captura del 30% del stock estimado. Este ciclo de manejo se repite anual o bienalmente, considerando los resultados de las estimaciones de stock obtenidas a partir de la evaluación más reciente, lo que puede ser considerado como un procedimiento "estático" o "carente de memoria", ya que no incorpora explícitamente la historia de las evaluaciones ejecutadas en el AMERB para estimar una cuota de captura sostenible.

La investigación sobre AMERB desarrollada hasta ahora se ha centrado en aspectos tales como sus impactos sobre la biodiversidad bentónica en comparación con áreas de libre acceso (Gelcich et al., 2008), las consecuencias de la medida para la gobernanza (e.g., Gelcich et al., 2010; Marín & Berkes, 2010) y el análisis del comportamiento de las organizaciones de pescadores titulares de AMERB (Bandin & Quiñones, 2014; Chavez et al., 2019; Gelcich et al., 2005). Más recientemente, se han incorporado elementos de modelación ecotrófica en la evaluación de largo plazo del ecosistema bentónico del AMERB Punta Choros en la Región de Coquimbo (González et al., 2021) y se ha analizado el desempeño de las AMERB a través del análisis de indicadores poblacionales, productivos, económicos, sociales e institucionales en las Regiones de Atacama y Coquimbo (Arias & Stotz, 2020) y últimamente en la Región del Biobío (Franco et al., 2021), donde se utilizó la metodología RAPFISH (Pitcher & Preikshot, 2001) para evaluar el estatus de sustentabilidad de la medida de administración. Todas estas investigaciones, han contribuido significativamente a la generación de conocimiento en torno a la efectividad de las AMERB, considerando una variedad de enfoques que cubren múltiples dimensiones. Sin embargo, a la fecha no se han realizado investigaciones que utilicen la información generada en las evaluaciones directas de AMERB para analizar la relación entre la estructura de las comunidades bentónicas y las condiciones

ambientales, y cómo la consideración de esta variabilidad ambiental puede aportar a mejorar el manejo de las especies objetivo.

Con base en estos antecedentes, la presente Tesis Doctoral se orienta a evaluar la relación que existe entre la variabilidad ambiental en AMERB de la zona centro-sur, la estructura de comunitaria del bentos submareal y la dinámica poblacional de especies explotadas.



## 2 HIPÓTESIS

La variabilidad en las condiciones oceanográficas interactúa con la geomorfología costera para determinar de manera predecible la estructura de las comunidades del bentos submareal y sus variaciones espaciales. A escala interanual, esta variabilidad afecta el éxito del reclutamiento de especies bentónicas, con efectos significativos sobre la abundancia y estructura de tamaños poblacional adulta.

## 3 OBJETIVOS

### 3.1 Objetivo General

Evaluar la relación entre la variabilidad de las condiciones oceanográficas de la zona costera en Chile centro-sur y la estructuración comunitaria y poblacional del bentos submareal.



### 3.2 Objetivos Específicos

1. Evaluar la relación que existe entre la variabilidad espacial de las condiciones ambientales en la zona costera y la estructura de las comunidades del bentos submareal.
2. Determinar el rol de la variabilidad temporal en las condiciones de la columna de agua sobre la estructura de las comunidades del bentos submareal.
3. Evaluar el efecto de la variabilidad ambiental sobre el reclutamiento y las tasas de captura aplicadas para la extracción sustentable de la macha *Mesodesma donacium* en playa Cucao, Región de Los Lagos.

## 4 METODOLOGÍA

### 4.1 Capítulo 1: Coastal geomorphology and oceanographic features shape subtidal benthic communities in management areas of central Chile

#### 4.1.1 Área y período de estudio

Entre octubre de 2015 y enero de 2016, se realizó la evaluación submareal de 30 AMERB ubicadas en la zona centro-sur de Chile ( $36^{\circ} 10'S - 37^{\circ} 45'S$ ). Los 30 sitios estudiados cubren una distancia lineal de 190 km, que representan más de 300 km de costa (Figura 2). La superficie de las AMERB evaluadas osciló entre 0,8 y 947,0 ha, con un 63% por debajo de 100 ha (ver histograma en la esquina superior izquierda de la Figura 2).

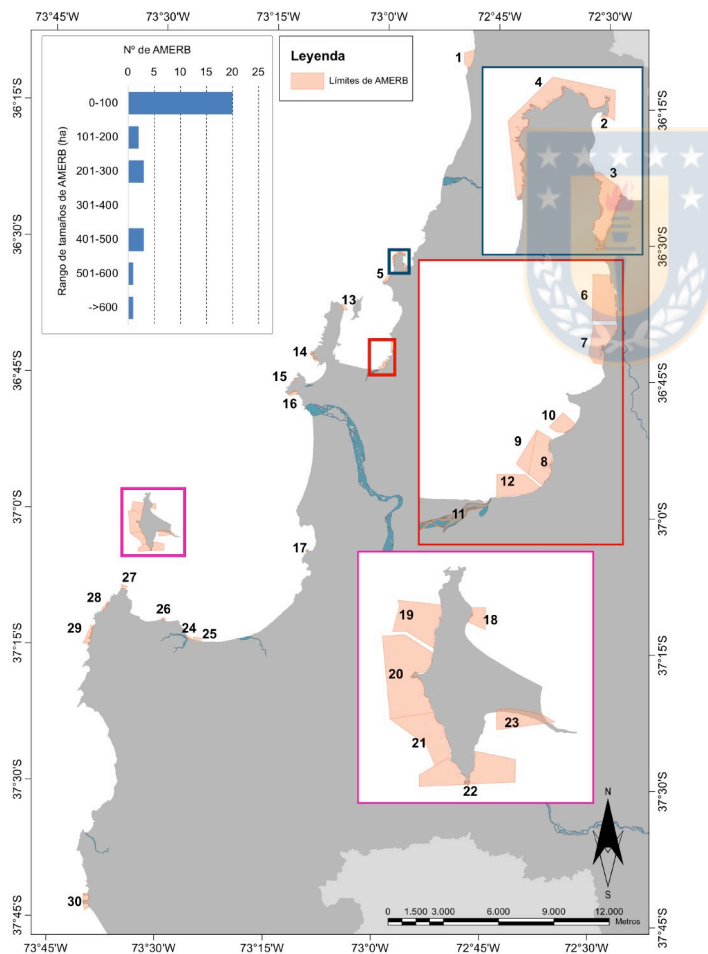


Figura 2. Área de estudio y ubicación de las 30 Áreas de Manejo y Explotación de Recursos Bentónicos (AMERB) analizadas. En el recuadro en la esquina superior

izquierda se indica la distribución de los tamaños de AMERB en términos de área de superficie (ha).

#### 4.1.2 Procedimiento de evaluación submareal

La información base para el análisis de la comunidad se obtuvo a partir de evaluaciones submareales realizadas por buzos científicos con demostrada experiencia en la identificación taxonómica de especies bentónicas presentes en la zona centro-sur. Los levantamientos submareales se diseñaron de manera de cubrir toda la superficie de cada AMERB hasta los 30 m de profundidad, utilizando al menos 40 puntos de observación por sitio. Cada uno de estos puntos de observación consistió en un transecto de 10 m × 2 m orientado en forma perpendicular a la línea de costa. En cada punto, se registraron las coordenadas geográficas en el extremo más profundo del transecto mediante GPS. Los buzos examinaron cada transecto desde el extremo más profundo hasta la zona de menor profundidad. Para cada transecto se registró el tipo de sustrato, la profundidad y la densidad de los principales grupos taxonómicos identificados.

Estos levantamientos produjeron un conjunto de datos que permitió la caracterización de patrones de distribución para múltiples especies en el mismo punto, incluida la densidad de especies desagregadas (e.g., lapas, erizos y cangrejos) que se contabilizaron dentro del transecto de 20 m<sup>2</sup> y la densidad de las especies de mayor agregación (e.g., choritos, almejas y navajuelas) dentro de cinco cuadrantes de 0,25 m<sup>2</sup>, dispuestos cada 2 m a lo largo del transecto. Además, y para el caso de aquellas especies de difícil recuento en el submareal (e.g., ascidias, cirripedios y algas rojas), se utilizó como una medida de la densidad relativa el porcentaje de cobertura dentro del transecto.

#### 4.1.3 Clasificación de datos biológicos

Las 100 especies bentónicas identificadas durante los estudios se clasificaron en grupos funcionales. Para las algas, los grupos funcionales se definieron de acuerdo a las características anatómicas y morfológicas de cada especie, siguiendo a Steneck & Dethier (1994). Para los invertebrados, se utilizó el análisis de rasgos biológicos (BTA) para explorar y definir el funcionamiento ecológico (Sigala et al., 2012; van der Linden et

al., 2012). El BTA combina datos estructurales cuantitativos con información sobre las características biológicas de cada taxón para caracterizar funcionalmente los conjuntos de especies (Bremner et al., 2006). Los criterios de clasificación (ver detalles en el Apéndice S1) son entonces una combinación de rasgos morfológicos y consideraciones ecológicas, y su propósito principal es capturar la estructura funcional de las comunidades submareales estudiadas.

Debido a las diferencias existentes en cuanto a las medidas de densidad utilizadas para diferentes taxa (número de individuos, cobertura, peso húmedo), el análisis comunitario utilizó como información de entrada la proporción con presencia de cada taxon por AMERB.

#### 4.1.4 Condiciones oceánicas superficiales

Para el análisis de las condiciones ambientales que caracterizan cada AMERB, se obtuvo series de tiempo a partir de imágenes compuestas de 7 días generadas por MODIS-Aqua para el período 2003-2016. En atención a la escala espacial de las AMERB, el análisis de series de tiempo derivadas de satélites utilizó como información de entrada imágenes con una resolución espacial de 1 km, que supera a la resolución típica de 4 km utilizada hasta ahora en la mayoría de los estudios publicados de esta región costera (e.g., Correa-Ramirez et al., 2007). Una menor resolución espacial puede dificultar la identificación de procesos o estructuras de variabilidad oceanográfica que podrían ser importantes en la estructuración de comunidades bentónicas cerca de la costa. Se debe destacar que el uso de datos de color del océano derivados del espectro-radiómetro MODIS-Aqua implica una ventaja en relación a otros sensores de color (e.g., SeaWiFS), porque además de proporcionar información sobre el color del océano (e.g. clorofila-a) permite estimar la temperatura de la superficie del mar (TSM), entregando así mediciones concomitantes y directamente comparables. Además, el mayor número de bandas espectrales en MODIS permite el uso de parámetros de color del océano que no están disponibles en sensores más antiguos como SeaWiFS.

Para cada sitio de estudio, se produjeron compuestos semanales con una resolución espacial de aproximadamente 1 km utilizando el software SEADAS (SeaWiFS Data Analysis System; National Aeronautics and Space Administration, NASA) para las siguientes variables:

- Temperatura Superficial del Mar (TSM)
- Clorofila-a superficial (Chl-a) y fluorescencia normalizada (nFLH) como indicadores de biomasa fitoplanctónica (i.e., disponibilidad de alimento)
- Reflectancia normalizada en 645 nm (nLw645) como indicador de la presencia de plumas de ríos en esta región (ver Saldías et al., 2016).

Para cuantificar la amplitud de la señal estacional en cada variable, y la variabilidad que no es explicada por el ciclo estacional (i.e., la varianza residual), se aplicó un análisis armónico a cada serie de tiempo y sitio siguiendo la metodología descrita por Thomson & Emery (2014). Además se calculó la media a largo plazo para cada serie de tiempo. Por lo tanto, se obtuvieron tres descriptores para cada una de las cuatro variables derivadas del satélite en cada sitio.

#### 4.1.5 Características topográficas

Las características topográficas consideradas en el análisis fueron la exposición de la costa y el porcentaje de sustrato rocoso dentro de cada AMERB. La evaluación cuantitativa de la exposición de la línea costera en cada AMERB se basó en el análisis del *fetch* (Baardseth, 1970), que es una medida de la longitud del agua sin obstrucciones sobre la cual el viento puede soplar desde una dirección específica. Para cuantificar el *fetch*, se consideró un conjunto de 40 radios (con espaciamentos de 9°) de una longitud de 300 km desde el centroide de cada AMERB, y luego se registró la distancia desde el centroide hasta la línea de costa más cercana a cada radio. El índice de exposición para un sitio determinado se calculó promediando todas esas distancias. Este procedimiento se implementó utilizando el paquete FETCH (Seers, 2017) disponible para R (<http://www.r-project.org>).



El porcentaje de sustrato rocoso en cada AMERB se determinó como el porcentaje promedio de sustrato de fondo duro registrado en las unidades de muestreo analizadas durante cada evaluación submareal.

#### 4.1.6 Variables relacionadas con la pesca

El análisis de los efectos potenciales de la pesca en las comunidades submareales de AMERB se basó en las estadísticas oficiales de desembarque, acumuladas entre 2000 y 2016, proporcionadas por el Servicio Nacional de Pesca y Acuicultura (SERNAPESCA). Adicionalmente, y considerando la existencia de pesca ilegal dentro de las AMERB (Bandin & Quiñones, 2014; Chávez et al., 2018), se incluyó el número de buzos de cada organización y, como medida de capacidad de vigilancia del AMERB, la distancia entre ésta y la caleta base de la organización de pescadores titular del AMERB.

#### 4.1.7 Análisis estadístico

##### 4.1.7.1 Escalamiento no métrico multidimensional (NMDS)

Se construyó una matriz de similitud de Bray-Curtis a partir de datos de presencia/ausencia por grupos funcionales. Se realizó una ordenación NMDS bidimensional para visualizar patrones de similitud en la estructura de la comunidad entre los AMERB. Posteriormente, se utilizó el análisis de varianza no paramétrico (PERMANOVA) para probar los efectos significativos de las variables ambientales y relacionadas con la pesca sobre los resultados de la ordenación. La significancia se estimó sobre la base de 9.999 permutaciones de residuos. Todos los cálculos se realizaron en R utilizando las bibliotecas *vegan* (Oksanen et al., 2019) y *MASS* (Venables & Ripley, 2002).

##### 4.1.7.2 Análisis de ruta

El análisis de ruta (*path analysis*) es una extensión de la regresión lineal múltiple (Legendre & Legendre, 1998) desarrollada originalmente por Wright (1934) como un método para estudiar los efectos directos e indirectos de las variables hipotetizadas como causas de las variables tratadas como efectos. Una de las ventajas de esta técnica es

que permite formular hipótesis *a priori* sobre las relaciones causales entre descriptores, examinando su viabilidad a partir de los coeficientes de regresión y correlación calculados entre estos descriptores (Pedhazur, 1997). Un diagrama de ruta es útil para mostrar gráficamente el patrón factible de relaciones causales entre un conjunto de variables, y consta de dos submodelos: el modelo interno y el modelo externo (Sánchez, 2013). El modelo interno, o estructural, muestra las relaciones entre las variables latentes, es decir, aquellas que resumen las respuestas de las variables o indicadores observados. El modelo externo, o de medición, consiste en aquellas medidas que crean variables latentes.

En este estudio, el diagrama de ruta propuesto (Figura 3, Tabla 1) expresa que la exposición de la costa (medida como *fetch*) influye sobre las variables ambientales utilizadas para caracterizar las condiciones de superficiales del océano, así como en la proporción de sustrato rocoso. Esto último en atención a que las bahías y otras áreas protegidas dentro de la zona de estudio, a menudo poseen una mayor proporción de sustrato blando que las áreas expuestas. Por otro lado, las actividades pesqueras también podrían verse afectadas por las condiciones ambientales, desarrollando un mayor esfuerzo pesquero en áreas con condiciones más favorables para la navegación (i.e., menor exposición). La presencia de algas podría estar asociada con la presencia de sustrato rocoso, en zonas más expuestas, donde las condiciones superficiales del océano indican condiciones de nutrientes más favorables. Finalmente, la presencia de invertebrados puede depender de manera diferente de cada una de las variables consideradas en este modelo conceptual.

Los cálculos para implementar este análisis se realizaron en R utilizando la biblioteca de modelos de mínimos cuadrados parciales PLSPM (Sánchez et al., 2017), siguiendo las recomendaciones de Sánchez (2013).

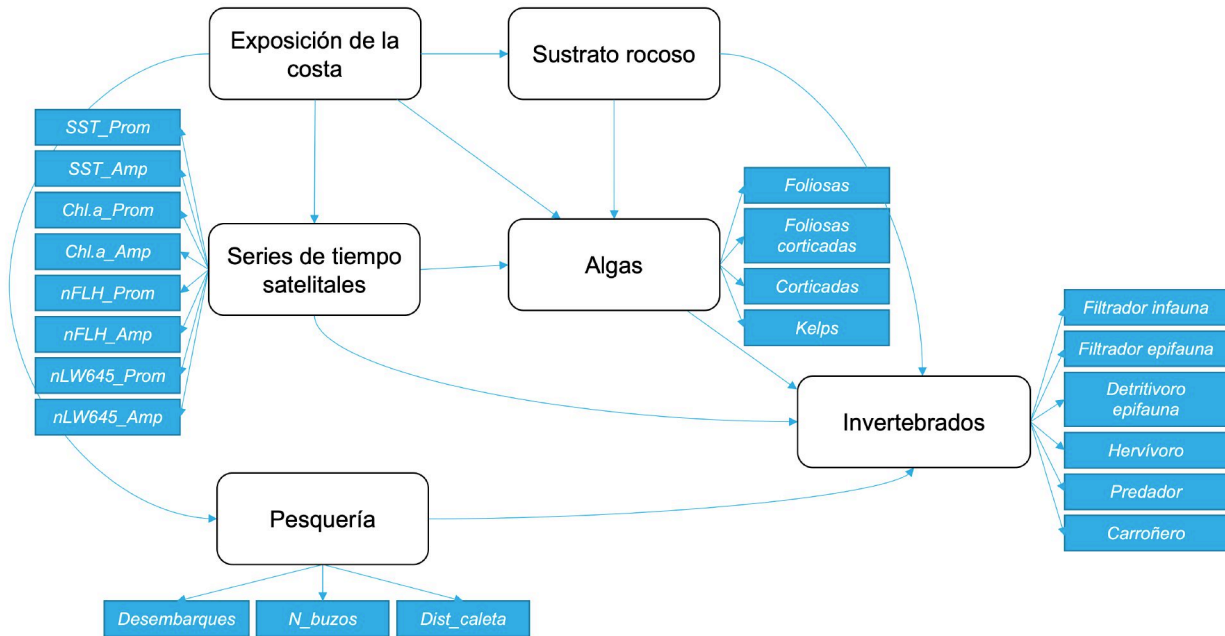


Figura 3. Esquema del modelo conceptual utilizado para el análisis de las variables que afectan a las comunidades submareales en AMERBs. Las flechas representan los efectos directos de una variable (recuadros) sobre otra. Los rectángulos azules y blancos representan variables externas e internas, respectivamente.

Tabla 1. Listado de variables independientes consideradas en el análisis, indicando la unidad de medida y fuente de información.

Tipo de variable	Variable	Código	Unidad de medida	Fuente
Características topográficas	Exposición de la línea de costa al viento	Fetch	%	Este estudio
	Porcentaje de sustrato rocoso en unidades de muestreo	Sustrato rocoso	%	Evaluación submareal
Series de tiempo satelitales	Temperatura superficial de mar promedio entre 2003 y 2017	SST_Prom	°C	
	Amplitud armónica de la temperatura superficial del mar entre 2003 y 2017	SST_Amp	°C	
	Concentración de clorofila-a promedio entre 2003 y 2017	Chl-a_Prom	mg m <sup>-3</sup>	
	Amplitud armónica de la concentración de clorofila-a entre 2003 y 2017	Chl-a_Amp	mg m <sup>-3</sup>	
	Fluorescencia normalizada promedio entre 2003 y 2017	nFLH_Prom	mW cm <sup>-2</sup> μm <sup>-1</sup> sr <sup>-1</sup>	MODIS-Aqua
	Amplitud armónica de la fluorescencia normalizada entre 2003 y 2017	nFLH_Amp	mW cm <sup>-2</sup> μm <sup>-1</sup> sr <sup>-1</sup>	
	Radiación superficial del mar normalizada a una longitud de onda de 645nm promedio entre 2003 y 2017	nLW645_Prom	mW cm <sup>-2</sup> μm <sup>-1</sup> sr <sup>-1</sup>	
Amplitud armónica de la radiación superficial del mar normalizada a una longitud de onda de 645nm entre 2003 y 2017	nLW645_Amp	mW cm <sup>-2</sup> μm <sup>-1</sup> sr <sup>-1</sup>		
Pesquería	Desembarques acumulados por AMERB entre 2000 y 2017	Desembarques	ton	Sernapesca
	Número de buzos en la organización titular del AMERB	N_buzos	Nº	
	Distancia desde el centro de la caleta a cada AMERB	Dist_caleta	km	Este estudio

## 4.2 Capítulo 2: Connecting spatial structure in subtidal benthic communities with temporal variability in bottom temperature and dissolved oxygen along an upwelling coast

### 4.2.1 Área y periodo de estudio

Para evaluar en qué medida la variabilidad de las condiciones ambientales del agua de fondo modula la estructura espacial de las comunidades bentónicas, se combinó registros continuos de temperatura y oxígeno disuelto en el agua de fondo con datos recopilados a partir de evaluaciones directas de comunidades bentónicas submareales desde AMERB (Figura 4). Los sitios de estudio analizados corresponden a AMERB evaluadas entre abril de 2017 y noviembre de 2018 (Tabla 2). Los registros de temperatura y oxígeno disuelto en las cercanías de cada uno de los sitios de muestreo se obtuvieron mediante sensores desplegados entre febrero de 2018 y febrero de 2019.

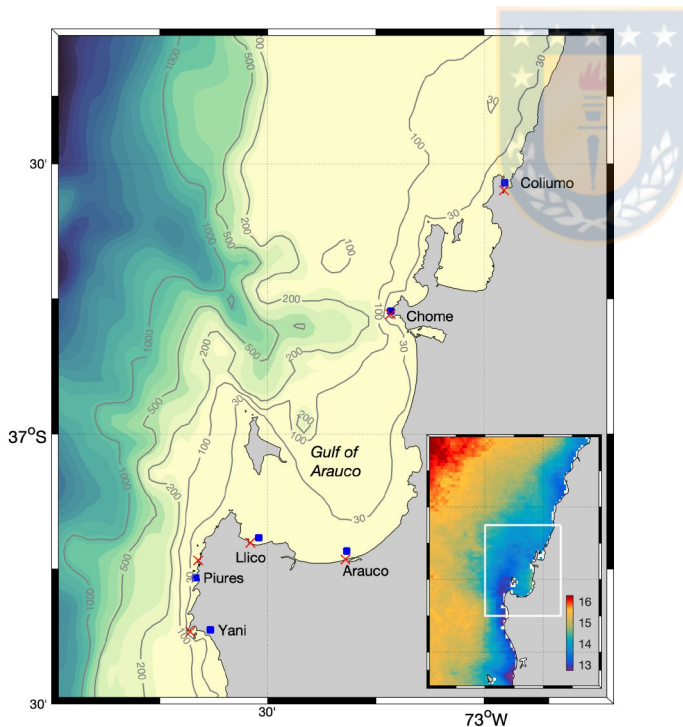


Figura 4. Ubicación geográfica de las AMERB (símbolos rojos) y de sitios de recopilación de registros continuos de la temperatura y oxígeno disuelto de fondo (símbolos azules). Se observa que la batimetría costera enfatiza la complejidad de la geomorfología costera en la región de estudio. El mapa insertado muestra la distribución media de la temperatura de la superficie del mar MODIS-Aqua ( $^{\circ}\text{C}$ ) entre 2003 y 2018.

#### 4.2.2 Comunidad bentónica

La comunidad bentónica de megafauna y macrófitas fue analizada a partir de evaluaciones submareales efectuadas en seis sitios que abarcaron cerca de 180 km de la costa central de Chile (Figura 4). En cada AMERB se obtuvo información sobre la composición de la comunidad bentónica mediante evaluación submareal directa, considerando unidades de muestreo que corresponden a un transecto de 10 x 2 m de largo, ubicado perpendicularmente a la línea de costa y considerando un mínimo de 40 unidades de muestreo por AMERB. En cada punto de muestreo, buzos científicos recorrieron desde el extremo más profundo al más superficial registrando la composición de especies y características asociadas al tipo de fondo.

Dependiendo del tipo de especie, se utilizó diferentes unidades de muestreo para obtener un conjunto de datos que permitió caracterizar los diferentes patrones de distribución en un mismo punto del espacio. Para las especies desagregadas que se pueden contar fácilmente, como lapas, erizos y jaibas, se registró su densidad dentro de cada transecto de 10 × 2 m. Para especies agregadas como mitílidos y almejas, se registró la densidad promedio observada dentro de cinco cuadrantes de 0,25 m<sup>2</sup>, dispuestos cada 2 m a lo largo del transecto. Además, y para el caso de aquellas especies de difícil recuento en el submareal (e.g., ascidias, cirripedios y algas rojas), se utilizó como una medida de la densidad relativa el porcentaje de cobertura promedio observado al interior de los cuadrantes evaluados.

Como medida de entrada al análisis se utilizó la densidad relativa para cada taxón, calculada como su densidad media dividida por la suma de todas las densidades dentro de un tipo dado de sustrato y taxa (e.g., invertebrados de fondo duro).

Adicionalmente, se determinó el tipo de sustrato por observación directa, estimando la proporción de sustratos duros (guijarros, cantos rodados, arcilla, planchón) y sustratos blandos (conchilla, arena, lodo) para cada unidad de muestreo. Para el análisis se utilizó como variable de entrada el porcentaje de sustrato rocoso promedio observado en las

unidades de muestreo evaluadas. Adicionalmente, se incluyó la profundidad promedio observada en las unidades de muestreo analizadas (Tabla 2).

Tabla 2. Información general para cada una de las seis AMERB incluidas en el análisis. La profundidad media y el porcentaje de sustrato rocoso corresponden a los promedios calculados para todas las unidades de muestreo evaluadas.

Sitio	Fecha	Unidades de muestreo	Número de taxa (S)	Profundidad media (m)	% Sustrato rocoso
Coliumo	18-Jul-2017	57	17	2,1	75
Chome	26-Mar-2018	69	15	6,1	100
Arauco	13-Apr-2018	45	5	6,5	0
Llico	03-Apr-2017	71	13	2,1	93
Piures	16-Apr-2017	94	20	4,2	100
Yani	17-Jun-2018	40	17	8,1	100

#### 4.2.3 Condiciones ambientales

Se obtuvo registros continuos de la temperatura y oxígeno disuelto de fondo a partir de sensores desplegados en las cercanías de cada AMERB entre febrero de 2018 y febrero de 2019. En cada ubicación, se amarró un registrador miniDOT (PME, EE. UU.) aprox. 2 m por encima del fondo, a una profundidad nominal de 20 m, programado para registrar la temperatura del agua y el oxígeno disuelto a intervalos de 10 minutos. Los datos de los registros fueron descargados cada 2 a 3 meses. Los datos recopilados fueron sometidos a control de calidad y convertidos en series de tiempo de frecuencia horaria. Posteriormente, se calcularon estadígrafos de cada serie de tiempo para caracterizar los regímenes locales de temperatura y variabilidad del oxígeno.

La temperatura se caracterizó mediante la mediana y el percentil 95 de cada distribución de temperatura; este último estadígrafo se utilizó para caracterizar los eventos de calentamiento experimentados por la comunidad bentónica. De manera similar, el oxígeno disuelto (OD) se caracterizó mediante la mediana y el percentil 5 de los valores registrados, indicando este último la condición más extrema de hipoxia en cada localidad. La variabilidad de alta frecuencia en temperatura y OD se cuantificó aplicando un filtro

coseno-Lanczos del tipo “pasa alta” para remover los períodos mayores de 24 h de cada serie de tiempo, y luego calculando el RMS (raíz cuadrada media) de la series filtrada, dividido por el RMS de la serie de tiempo sin filtrar. En cuanto a la hipoxia, se calculó la fracción de mediciones con OD < 2 mg/l para cada serie de tiempo. Adicionalmente, a partir de la duración de todos los eventos de hipoxia encontrados en cada registro horario, se utilizó la mediana y el percentil 95 como descriptores de las exposiciones típicas (más frecuentes) y más prolongadas de organismos bentónicos a aguas hipóxicas, respectivamente. Los eventos de hipoxia fueron definidos como los casos de más de dos mediciones consecutivas de OD < 2 mg/l.

#### 4.2.4 Análisis estadístico

Para observar las diferencias en cuanto a la estructura de la comunidad bentónica entre los sitios evaluados, se realizó una ordenación bidimensional mediante Escalamiento No Métrico Multidimensional (NMDS) utilizando la función metaMDS del paquete *vegan* v2.6-5 (Oksanen et al., 2019) en R. Los centroides de especies y AMERB se graficaron en conjunto en un diagrama biplot para visualizar las asociaciones entre las especies y los sitios. La significancia estadística de las relaciones entre la estructura emergente de la ordenación NMDS y las condiciones ambientales que caracterizan cada sitio fue evaluada mediante PERMANOVA. Los diferentes estadígrafos de variabilidad asociados con la temperatura y el oxígeno, además del porcentaje de sustrato rocoso fueron considerados como factores independientes, utilizando la función **adonis** de *vegan*, con valores *p* para la estadística de prueba pseudo-F basada en 999 permutaciones. Los factores identificados como estadísticamente significativos ( $p < 0.05$ ) fueron posteriormente utilizados en un PERMANOVA combinado, orientado a determinar el porcentaje máximo de varianza en la ordenación NMDS que pueden explicar de manera conjunta. El ajuste resultante de métricas ambientales seleccionadas a la ordenación NMDS se incluyó en los biplots utilizando la función **envfit** de *vegan*.



### 4.3 Capítulo 3: Harvest rate for a benthic species with highly variable recruitment, the case of the surf clam *Mesodesma donacium* in northern Patagonia, Chile

#### 4.3.1 Área de estudio y fuentes de datos

El área de estudio corresponde a playa Cucao (42°36'S - 74°08'W), ubicada en la costa occidental de la isla de Chiloé, en el extremo norte de la Patagonia chilena (Figura 5). Durante la última década, Cucao ha sido una de las principales zonas de captura de la macha (*Mesodesma donacium*), con tres organizaciones de pescadores artesanales que poseen derechos de uso territorial desde el 2015, luego de la implementación del AMERB Cucao.

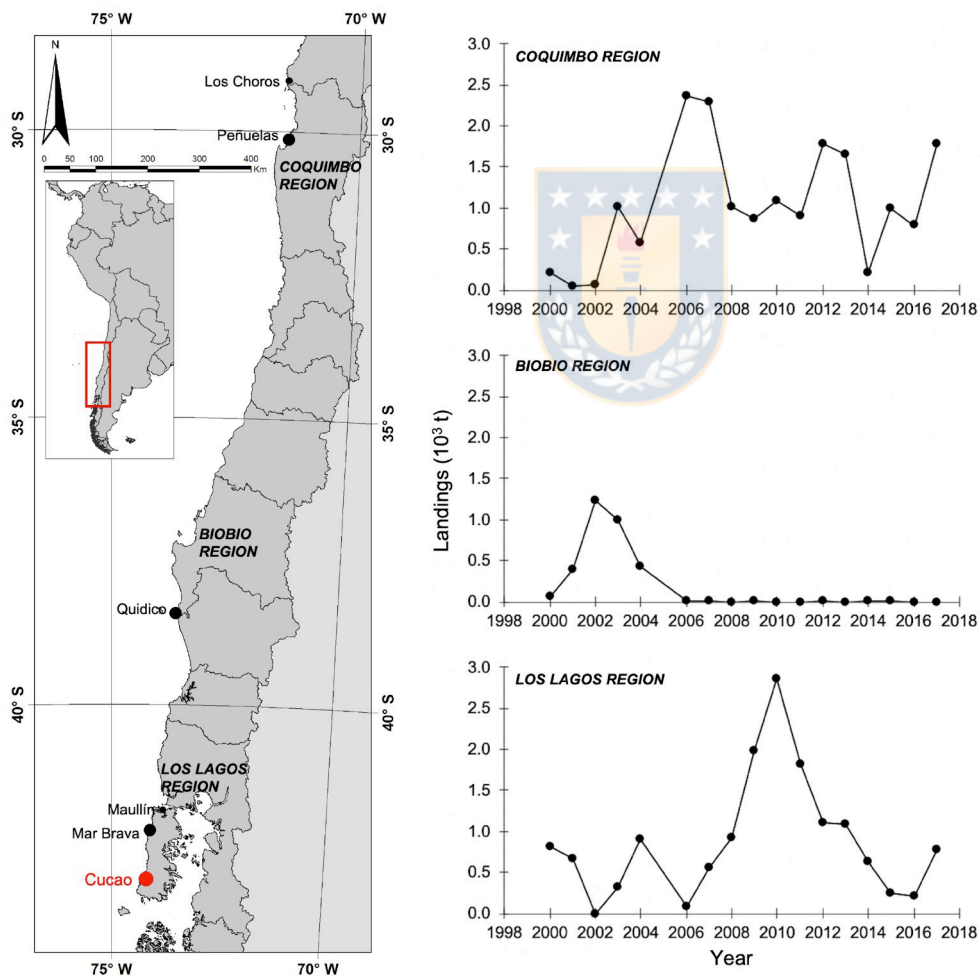


Figura 5. Principales puntos de desembarque de macha (*M. donacium*) a lo largo de la costa chilena (izquierda) y evolución de los desembarques regionales a partir del 2000. Fuente: Servicio Nacional de Pesca y Acuicultura ([www.sernapesca.cl/anuarios](http://www.sernapesca.cl/anuarios)).

Los datos de entrada al análisis provienen de seis evaluaciones directas poblacionales realizadas entre 2011 y 2017 (Tabla 3). Hasta 2015, se realizaron evaluaciones directas orientadas al establecimiento de cuotas de captura anuales bajo la medida administrativa llamada “pesca de investigación”, basada en evaluaciones a partir de las cuales se propusieron cuotas de captura globales para la zona (Leal et al., 2014). A diferencia del régimen AMERB, estas cuotas propuestas y posteriormente evaluadas por SUBPESCA no incluían derechos de uso territoriales y podían ser extraídas por cualquier pescador artesanal de la Región de Los Lagos registrado en la pesquería. Desde 2015, los datos de las evaluaciones se convirtieron en información de entrada para la captura de machas bajo el sistema AMERB. El enfoque para establecer la cuota de cosecha no cambió después de 2015.

Tabla 3. Resumen de las evaluaciones anuales de macha *Mesodesma donacium* en playa Cucao, utilizadas para acondicionar el modelo operativo. La tasa de cosecha ( $\mu$ ) se calculó como la relación entre la Cuota y la Biomasa vulnerable.

<b>Resultados de evaluaciones directas</b>	<b>2011*</b>	<b>2012*</b>	<b>2013*</b>	<b>2014*</b>	<b>2015**</b>	<b>2017**</b>
Fecha de la evaluación	14-Jun	30-Mar	26-Abr	14-Ene	04-Dic	31-Ene
Unidades de muestreo (cuadrantes)	647	1063	328	1116	800	236
Densidad promedio (ind/m <sup>2</sup> )	110,5	213,2	441,5	197,5	359,1	78,7
Superficie del banco (ha)	69,4	112,7	117,2	70,7	108,7	120,6
Abundancia (10 <sup>3</sup> individuos)	72.530	221.053	203.711	68.008	385.039	94.972
Biomasa (ton)	1.356,2	4.638,8	5.407,2	1.687,1	3.257,5	1.618,3
Biomasa vulnerable (ton)	1.261,3	4.459,9	5.398,6	1.646,3	1.992,4	1.539,5
Cuota (10 <sup>3</sup> individuos)	16.671	52.173	44.578	8.878	24.628	19.06
Cuota (ton)	347	1.169	1.350	356	450	403
<b>Cuota/Biomasa vulnerable (<math>\mu</math>%)</b>	<b>27,5</b>	<b>26,2</b>	<b>25,0</b>	<b>21,6</b>	<b>22,6</b>	<b>26,2</b>
Captura efectiva (ton)	199	662	800	304	101	592

\* Datos obtenidos desde Fundación Chiquihue (2012)

\*\* Datos obtenidos a partir de Informes Técnicos de AMERB (ITA-SUBPESCA). Para el modelo operacional las evaluaciones de finales de 2015 fueron asignadas al año 2016.

#### 4.3.2 El ciclo de manejo y las reglas de control de la cosecha.

El ciclo de manejo de la macha en el AMERB Cucao consta de tres etapas (Figura 6). Primero, un equipo de técnicos y taloneros locales lleva a cabo estudios de evaluación de poblaciones anuales que comprenden el muestreo de la densidad, la estructura del tamaño y la relación longitud-peso de las especies objetivo (ver Tabla 3). La evaluación permite obtener estimadores de abundancia y biomasa de las especies comerciales evaluadas en el AMERB. La estimación de la biomasa está estructurada por tamaños, lo que permite estimar la biomasa vulnerable, definida como individuos de más de 50 mm de longitud anteroposterior (tamaño mínimo de extracción para la macha). El equipo de evaluación de stock recomienda una cuota y envía los resultados de su análisis, junto con las bases de datos, a la Subsecretaría de Pesca y Acuicultura (SUBPESCA). Actualmente, la cuota de captura autorizada para la macha en Cucao oscila alrededor del 25% de la biomasa vulnerable (Tabla 3). Por lo tanto, la regla de control de captura (RCC) es empírica y utiliza la biomasa vulnerable estimada como índice de estado. Por lo tanto, la RCC consiste en una tasa de cosecha constante del 25% de la biomasa vulnerable:

$$1) \quad Q_i = 0.25B_i$$

donde  $B_i$  es la biomasa vulnerable en el año  $i$ , y  $Q_i$  es la cuota de captura de macha propuesta. Una vez que SUBPESCA aprueba la cuota, los pescadores pueden efectuar la cosecha desde el AMERB. En el momento de la cosecha, las capturas son monitoreadas y registradas e informadas al Servicio Nacional de Pesca y Acuicultura (SERNAPESCA).

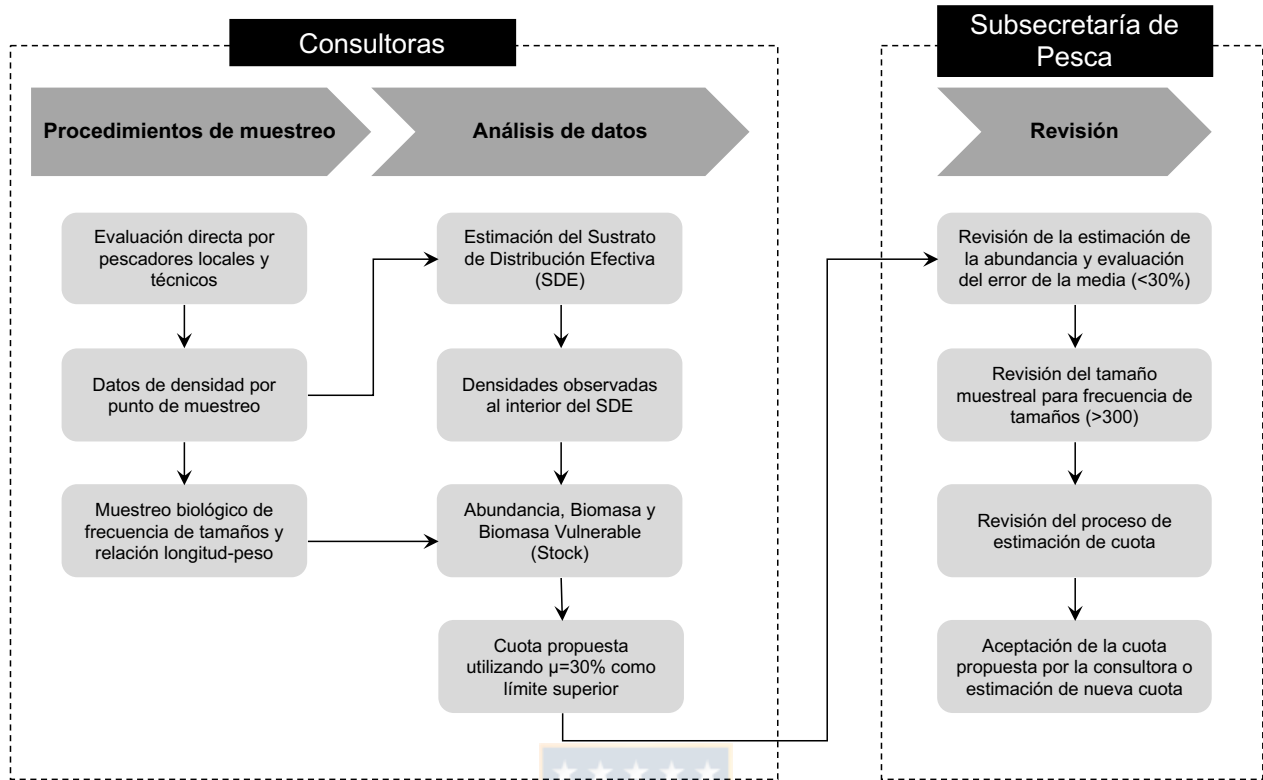


Figura 6. Procedimiento de evaluación de macha *M. donacium* en el AMERB Cucao.

#### 4.3.3 Reglas de control de captura alternativas

Para comparar la tasa de cosecha actual ( $\mu = 25$ ) con otros escenarios, se consideraron valores alternativos de  $\mu = 0$ ,  $\mu = 10$ ,  $\mu = 15$  y  $\mu = 30$  de la biomasa vulnerable. La tasa de cosecha  $\mu = 0$  se incluyó solo como una condición de referencia para evaluar la dinámica poblacional en ausencia de explotación. La tasa de captura  $\mu = 30$  es la captura máxima permitida actualmente por SUBPESCA.

#### 4.3.4 Dinámica poblacional

##### 4.3.4.1 Abundancia

Se condicionó un modelo de dinámica poblacional a parámetros conocidos de la historia de vida de la macha, utilizando información sobre la biomasa total y la estructura tamaños obtenida a partir de las evaluaciones directas (Tabla 3). La dinámica poblacional de la

macha consistió en un modelo integrador de evaluación de stock estructurado por tamaño (Sullivan et al., 1990; Punt et al., 2013), expresado por:

$$2) \quad \mathbf{N}_i = \mathbf{GN}_{i-1}\mathbf{S}_{i-1} + \mathbf{R}_i$$

donde  $\mathbf{N}_i$  es un vector columna de tamaño  $L$  (número de clases de talla) que contiene el número por talla de la población al comienzo del año ( $i$ ),  $\mathbf{G}$  es una matriz de transición de crecimiento (dimensión  $L \times L$ ) que determina el crecimiento entre clases de talla (ver abajo). La matriz  $\mathbf{S}_i$  es una matriz de supervivencia (dimensión  $L \times L$ ), con términos diagonales iguales a la tasa de supervivencia ( $\exp(-Z_{t-1})$ ), donde  $Z$  representa la tasa de mortalidad total, y  $\mathbf{R}_i$  es un vector columna de tamaño  $L$  que contiene el reclutamiento para cada clase de talla al final del año (o al comienzo del año siguiente, ver abajo).

#### 4.3.4.2 Mortalidad

La tasa de mortalidad total queda expresada por  $Z = F + M$ , donde  $F$  es la mortalidad por pesca y  $M$  es la tasa de mortalidad natural. Se estimó  $M = 0,3 \text{ año}^{-1}$  utilizando el modelo empírico de Brey y Cage (1997) para invertebrados bentónicos. La tasa de mortalidad por pesca por clase de talla durante un año determinado fue:

$$3) \quad F_{i,l} = s_l F_i$$

donde  $F_i$  es la tasa de mortalidad por pesca durante el año  $i$  y  $s_l$  es la selectividad a la talla  $l$ , definida por:

$$4) \quad s_l = 0 \text{ if } l < 50; \text{ or } s_l = 1 \text{ if } l \geq 50$$

La selectividad en la ecuación 4 es una función en “filo de cuchillo” al tamaño mínimo legal ( $l_c = 50 \text{ mm}$ ).

#### 4.3.4.3 Reclutamiento

La dinámica del reclutamiento siguió una relación stock-recluta (RSR) de Beverton-Holt, afectada multiplicativamente por un forzante ambiental, y descrita por:

$$5) \quad R_i = \frac{4hR_0S_{i-1}}{(1-h)S_0+(5h-1)S_{i-1}} e^{\epsilon_i - 0.5\sigma_R^2} E_i$$

donde  $R_0$  y  $S_0$  son el reclutamiento promedio y biomasa desovante antes de la explotación, respectivamente. El parámetro  $h$  representa la inclinación o “steepness” de la RSR (Dorn, 2002; Francis, 1992; Lee et al., 2012),  $\epsilon_i$  es la desviación anual, que siguió a una distribución normal  $N(0, R)$ , y  $E_i$  es el forzamiento ambiental multiplicador. Se adoptó el supuesto que  $R_0$  es igual al reclutamiento promedio durante 2011-2017 y se fijó el valor de  $h$  en 0,7 considerando estimaciones para la macha del Atlántico *Spisula solidissima* (Hennen et al., 2018; Powell et al., 2015).

En la ecuación 5, el forzamiento ambiental ( $E_i$ ) representa una secuencia temporal de fracasos ( $E_i = 0.1$ ) y éxitos ( $E_i = 1$ ) del reclutamiento. Se generó una secuencia de fracasos (reclutamiento no observado) y éxitos (reclutamiento observado) durante siete años, de acuerdo a la abundancia observada de reclutas (i.e., longitud inferior a 10 mm). De esta forma, la secuencia de eventos fue [Fracaso, Éxito, Éxito, Éxito, Fracaso, Fracaso, Éxito]. Una vez establecida la secuencia de reclutamiento, se ajustó la distribución subyacente de la Cadena de Markov utilizando máxima verosimilitud con el paquete "markovchain" para R (Spedicato, 2017). Posteriormente, se utilizó 50 réplicas de bootstrap para estimar una Cadena de Markov discreta de 2 dimensiones, definiendo el estatus de reclutamiento en fracasos y éxitos, utilizando secuencias de número de reclutas para condicionar las estimaciones de reclutamiento en el modelo poblacional. Se asumió que los fracasos produjeron un 10% de los reclutas esperados y que el éxito produjo un 100% de los reclutas. El valor del 10% para los fracasos es una elección conservadora, teniendo en cuenta que las fallas en el reclutamiento pueden producir disminuciones por debajo de ese porcentaje.

Por último, el reclutamiento anual se distribuyó en clases de longitud de acuerdo con una probabilidad normal a la talla, es decir,

$$6) \quad r_l = \int_l^{l+1} \frac{1}{\sqrt{2\pi\sigma^2}} e^{-(l-l_r)^2/2\sigma^2} dl$$

donde  $l_r$  es la longitud media de reclutamiento,  $l$  es la clase de longitud, y  $\sigma^2$  es la varianza de la longitud de reclutamiento.

#### 4.3.4.4 Modelos de observación

Los modelos de observaciones consistieron en la cosecha anual total y la biomasa total determinada a partir de las evaluaciones directas. La captura por número se estimó de acuerdo con la ecuación de captura de Baranov, es decir,

$$7) \quad C_{i,l} = F_{i,l} N_l (1 - e^{-Z_{i,l}}) / Z_{i,l}$$

donde  $C_{i,l}$  es la captura en longitud en el año. La cosecha anual total ( $Y_i$ ) se estimó en:

$$8) \quad Y_i = \sum_l W_l C_{i,l}$$

donde  $W_l$  es el peso promedio en la clase de longitud  $l$ .

La composición de longitudes en la población se estimó mediante:

$$9) \quad p_{i,l} = \frac{N_{i,l}}{(\sum_l N_{i,l})}$$

La biomasa total ( $TB$ ) en el momento de la evaluación (dentro del año) siguió la expresión:

$$10) \quad TB_i = \psi \sum_l W_l N_{i,l} e^{-\tau Z_{i,l}}$$

donde  $\psi$  es el coeficiente de capturabilidad que se supone igual a 0,99,  $v_l$  es la selectividad de la evaluación en longitud y se supone constante e igual a 1 para todas las clases de longitud, y  $\tau$  es la época del año en que se llevó a cabo la evaluación directa (Tabla 3). Luego se modeló la biomasa vulnerable en las evaluaciones directas ( $B_i$ ) de acuerdo con:

$$11) \quad B_i = \psi \sum_l s_l W_l N_{i,l} e^{-\tau Z_{i,l}}$$

La biomasa total corresponde a la suma de los productos entre la abundancia y el peso promedio en longitud, y la biomasa desovante queda determinada por:

$$12) \quad S_i = \sum_l m_l W_l N_{i,l} e^{-T_s Z_{i,l}}$$

donde  $m_l$  es la ojiva de madurez,  $T_s$  es el comienzo del período de desove dentro de un año (establecido en 0,81). Los parámetros desconocidos del modelo se estimaron ajustando la dinámica poblacional a los datos de terreno (Tablas 3 y 4). La función

objetivo consistió en funciones negativas de log-verosimilitud y probabilidad penalizada (Tablas 4 y 5).

Se utilizó ADMB (Fournier et al., 2012) para implementar el procedimiento de estimación y la fase de proyección en la que se simuló un horizonte de 20 años. La simulación consistió en: a) muestreo desde el modelo ajustado a través de Cadena de Markov - Monte Carlo (MCMC), y b) simulación de una secuencia futura de fallas y éxitos del reclutamiento utilizando la probabilidad de transición de la Cadena de Markov subyacente. Se utilizó 200 simulaciones MCMC obtenidas de 10.000 muestras guardadas cada 50 iteraciones mediante el algoritmo Metropolis implementado en ADMB.





Tabla 4. Configuración general del modelo poblacional de la macha *Mesodesma donacium* en playa Cucao.

Proceso	Definición	Parámetro o vector	Valor	Previo	Penalización	Estimación
Crecimiento	Longitud asintótica de FCVB	$L_{\infty}$	fijo	93,4 mm	-	93,4 mm
	Coefficiente de crecimiento de FCVB	$K$	estimativo	0,25 año <sup>-1</sup>	Ec. T5.1	0,21 año <sup>-1</sup>
	Desviación estándar para la penalización K	$\sigma_k$	fijo	0,1	Ec. T5.1	-
	Longitud de Reclutamiento	$l_r$	estimativo	20 mm	-	8,8 mm
	Desviación estándar de $l_r$	$\sigma$	estimativo	1,5 mm	-	2,72 mm
	Forma de incremento en el crecimiento	$\beta_r$	estimativo	0,2	-	0,313
Mortalidad	Tasa de mortalidad natural	$M$	fijo	0,3	-	-
	Mortalidad pesquera	$F_i$	estimativo	$\log(F_i)$	$\sim U(-6, 1,39)$	3
Reclutamiento	Steepness de RSR	$h$	fijo	0,7	-	-
	Reclutamiento promedio sin explotar	$\bar{R}$	estimativo	$\log(R_0)$	-	38,5 10 <sup>6</sup>
	Desviación estándar del reclutamiento	$\sigma_R$	fijo	0,4	-	-
	Desviaciones del reclutamiento (escala logarítmica)	$\varepsilon_i$	estimativo	$\varepsilon_i \sim N(0, \sigma_R)$	Ec. T5.2	3
Capturabilidad	Coefficiente de capturabilidad de evaluaciones	$\psi$	estimativo	0,99	Ec. T5.3	0,99
	Desviación estándar para la penalización $\psi$	$\sigma_{\psi}$	fijo	0,1	Ec. T5.3	-
Selectividad	Selectividad de la pesca	$s_l$	fijo	-	-	-
	Selectividad de la evaluación	$v_l$	fijo	-	-	-
Reproducción	Ojiva de madurez	$m_l$	fijo	-	-	-
	Steepness	$h$	fijo	0,7	-	-
	Tiempo de desove	$T_s$	fijo	0,81	-	-

FCVB: Función de crecimiento de von Bertalanffy.

Tabla 5. Penalizaciones ( $\rho_j$ ) y funciones log-verosimilitud negativas ( $\ell_j$ ) que contribuyen a la función objetivo ( $f$ ) en la estimación de parámetros desconocidos ( $\theta_k$ ) para el modelo operacional de la macha. Desviaciones estándar para el ajuste: desviación estándar para la cosecha total  $\sigma_Y = 0,01$ ; desviación estándar para la biomasa total de la evaluación directa  $\sigma_B = 0,1$ ; tamaño efectivo para la composición de tallas multinomial  $\omega_j$ .

Componentes	Ecuación	Número
Coefficiente de crecimiento de FCVB	$\rho_2 = \frac{(\log(\hat{K}/K))^2}{2\sigma_K}$	T5.1
Desviaciones de reclutamiento (escala logarítmica)	$\rho_1 = \frac{1}{2\sigma_R} \sum_i \varepsilon_i^2$	T5.2
Coefficiente de capturabilidad de evaluaciones	$\rho_3 = \frac{(\log(\hat{\psi}/\psi))^2}{2\sigma_\psi}$	T5.3
Cosecha anual total	$\ell_1 = \frac{1}{2\sigma_Y^2} \sum_{i=1}^n (\log(\hat{Y}_i/Y_i))^2$	T5.4
Biomasa de la evaluación	$\ell_2 = \frac{1}{2\sigma_B^2} \sum_{i=1}^n (\log(\hat{T}B_i/TB_i))^2$	T5.5
Composición de longitudes de la evaluación	$\ell_3 = \omega_i \sum_{i=1}^n \sum_l p_{i,l} \log(\hat{p}_{i,l})$	T5.6
Función objetivo	$f = \sum_j \ell_j + \sum_j \rho_j$	T5.7

#### 4.3.4.5 Rendimiento de las Tasas de Captura

Se resumió las trayectorias del reclutamiento, biomasa desovante y mortalidad por pesca resultantes de la modelación utilizando intervalos de confianza del 95% y 80%, obtenidos mediante la aplicación del método de percentiles a todas las realizaciones obtenidas por MCMC. Para cuantificar el agotamiento de la población se calculó la relación entre la biomasa de desove en un año determinado y la biomasa de desove promedio no explotada. Ante la falta de puntos de referencia explícitos en el plan de manejo para la biomasa desovante de machas, se consideró una reducción predeterminada de la biomasa desovante al 40% del escenario promedio no explotado, es decir,  $S_{\text{target}} = 0.4 S_0$ .

Por lo tanto, las tasas de explotación que generan disminuciones en la biomasa más allá del nivel objetivo se consideraron insostenibles para la población de machas. Se calculó la probabilidad de mantener la biomasa desovante por encima de este objetivo como

$Pr[S_i / S_{\text{target}} > 1]$ . Por el contrario, la probabilidad de un colapso se calculó considerando reducciones en la biomasa por debajo del 50% del punto de referencia objetivo, es decir,  $Pr[S_i / S_{\text{target}} \leq 0.5]$ . Se consideró "buen desempeño" los casos en los que las tasas de explotación generaron probabilidades  $> 50\%$  de alcanzar el objetivo, mientras que los casos con una probabilidad de colapso superior al 10% fueron considerados como "mal desempeño".



## 5 RESULTADOS

### 5.1 Capítulo 1: Coastal geomorphology and oceanographic features shape subtidal benthic communities in management areas of central Chile

Paper published in Aquatic Conservation: Marine and Freshwater Ecosystems, 2021

#### Abstract

1. The spatial variation in community structure among 30 areas for the management and exploitation of benthic resources (AMEBRs) in central Chile was assessed from surveys conducted during the same spring–summer season. One hundred taxa identified in the subtidal surveys were grouped into 10 functional groups.
2. The influence and relative importance of external factors over benthic associations were assessed through nonmetric multidimensional scaling (NMDS) and path analysis. Three main categories of external factors were considered: ‘terrain traits’ (e.g., coastline exposure), ‘surface-ocean conditions’ (e.g., sea surface temperature, SST), and ‘fishery-related variables’ (e.g., cumulative landings).
3. The NMDS revealed a strong association between benthic community structure and both terrain and surface-ocean conditions (42% of variance explained by permutational multivariate analysis of variance), but not with fishery-related variables. Assemblages typical of rocky substrates were associated with larger seasonal fluctuations in SST and surface chlorophyll a. The presence of soft-bottom functional groups was associated with higher levels of surface fluorescence and larger seasonal fluctuations in a satellite-derived proxy for river-plume influence (nLw645).
4. A path analysis model for hard-bottom communities reached a 49% goodness of fit (GOF), with the presence of epifaunal filter-feeders, grazers, predators, and scavengers being significantly correlated with leathery and corticated foliose algae, which in turn depend on the fraction of rocky substrate in the AMEBR; the fraction of rocky substrate is positively correlated with coastline exposure.
5. The model for soft-bottom communities reached a 52% GOF with the presence of infaunal filter-feeders and epifaunal detritivores depending directly on SST and surface chlorophyll a. The fishery-related variables considered in the model had no apparent effect on the structure of either type of subtidal community.

6. These results provide a hierarchy of physical–biological associations determining the functional composition of subtidal benthic communities in management areas along central Chile. This knowledge may improve future assessments of ecosystem response to changes in environmental conditions and management strategies.



# Coastal geomorphology and oceanographic features shape subtidal benthic communities in management areas of central Chile

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## KEYWORDS

AMEBRs, benthic communities, Central Chile, coastal management, subtidal, TURF

## 1 | INTRODUCTION

The study of patterns in species distributions and the mechanisms that generate them has been one of the main areas of research in ecology and evolutionary biology (Pianka, 1966). Identifying the scales at which variability occurs in space and time is necessary to understand factors and processes that generate patterns in the biotic and abiotic components of ecosystems (Levin, 1992). Marine communities consist of groups of populations structured by multiple factors over a range of spatial scales (Grantham, Eckert, & Shanks, 2003). The proper management and conservation of marine communities depend on understanding these factors, particularly in the context of a changing climate. Also, understanding the forces that modulate the spatial and temporal variation of the composition, abundance, and diversity of marine communities is critical for the design and implementation of conservation measures, as well as the spatial management of coastal habitats at scales that are relevant to key biological and ecological processes, beyond administrative or political considerations (Carr et al., 2017; Reiss, Hoarau, Dickey-Collas, & Wolff, 2009).

The structure and functioning of coastal benthic communities are closely linked to substrate features, such as bottom type (hard or soft), grain size (in soft-bottom habitats), and spatial heterogeneity, as well as to the hydrodynamics and productivity of the overlying water column. The interaction of meteorological and oceanographic processes over a range of spatio-temporal scales shapes the patterns of coastal circulation and productivity, which in turn determine the supply of food, nutrients, and propagules to benthic communities (Blanchette, Wieters, Broitman, Kinlan, & Schiel, 2009; Gaines, Brown, & Roughgarden, 1985; Largier, 2019; Menge & Menge, 2013; Roughgarden, Gaines, & Possingham, 1988). Although the relationship between community structure and environmental factors is complex and often nonlinear (Anderson et al., 2008), a small number of environmental variables may explain a substantial fraction of the variability in community structure (Legendre, Borcard, & Peres-Neto, 2005).

Topography and geomorphology, and their interaction with coastal winds, modulate coastal circulation and therefore strongly influence the hydrographic and physical-chemical conditions of near-shore waters. Coastal upwelling has a strong influence on water-column properties and their spatio-temporal variability in the near-shore (e.g. Tapia, Largier, Castillo, Wieters, & Navarrete, 2014), as well as on the patterns of larval dispersal and settlement for many species of benthic invertebrates (e.g. Barth et al., 2007; Navarrete, Wieters, Broitman, & Castilla, 2005), thus influencing the spatial distribution, population dynamics, and even genetic structure of coastal populations (Barshis et al., 2011). At the community level, geographic changes in the local regime of coastal upwelling appear to have a strong effect on species interactions, recruitment rates, and food supply to rocky intertidal habitats (Menge & Menge, 2013). In addition to

upwelling effects, coastal exposure has a strong influence on the local distribution of intertidal benthic communities (Burrows, 2012), through the changing effect of waves on larval transport to settlement sites (Morgan, Shanks, MacMahan, Reniers, & Feddersen, 2018; Navarrete et al., 2015), as well as on post-settlement survival (Pineda, Porri, Starczak, & Blythe, 2010). Substrate type, on the other hand, is critical for the pattern of larval settlement in benthic species with a planktonic larval phase, in which the selection of the substrate before settlement has a strong evolutionary basis (Morse, 1990).

Over the past decade, many studies have addressed the spatial structuring of intertidal benthic communities by coastal topographic features and changing oceanographic regimes (e.g. Broitman et al., 2011; Wieters, Broitman, & Branch, 2009). Comparatively little is known about the factors that shape subtidal benthic communities over similar spatial scales, however. This partly arises from a lack of information with sufficient spatial coverage and the lack of consistency in methods of observation. In this context, the areas for the management and exploitation of benthic resources (AMEBRs), a territorial use rights in fisheries (TURF) programme established for the management of coastal areas in Chile since 1991, provide a rich source of information on the structure of subtidal communities at many sites, spanning scales of 10–100 km. Legally organized artisanal fishers are assigned temporary rights to exploit benthic species within defined coastal areas that vary in size from less than 1 ha to more than 4,000 ha, with maximum depths ranging from approximately 5 m to greater than 100 m (<http://www.subpesca.cl/portal/619/w3-article-79986.html>). Fishers are required to develop a management plan for sustainable harvesting in an AMEBR, including compulsory annual or biannual surveys of the benthic communities, which are typically conducted by private consultants sought and hired by the fishers themselves. Data from these benthic surveys, along with estimates of abundance for the species of commercial interest, are submitted to the Chilean Undersecretariat of Fisheries (SUBPESCA, Ministry of Economy). Although researchers can eventually access the benthic-community data, the information from surveys conducted by different technical teams may not always be comparable because of differences in sampling strategies and protocols. This flaw in the data has thus far hindered analyses that go beyond the scale of a single AMEBR and span a larger section of the Chilean coast.

The research on AMEBRs published thus far has focused on aspects such as their positive effects on benthic biodiversity (Gelcich, Godoy, Prado, & Castilla, 2008), their implications for governance (e.g. Gelcich et al., 2010; Marin & Berkes, 2010), and the behavioural patterns of fishers in charge of AMEBRs (Bandin & Quiñones, 2014; Gelcich, Edwards-Jones, & Kaiser, 2005). There is, however, a lack of studies on the connection between spatial changes in oceanographic conditions and changes in the underlying benthic communities. This is a critical aspect to study given the current and projected climate

scenarios, the expected impact on the physics, chemistry, and productivity of coastal waters and, by extension, on the structure and functioning of coastal ecosystems (see Doney et al., 2012). As climate change and the pressure imposed by fishing on marine ecosystems can have a synergistic effect (Perry et al., 2010), it is also necessary to consider the role that harvesting rates and other fishery-related variables may play in shaping the spatial pattern of subtidal benthic community structure.

In this contribution, data from 30 surveys conducted by the same technical team at AMEBRs spanning approximately 200 km of the central Chilean coast are used to assess the relationship between spatial changes in the community structure of subtidal benthos and differences among AMEBRs in terms of environmental and fishery-related variables. The selected environmental variables were used as proxies for the influence of coastal upwelling, exposure to wave action, and river plumes. Through their effects on the supply and/or retention of nutrients, local productivity, and larval settlement on subtidal habitats, these factors are expected to shape the community structure in the subtidal benthos of central Chile and other regions with a similar oceanographic regime. A better understanding of these relationships may contribute to the conservation of coastal ecosystems, and the implementation of sustainable management strategies for exploited benthic species.

## 2 | METHODS

### 2.1 | Area and study period

Between October 2015 and January 2016 (i.e. austral spring–summer), 30 AMEBRs were surveyed in central Chile (36°10'S–37°45'S). The 30 sites surveyed span a linear distance of 190 km that corresponds to more than 300 km of shoreline (Figure 1). The surface area of the AMEBRs surveyed ranged from 0.8 to 947.0 ha, with 63% being <100 ha (see histogram in Figure 1).

The coast of central Chile (36–38°S) is characterized by a complex coastline that includes a system of nested embayments oriented towards the equator: Gulf of Arauco, Concepción Bay, and Coliumo Bay. Two submarine canyons and a major cape at the southern tip of the gulf (Punta Lavapié) strongly influence coastal circulation and promote a high degree of spatial and temporal variability in nearshore oceanographic conditions (Sobarzo, Bravo, Donoso, Garcés-Vargas, & Schneider, 2007). On the other hand, freshwater discharges from the two main rivers in this region (Biobío and Itata) are highly seasonal (Saldías, Sobarzo, Largier, Moffat, & Letelier, 2012), and play an important hydrographic and biogeochemical role over the continental shelf (Iriarte, Vargas, Tapia, Bermúdez, & Urrutia, 2012). Combined with seasonal changes in solar radiation and ocean–atmosphere heat flows, these factors determine a high degree of spatial heterogeneity in environmental conditions as well as in productivity (Henriquez et al., 2007), which is likely to affect benthic communities both directly and indirectly.

### 2.2 | Benthic surveys

Base information for community analysis was obtained from benthic surveys conducted by scientific divers with extensive experience in the field identification of subtidal species. Subtidal surveys were designed so that the entire surface area with a depth of <30 m was covered, using at least 40 observation points per AMEBR. Each of these observation points consisted of a 10-m × 2-m transect oriented in a cross-isobath fashion. At each point, geographic coordinates at the deepest end of the transect were recorded from a global positioning system (GPS). Divers surveyed each transect from the deepest to the shallowest ends. Substrate type, depth, and density of the main taxonomic groups identified were recorded for each transect. More details on the surveying procedure are provided in Appendix S1.

These benthic surveys produced a dataset that allowed the characterization of distribution patterns for multiple species at the same points in space, including the density of disaggregated species (e.g. limpets, urchins, and crabs) within the 20-m<sup>2</sup> transect and the density of aggregated species (e.g. mussels, clams, and macroalgae) averaged over five 0.25-m<sup>2</sup> quadrats, arranged every 2 m along the transect. Additionally, the percentage cover, averaged across quadrats in each transect, was used as a measure of the relative density for species that are difficult to count individually in the subtidal (e.g. barnacles and ascidians).

### 2.3 | Classification of biological data

The 100 benthic species identified during the surveys were classified into functional groups. For algae, functional groups were defined following Steneck and Dethier (1994), who proposed a classification based on anatomical and morphological features that often respond to ecological characteristics. For invertebrates, biological trait analysis (BTA) was used to explore and define ecological functioning (Sigala, Reizopoulou, Basset, & Nicolaidou, 2012; van der Linden et al., 2012). BTA combines quantitative structural data with information on the biological features of each taxon to functionally characterize species assemblages (Bremner, Rogers, & Frid, 2006). The classification criteria (see details in Appendix S2) are then a combination of morphological traits and ecological considerations, and their primary purpose is to capture the functional structure of the subtidal communities surveyed.

As a result of the differences in density measurements collected for different taxa (number of individuals, coverage, wet weight), the analysis was based on the proportion of transects within each AMEBR that contained each taxon.

### 2.4 | Surface ocean conditions

Given the spatial scale of AMEBRs, the analysis of satellite-derived time series was based on images with a resolution of approximately

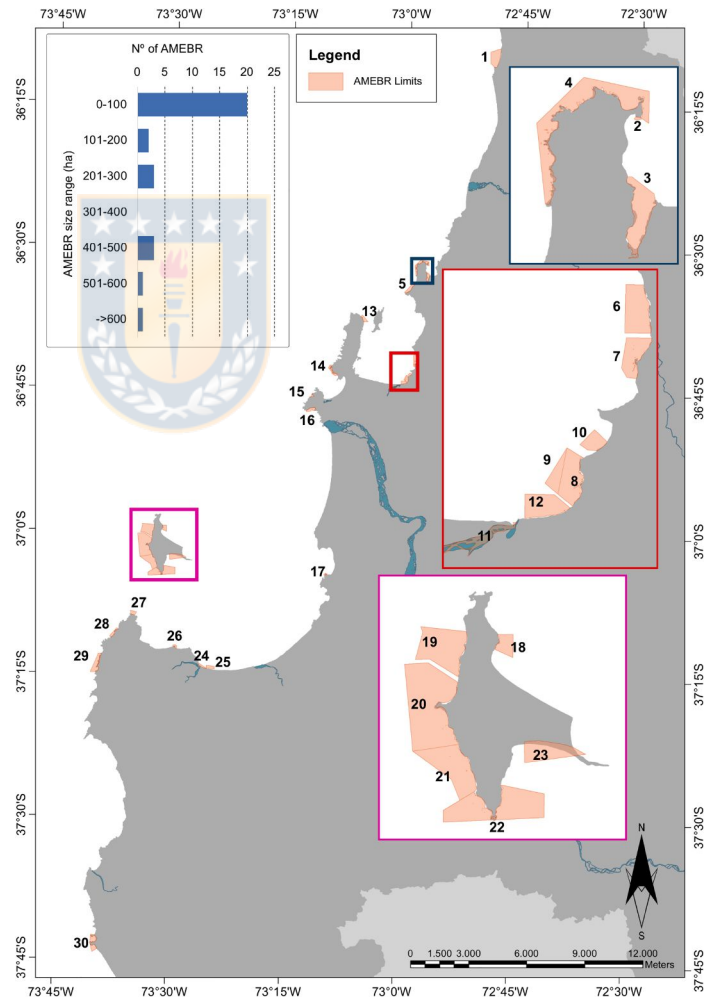


1 km; this is higher than the typical 4-km resolution used thus far in most published studies of this coastal region (e.g. Correa-Ramirez, Hormazabal, & Yuras, 2007). A coarser resolution may hinder the identification of relevant features near the coastline, thus limiting the identification of processes that might be important in structuring benthic communities nearshore. Also, it must be noted that using ocean colour data derived from the moderate resolution imaging spectro-radiometer (MODIS) on board the Aqua satellite implies an advantage, compared with other colour sensors (e.g. the sea-viewing wide field-of-view sensor, SeaWiFS), because it delivers information on both ocean colour (chlorophyll *a*, Chl *a*; normalized fluorescence line height, nFLH; and normalized water-leaving radiance at a wavelength of 645 nm, nLw645) and sea surface temperature (SST), thereby allowing the analysis to use concomitant and directly

comparable measurements. Also, the increased number of spectral bands in MODIS allows the use of ocean colour parameters such as nFLH that are not available in SeaWiFS.

For each study site, environmental time series were extracted from 7-day composites of MODIS-Aqua imagery available for the period 2003–2016. Composites with a spatial resolution of approximately 1 km were produced using SEADAS (SeaWiFS Data Analysis System; National Aeronautics and Space Administration, NASA) for the following variables: SST, Chl *a*, and nFLH, as proxies for phytoplankton biomass (i.e. food availability), and normalized water-leaving radiance at a wavelength of 645 nm (nLw645) as a proxy for the presence of river plumes in this region (see Saldías et al., 2016).

To quantify the amplitude of the seasonal signal in each variable, and the variability that is not explained by the seasonal cycle



**FIGURE 1** Study area and location of the 30 areas for the management and exploitation of benthic resources (AMEBRs) surveyed in central Chile. The inset in the top-left corner shows the distribution of AMEBR sizes in terms of surface area (ha)

(i.e. residual variance), harmonic analysis was applied to each time series and site. The long-term mean was also computed for each time series. Thus, three descriptors were obtained for each of the four satellite-derived variables at each site.

## 2.5 | Terrain traits

Terrain traits considered in the analysis were coastline exposure and percentage of rocky substrate within each AMEBR. Quantitative assessment of the coastline exposure at each of the 30 AMEBRs was based on the analysis of fetch, i.e. the length of unobstructed water over which the wind can blow from a specific direction. To quantify the fetch, 40 radii (9° spacing) of length 300 m were drawn from each point, and the distance from the centre to the nearest shoreline was then recorded for each radius. The coastal exposure index for a given site was computed by averaging all such distances. This procedure was implemented using the `FETCH` package (Seers, 2017) available for R (<http://www.r-project.org>).

The percentage of rocky substrate in each AMEBR was determined as the average percentage of hard-bottom substrate recorded in the sampling units visited during each subtidal survey.

## 2.6 | Fishery-related variables

The analysis of potential fishing effects on the AMEBR subtidal communities was based on official landing statistics, accumulated between 2000 and 2016, provided by the Chilean National Fisheries Service (Servicio Nacional de Pesca y Acuicultura, SERNAPESCA). Additionally, and considering the existence of poaching within AMEBRs (Bandin & Quiñones, 2014; Chávez, Murphy, & Stranlund, 2018), the number of divers in each organization and, as a measure of surveillance capacity, the distance between the AMEBR and the association's base cove were included.

## 2.7 | Statistical analysis

### 2.7.1 | Nonmetric multidimensional scaling (NMDS)

A Bray-Curtis similarity matrix was constructed from presence/absence data by functional groups. A two-dimensional NMDS ordination was performed to visualize patterns of similarity in community structure among AMEBRs. Later, non-parametric analysis of variance (PERMANOVA) was used to test for significant effects of environmental and fishery-related variables over the ordination results. Significance was estimated based on 9,999 permutations of residuals. All computations were performed in R using the libraries `VEGAN` (Oksanen et al., 2017) and `MASS` (Venables & Ripley, 2002).

### 2.7.2 | Path analysis

Path analysis is an extension of multiple linear regression (Legendre & Legendre, 1998) developed by Wright (1934) as a method to study the direct and indirect effects of hypothesized variables as causes of variables treated as effects. One of the advantages of path analysis is that it allows the formulation of a priori hypotheses on the causal relationships between descriptors, examining their feasibility by observing the regression and correlation coefficients calculated between these descriptors (Pedhazur, 1997). A path diagram is useful to show graphically the feasible pattern of causal relationships among a set of variables (Pedhazur, 1997). A full path model consists of two submodels: the inner model and the outer model (Sanchez, 2013). The inner (or structural) model is the part that pertains to the relationships among latent variables (i.e. variables that summarize the responses of several observed variables or indicators), and the outer (or measurement) model consists of those measures that create latent variables (for a more detailed explanation, see Appendix S3).

In this study, coastline exposure (i.e. fetch) was expected to directly influence the environmental variables used to characterize surface-ocean conditions as well as the proportion of rocky substrate (see Figure 2), as bays and other areas sheltered from wave action often have a higher proportion of soft substrate than exposed areas. On the other hand, fishing activities could also be affected by environmental conditions, with greater fishing effort in areas with more favourable conditions for navigation (i.e. less exposure). The presence of algae could be associated with the presence of rocky substrate, coastline exposure, and surface-ocean features indicative of more favourable nutrient conditions. Finally, the presence of invertebrates may depend differently on each of the endogenous and exogenous variables considered in this conceptual model.

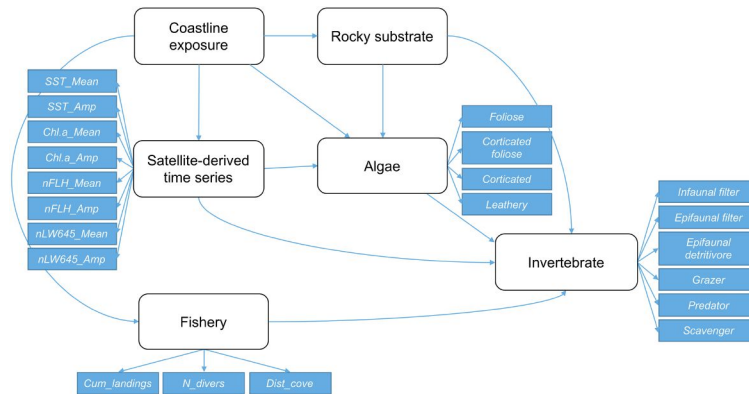
Computations to implement this analysis were performed in R using the partial least-squares modelling library `PLSPM` (Sanchez et al., 2017), and following the recommendations of Sanchez (2013).

## 3 | RESULTS

### 3.1 | Biological data and explanatory variables

One hundred taxa were identified across the 30 AMEBRs surveyed. The classification of those taxa into functional groups revealed high among-site variability in community composition. Foliose algae and infaunal filter-feeders were present in 13 and 14 sites, respectively (<47%), whereas corticated algae, epifaunal filter-feeders, grazers, predators, and scavengers were present in 26 AMEBRs (>85%). The poorest sites (with fewer than four functional groups) were located in sheltered sections of Concepcion Bay and the Gulf of Arauco (sites 11 and 25 in Figure 1), whereas all 10 functional groups were present at sites located in semi-exposed sections of Concepcion Bay and south of San Vicente Bay (sites 13 and 15 in Figure 1).

**FIGURE 2** Schematic of the conceptual model used in this analysis for variables affecting subtidal communities in areas for the management and exploitation of benthic resources (AMEBRs). Arrows depict direct effects of one variable (boxes) on another. Blue and white rectangles represent outer and inner variables, respectively. For a detailed description of inner variables and outer variables, see Appendix S3



**TABLE 1** List of independent variables inputted into the analysis, indicating the units of measure and the source of the information

Type of variable	Variable	Code	Unit	Source
Surface ocean conditions	Average of sea surface temperature (SST) for 2003–2017	SST_Mean	°C	MODIS-Aqua
	Harmonic amplitude of SST for 2003–2017	SST_Amp	°C	
	Average of surface chlorophyll <i>a</i> (Chl <i>a</i> ) concentration for 2003–2017	Chl <i>a</i> _Mean	mg m <sup>-3</sup>	
	Harmonic amplitude of Chl <i>a</i> concentration for 2003–2017	Chl <i>a</i> _Amp	mg m <sup>-3</sup>	
	Average of normalized fluorescence line height (nFLH) for 2003–2017	nFLH_Mean	mW cm <sup>-2</sup> μm <sup>-1</sup> sr <sup>-1</sup>	
	Harmonic amplitude of nFLH for 2003–2017	nFLH_Amp	mW cm <sup>-2</sup> μm <sup>-1</sup> sr <sup>-1</sup>	
	Average of normalized water-leaving radiance at 645 nm (nLw645) for 2003–2017	nLw645_Mean	mW cm <sup>-2</sup> μm <sup>-1</sup> sr <sup>-1</sup>	
	Harmonic amplitude of nLw645 for 2003–2017	nLw645_Amp	mW cm <sup>-2</sup> μm <sup>-1</sup> sr <sup>-1</sup>	
Terrain traits	Coastline exposure	Fetch	%	This study
	Percentage of rocky substrate in total sampling units	Rocky_sub	%	Direct subtidal evaluation
Fishery-related variables	Cumulative landings by AMEBR for 2000–2017	Cum_landings	ton	National Service of Fisheries
	Number of divers in fishers' organization of AMEBR	N_divers	<i>n</i>	
	Distance from the centre of each AMEBR to the main cove of the fishers' organization	Dist_cove	Km	This study

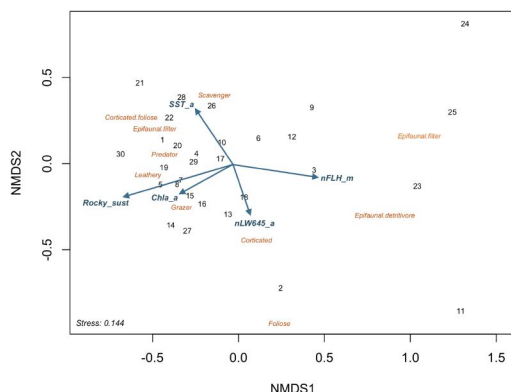
The variables selected as explanatory factors are listed in Table 1. Only the long-term mean and seasonal amplitudes of each satellite-derived time series were used, as the residual variance and seasonal amplitude were highly correlated for all variables and sites.

### 3.2 | NMDS and PERMANOVA

The NMDS ordination (Figure 3) revealed that along the first axis (NMDS1) there is a clear separation between sites characterized by the presence of infaunal filter-feeders and epifaunal detritivores (right side of the plot in Figure 3) from sites where foliose corticated algae, epifaunal filter-feeders, predators, and leathery algae are present (left

side of the same plot). The central position of corticated algae in the ordination was consistent with their presence in most of the sites (see Appendix S3). The presence of foliose algae, on the other hand, was associated with sites 2 and 4, which correspond to neighbouring sites located in Coliumo Bay (see Figure 1).

A PERMANOVA analysis of the Bray–Curtis distance matrix, performed independently for each set of external factors, revealed that satellite-derived variables accounted for approximately 40% of the NMDS ordination, with the seasonal amplitude of SST and Chl *a*, as well as mean fluorescence (nFLH) appearing as statistically significant sources of variation (Table 2). The terrain-related variables of coastline exposure and rocky substrate were both statistically significant, and together explained 33% of the variability. Finally, none of the



**FIGURE 3** Nonmetric multidimensional scaling (NMDS) biplot showing the relationship between community structure and environmental variables found to be significant via PERMANOVA. Numbers correspond to areas for the management and exploitation of benthic resources (AMEBRs), ordered from north to south (see Figure 1), blue labels correspond to environmental variables, with the strongest effects on the ordination of functional groups (orange labels)

variables associated with the fishery appeared to be statistically significant factors in the model.

A model that combined the variables found to be statistically significant factors ('Selected variables' in Table 2) explained 42% of the total variance. In this case, however, coastal exposure was no longer significant as an explanatory variable, which is probably because of its high correlation with the selected satellite variables as well as with the percentage of rocky substrate. When the explanatory variables found to be statistically significant in this model were superimposed on the ordination of Figure 3, it became apparent that the segregation of sites along the first NMDS axis is strongly influenced by the presence of rocky substrate and the amplitude of seasonal fluctuations in surface Chl *a*. Sites with higher fractions of rocky substrate and greater fluctuations in Chl *a* are dominated by foliose corticated algae, epifaunal filter-feeders, predators, leathery algae, and grazers. Sites where infaunal filter-feeders and epifaunal detritivores are dominant, on the other hand, are characterized by higher mean levels of fluorescence (indicative of higher planktonic productivity). The analysis also revealed that corticated foliose algae, epifaunal filter-feeders, and scavengers are associated with greater amplitudes in the SST seasonal cycle, whereas foliose algae are associated with greater seasonal fluctuations (i.e. amplitude) of the river-plume satellite proxy (nLw645).

### 3.3 | Path analysis

The evaluation of the conceptual model shown in Figure 4 yielded a 41% goodness of fit, and revealed strong correlations between coastline exposure, the percentage of rocky substrate, and the satellite-derived variables, but not between the coastline exposure and

fishery-related variables. In this first model, the presence of invertebrates was only explained significantly by the percentage of rocky substrate. The presence of algae, the satellite-derived variables, or variables pertaining to the fishery did not show significant results. The presence of algae could not be explained significantly by any of the endogenous variables considered in the model. Foliose and corticated algae showed positive correlations with the latent variable 'Algae', whereas the presence of leathery and corticated foliose algae showed negative correlations. As for invertebrates, infaunal filter-feeders and epifaunal detritivores showed negative correlations with the inner latent variable 'Invertebrate', whereas epifaunal filter-feeders, grazers, predators, and scavengers were positively correlated.

As a requirement for a path-analysis model is that all indicators in the reflective block (outer model) are positively correlated (Sanchez, 2013), and considering that the results from the first model suggested the existence of distinct paths for functional groups of algae and invertebrates (i.e. those with positive and negative loadings in the NMDS), independent models were implemented for hard-bottom and soft-bottom communities. In these models, nonsignificant relationships and the outer variables with low correlations were discarded from each model (Figure 5).

The model for hard-bottom communities (Figure 5a) explained approximately 50% of the variance and showed that the presence of epifaunal filter-feeders, grazers, predators, and scavengers is significantly associated with the presence of leathery and corticated foliose algae, and that these algae respond positively to the presence of rocky substrate, which in turn is positively correlated with coastline exposure. In this case, the presence of leathery and corticated foliose algae did not appear significantly correlated with the amplitude of seasonal fluctuations in SST, Chl *a*, or nLw645. The presence of invertebrates, on the other hand, was not significantly correlated with the fishery-related variables (Figure 5a).

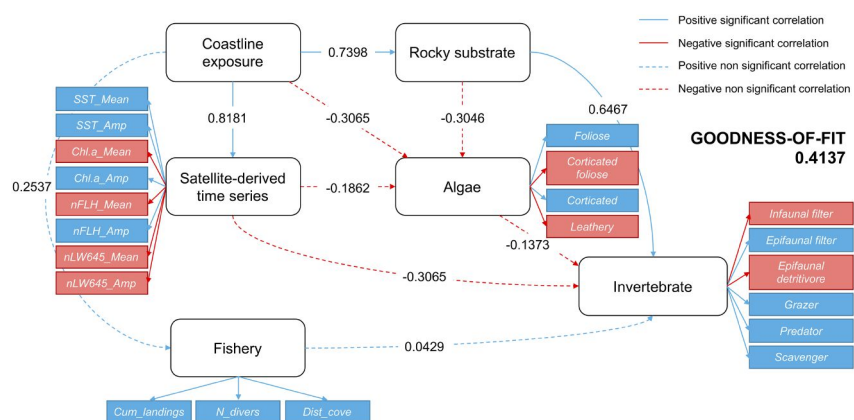
The model for soft-bottom communities (Figure 5b) explained 52% of the variance and revealed that infaunal filter-feeders and epifaunal detritivores are positively correlated with mean Chl *a* and the inverse of SST amplitude (i.e. low seasonal variability in SST). Both variables were negatively correlated with coastline exposure and showed significant correlations with the presence of foliose and corticated algae. The presence of soft-bottom invertebrates was not significantly correlated with either of the selected fishery-related variables.

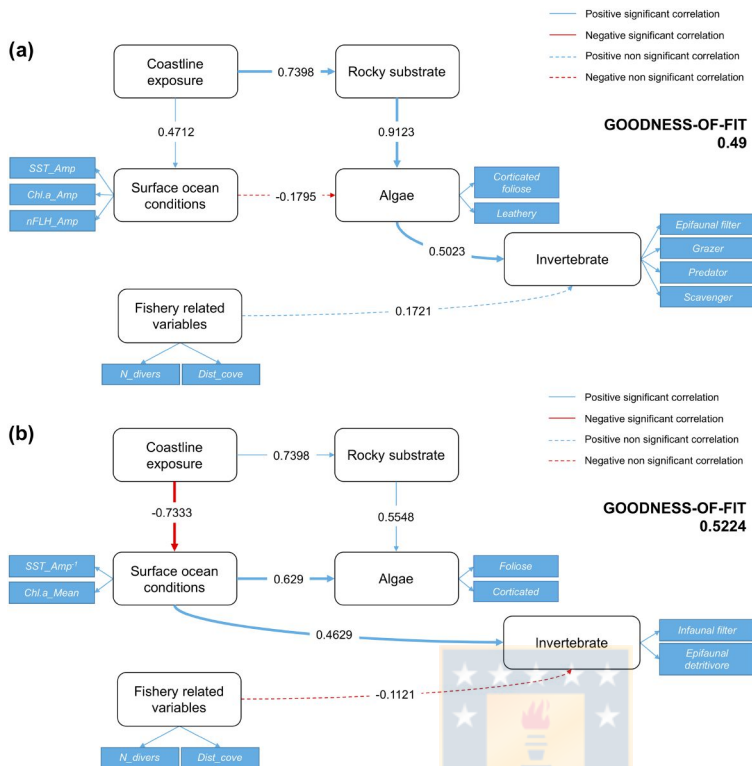
## 4 | DISCUSSION

The results highlight the preponderance of coastline exposure as a modulator of substrate type and water-column conditions in the study area and reveal differences in the effect of oceanographic variables on hard-bottom versus soft-bottom communities. In hard-bottom communities, the percentage of rocky substrate appears to modulate the presence of brown and foliate-corticated algae, and the subsequent effect of these algae on the presence of invertebrates such as epifaunal filter-feeders, grazers, predators, and scavengers. In soft-

**TABLE 2** Results of PERMANOVA analysis of benthic community structure for 30 AMEBRs

Variables	Source of variation	df	SS	MS	F Model	R <sup>2</sup>	P (>F)
Surface ocean conditions	SST_Mean	1	0.0706	0.0707	0.5519	0.0158	0.768
	SST_Amp	1	0.3930	0.3930	3.0705	0.0879	0.016 *
	Chl <i>a</i> _Mean	1	0.1817	0.1817	1.4196	0.0407	0.204
	Chl <i>a</i> _Amp	1	0.3148	0.3149	2.4597	0.0704	0.045 *
	nFLH_Mean	1	0.3310	0.3310	2.5857	0.0741	0.036 *
	nFLH_Amp	1	0.0420	0.0420	0.3283	0.0094	0.902
	nLW645_Mean	1	0.1637	0.1637	1.2792	0.0366	0.288
	nLW645_Amp	1	0.2849	0.2849	2.2260	0.0637	0.069
	Residuals	21	2.6881	0.1280		0.6014	
Total	29	4.4700			1.0000		
Terrain traits	Fetch	1	0.8772	0.8772	7.9724	0.1962	0.001 *
	Rocky_subst	1	0.6220	0.6221	5.6536	0.1392	0.004 *
	Residuals	27	2.9707	0.1100		0.6646	
	Total	29	4.4700			1.0000	
Fishery related variables	Cum_landings	1	0.0663	0.0663	0.4077	0.0148	0.823
	N_divers	1	0.1489	0.1489	0.9154	0.0333	0.47
	Dist_cove	1	0.0268	0.0268	0.1650	0.0060	0.984
	Residuals	26	4.2280	0.1626		0.9459	
	Total	29	4.4700			1.0000	
Selected variables	SST_Amp	1	0.2826	0.2826	2.6183	0.0632	0.026 *
	Chl <i>a</i> _Amp	1	0.2683	0.2683	2.4851	0.0600	0.035 *
	nFLH_Mean	1	0.4331	0.4331	4.0124	0.0969	0.003 *
	nLW645_Amp	1	0.3089	0.3089	2.8612	0.0691	0.026 *
	Rocky_subst	1	0.5864	0.5864	5.4320	0.1312	0.002 *
	Residuals	24	2.5907	0.1080		0.5796	
	Total	29	4.4700			1.0000	

\*Significant effects, with  $\alpha = 0.05$ .**FIGURE 4** Path analysis of the complete model, i.e. including all variables and correlations. The colour and type of arrow lines indicate the sign and significance of the correlations (see legend). Thicker lines represent the primary sequence of the correlations identified



**FIGURE 5** Evaluation of separate path-analysis models for (a) hard-bottom communities and (b) soft-bottom communities. The colour and type of arrow lines indicate the sign and significance of the correlations (see legend). Thicker lines represent the primary sequence of the correlations identified

bottom communities, surface ocean conditions are the main factor explaining the presence of infaunal filter-feeders and epifaunal detritivores. The presence of soft-bottom zones in sheltered or semi-exposed places may provide suitable conditions for the settlement of some invertebrate larvae without a significant influence of other taxonomic groups in structuring benthic communities.

#### 4.1 | Using AMEBRs to study subtidal benthic communities

Currently there are more than 500 operational AMEBRs along the Chilean coast, and all of them must conduct periodic benthic surveys (annual or biennial) to assess the abundance of focal species and check the state of benthic communities. Despite this wealth of information, most of the studies on AMEBRs that have been published thus far focus on their implications for governance (Castilla & Gelcich, 2008; Gelcich et al., 2010; Marín & Berkes, 2010), or the behavioural patterns of fishers that benefit from these management areas (Bandin & Quiñones, 2014; Gelcich et al., 2005). Only two published studies have dealt with the effects of AMEBRs on the benthic community: one is based on observations from three sites (Gelcich et al., 2008), whereas the other uses data from surveys conducted

over 20 years at a single AMEBR (Molina et al., 2014). This general lack of spatial replication and geographic coverage hinders efforts to test whether changes in community structure are forced from the top down, through changes in predator density or fishing pressure, or result from changes in the pattern of environmental variability.

In this contribution, the spatial dimension was considered by analysing data from 30 AMEBRs, surveyed quasi-simultaneously, spanning approximately 200 km along the central Chilean shoreline. Combining community information derived from compulsory AMEBR surveys to analyse spatial variability in benthic community structure is a novel approach, and more so when the emerging patterns in benthic community structure are compared with among-site variability in terrain features, surface ocean conditions, and fishery-related variables. Our results show that environmental factors can be combined to predict, to some extent, the type of benthic community expected for a given site, thus contributing to the understanding of factors that are mostly responsible for the spatial structuring of subtidal benthos. Understanding how coastal populations are geographically structured according to oceanographic variability is fundamental to further understand biodiversity and evolutionary processes, as well as to address conservation challenges (Barshis et al., 2011) or to identify areas where anthropogenic impacts should be reduced (Burrows, 2012).

## 4.2 | Predicting benthic community structure

The development of statistical models has a wide application in ecology and has provided inferences about habitat relationships, the presence of taxonomic groups, and the effects of human disturbance (Latimer, Wu, Gelfand, & Silander, 2006). Most statistical approaches in ecology assume direct and simultaneous effects between independent and dependent variables (e.g. generalized linear or linear models) or identify direct patterns related to multivariate components (e.g. ordination analysis including multidimensional nonmetric scaling and canonical correspondence analysis). Statistical techniques that quantify direct and indirect effects, such as path analysis, can provide valuable insight on how different variables affect, in a sequential fashion, the structure and dynamics of aquatic communities and ecosystems (Hitchman, Mather, Smith, & Fencl, 2018). Furthermore, the application of path analysis allows for an estimation of the strength and direction of relationships in complex causal schemes with multiple dependent variables (Li, 1975). The causal scheme on which the path analysis is based considers the formulation of hypotheses as to potential effects (Shipley, 1997), thus allowing predictions about the distribution patterns of species.

The models formulated in this study using path analysis gave insight into the sequence of causal relationships that are most likely to structure coastal benthic communities in the study area. Long-term climate predictions for eastern boundaries such as the Chilean coast indicate more intense wind and upwelling (Bakun, 1990), especially in mid- to high-latitudes (García-Reyes et al., 2015; Schneider, Donoso, Garcés-Vargas, & Escribano, 2017). Such changes may have a substantial effect on the levels of coastal exposure and, therefore, on the structure of subtidal communities. Thus, an approach such as the one presented here may contribute to the preliminary classification of areas according to their suitability for different uses (e.g. aquaculture, harvesting of benthic invertebrates, conservation purposes) given future scenarios of physical forcing. A better classification of coastal areas according to their benthic community structure and local environmental regimes is relevant in the context of coastal management and, particularly, for the allocation of territorial rights.

Today there is global interest in establishing small-scale aquaculture activities in coastal areas, in response to the stagnation and decline of fisheries since the late 1980s (Food and Agriculture Organization of the United Nations, 2016). In Chile, as in other coastal states, small-scale aquaculture represents a focus of particular interest for development policies, especially considering the territorial rights conferred to organizations of artisanal fishers through AMEBRs. The extent to which spatial differences in environmental forcing may affect the suitability of a certain area for a particular productive activity has not been explicitly considered, however.

The results show that in this upwelling system, through simple measurements such as coastline exposure and substrate type, it is possible to establish a priori – and with a reasonable degree of certainty – the type of species that can naturally thrive in a given subtidal area and, therefore, the type of species that can be cultivated,

restored, or managed successfully. It remains to be determined whether the relationship found here still holds for subtidal areas in other sections of the Chilean coast as well as in other regions with similar regimes of environmental forcing.

## 4.3 | Limitations of the analysis and future steps

Despite the well-documented association between spatial patterns in surface ocean conditions and changes in the structure of intertidal benthic communities (e.g. Broitman, Navarrete, Smith, & Gaines, 2001; Menge & Menge, 2013; Navarrete et al., 2005), the satellite-derived variables used to characterize AMEBRs did not contribute substantially to predicting the community structure of subtidal benthos. This is partly because most satellite measurements are restricted to a thin surface layer, which may not always reflect the subsurface or near-bottom conditions adequately. Additionally, near-shore waters exhibit strong variability at temporal scales shorter than those captured by the weekly composites used in this study. The spatio-temporal scales at which a specific sea surface feature affects benthic community structure, and the mechanisms through which such connection takes place, are aspects that remain unresolved and warrant further research.

Other variables not considered in this study and that cannot be measured from satellites, such as near-bottom oxygen concentrations and pH levels, as well as some measure of organic matter content in the sediment, may help to explain the unresolved spatial variability in subtidal benthic communities. The intrusion of low-oxygen waters into the coastal zone has been proposed as a critical structuring factor for benthic communities in central Chile (Gallardo et al., 2004) and other upwelling regions. Furthermore, and similarly to what has been documented for the Oregon coast (Grantham et al., 2004), massive die-offs of benthic organisms caused by the nearshore intrusion of hypoxic subsurface waters of equatorial origin have been reported for central Chile (Hernández-Miranda, Veas, Labra, Salamanca, & Quiñones, 2012).

Including variables that pertain to the extractive activity in the AMEBRs did not yield significant relationships for either of the cases analysed here. This was a striking result, given that fishing is expected to increase the variability in abundance of exploited species (Anderson et al., 2008; Stenseth & Rouyer, 2008), and to affect the associated communities, as it has been shown for an individual AMEBR (Molina et al., 2014). The absence of clear responses to fishing pressure is probably because the analysis presented here was carried out on functional groups, whereas the effect of the catch is species specific. The existence of fishing effects on the population structure of certain species will be addressed in a future contribution. Finally, illegal catches and poaching were not considered among the metrics used to characterize human intervention in AMEBRs, despite their potential importance in the region (see Bandin & Quiñones, 2014; Chávez et al., 2018). Gathering the information required to index these illegal activities for each of the 30 AMEBRs requires surveying work that was beyond the scope of our study.

When excessive extraction pressure is put on a species, there may be a replacement of species with similar function in the ecosystem, which may mask the effect of the fishery on community structure. This is especially the case when the analysis of community structure is based on functional traits rather than taxonomic units, as compensation and compensatory dynamics may keep aggregate community properties stable, even though species composition might change over time (Gonzalez & Loreau, 2009). According to Mouchet, Villéger, Mason, and Moullot (2010), two or more species are considered redundant for a process in the ecosystem when the absence of one or more of these species does not significantly affect this process. Thus, functional redundancy can favour ecosystem resilience to current and future perturbations (Braeckman, Rabaut, Vanaverbeke, Degraer, & Vincx, 2014; Francisco & de la Cueva, 2017).

## 5 | CONCLUSIONS

1. The functional structure of subtidal benthic communities in the upwelling coast of central Chile is mainly determined by physical attributes, such as coastal exposure, SST, and Chl *a* concentration, without the detection of significant effects of variables associated with fishing activity. Although the commercial extraction of benthic species is effectively a factor that alters the taxonomic composition of these communities, it does not have a noticeable effect in terms of their functional composition.
2. The chain of significant correlations found using path analysis differed between hard-bottom and soft-bottom communities. In hard-bottom communities, the presence of filter-feeders, herbivores, predators, and scavengers was significantly correlated with the presence of foliose, leathery, and corticated algae, which in turn were significantly correlated with coastal exposure. In soft-bottom communities, infaunal filter-feeders and epifaunal detritivores were positively correlated with weaker variability in SST and higher mean concentrations of surface Chl *a*. In contrast, foliose and corticated algae were significantly correlated with the fraction of rocky substrate and coastline exposure.
3. These results show that environmental factors strongly influenced by coastal geomorphology may explain over 50% of the variability in the structure of subtidal benthic communities from central Chile and, potentially, other regions with similar oceanographic regimes.
4. In terms of management, these results indicate that in soft-bottom environments with higher productivity and more thermal stability it would be feasible for AMEBRs to implement production systems or management actions for epifaunal and infaunal filter-feeders (e.g. mussels and clams). Hard-bottom areas exposed to stronger environmental variability would be better suited for productive systems or management actions based on macroalgae, epifaunal filter-feeders, herbivores, and carnivores.

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## CONFLICT OF INTERESTS

The authors declare that they have no conflicts of interest.

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#### SUPPORTING INFORMATION

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## 5.2 Capítulo 2: Connecting spatial structure in subtidal benthic communities with temporal variability in bottom temperature and dissolved oxygen along an upwelling coast

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### Abstract

While spatial patterns in the structure of intertidal communities have been linked to changes in surface-ocean conditions indicative of coastal advection, nutrient supply, and productivity, less is known as to environmental features that, in addition to substrate type, are most influential in structuring subtidal benthic communities. Here we analyze data from subtidal benthic surveys conducted at six sites spanning ca. 180 km of shoreline along the upwelling coast of central Chile. Using continuous records of temperature and dissolved oxygen in bottom waters from each site, we tested whether among-site differences in community structure can be better explained by considering features of local environmental variability in addition to changes in substrate type. Starting from the NMDS ordination of benthic sites based on the presence and relative abundance of 29 species, we used PERMANOVA to test the explanatory power of substrate type and nine indices of environmental variability derived from in situ records. Three indices, namely the high-frequency variability and 95th percentile of bottom temperatures together with an index for the duration of hypoxia events, explained individually as much of the total variance as substrate type alone (ca. 30%). When combined into a single PERMANOVA analysis, these four factors explained 84% of the total variance in the NMDS-based ordination of benthic communities across the study region. A comparison of the benthic species ordination and environment-based site ordination suggests that soft-bottom species such as the razor clam *Ensis macha*, the snail *Chorus giganteus*, and the crab *Cancer setosus*, might be physiologically more tolerant to more rigorous conditions in terms of more intense warming and longer hypoxia events. Hard bottom species such as the gastropods *Concholepas concholepas* and *Fissurella sp.* and the barnacle *Austromegabalanus psittacus* thrive in environments where the temperature is lower on average but highly variable and where hypoxic conditions are intense but more intermittent. Our findings highlight the structuring role of the variability and the occurrence of extreme conditions,

rather than the most frequent levels, in bottom-water properties such as temperature and dissolved oxygen. These two properties are closely intertwined in this and other coastal upwelling regions and are susceptible to change widely under future climate scenarios.





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## Connecting spatial structure in subtidal benthic communities with temporal variability in bottom temperature and dissolved oxygen along an upwelling coast

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### ABSTRACT

While spatial patterns in the structure of intertidal communities have been linked to changes in surface-ocean conditions indicative of coastal advection, nutrient supply, and productivity, less is known as to environmental features that, in addition to substrate type, are most influential in structuring subtidal benthic communities. Here we analyze data from subtidal benthic surveys conducted at six sites spanning ca. 180 km of shoreline along the upwelling coast of central Chile. Using continuous records of temperature and dissolved oxygen in bottom waters from each site, we tested whether among-site differences in community structure can be better explained by considering features of local environmental variability in addition to changes in substrate type. Starting from the NMDS ordination of benthic sites based on the presence and relative abundance of 29 species, we used PERMANOVA to test the explanatory power of substrate type and nine indices of environmental variability derived from *in situ* records. Three indices, namely the high-frequency variability and 95th percentile of bottom temperatures together with an index for the duration of hypoxia events, explained individually as much of the total variance as substrate type alone (ca. 30%). When combined into a single PERMANOVA analysis, these four factors explained 84% of the total variance in the NMDS-based ordination of benthic communities across the study region. A comparison of the benthic species ordination and environment-based site ordination suggests that soft-bottom species such as the razor clam *Ensis macha*, the snail *Chorus giganteus*, and the crab *Cancer setosus*, might be physiologically more tolerant to more rigorous conditions in terms of more intense warming and longer hypoxia events. Hard bottom species such as the gastropods *Concholepas concholepas* and *Fissurella* sp. and the barnacle *Austromegabalanus psittacus* thrive in environments where the temperature is lower on average but highly variable and where hypoxic conditions are intense but more intermittent. Our findings highlight the structuring role of the variability and the occurrence of extreme conditions, rather than the most frequent levels, in bottom-water properties such as temperature and dissolved oxygen. These two properties are closely intertwined in this and other coastal upwelling regions and are susceptible to change widely under future climate scenarios.

### 1. Introduction

Understanding the relationship between community structure and environmental variability makes it possible to establish the range of conditions under which it is feasible to find certain species. In coastal areas, this kind of understanding allows for more effective conservation and management plans, including better allocation of activities such as

fishing and aquaculture. In a climate-change context, it is relevant to determine the potential of species to adapt to changing environmental conditions and the effects of this variability on the dynamics of coastal communities, biodiversity, and ecosystem functioning (Kordas et al., 2011).

The composition and functioning of marine benthic communities vary in close connection with the changes in their physical environment.

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Substrate type is a first-order structuring factor that, in coastal environments, depends strongly on shoreline exposure and bathymetry, as well as on wave action and the influence of river plumes (Burrows 2012; Forrest et al., 2010). Secondly, the physical-chemical conditions of bottom waters contribute to the spatial structuring of coastal benthos through their effect on the behavior, physiology, and survival of different benthic species (Bremner et al., 2006).

In coastal upwelling regions, the recurrent intrusion of cold, oxygen-deficient waters into nearshore habitats brings about many physiological challenges for benthic organisms, especially for sessile species (Grantham et al., 2004; Thiel et al., 2007; Hernandez-Miranda et al., 2012). The shores of central Chile are strongly influenced by coastal upwelling which, as in other regions with a similar oceanographic regime, interacts with the complexities of shoreline morphology to produce an array or “mosaic” of local environmental regimes (Tapia et al., 2009; Chan et al., 2017) that ultimately shape coastal benthic

communities (Broitman et al., 2001; Wieters et al., 2009).

While the connection between community structure and variability in nearshore sea-surface conditions has been amply documented for intertidal benthos (e.g., Broitman et al., 2001; Navarrete et al., 2005; Blanchette et al., 2008), less is known as to the extent to which subtidal benthic communities are shaped by the variability in physical-chemical conditions of bottom waters, particularly by frequent drops and increases in temperature and oxygen concentrations during the intensification and relaxation of coastal upwelling. Thus far, research focused on the effects of drops in the oxygen content of coastal waters has revealed a wide range of responses, from behavioral effects that modify the species composition (Riedel et al., 2014; Gallo et al., 2020) to sub-lethal and lethal effects (Vaquer-Sunyer and Duarte, 2011) that ultimately alter the structure and function of benthic communities (Villnäs et al., 2012).

The intensity and periodicity of hypoxia in nearshore bottom waters

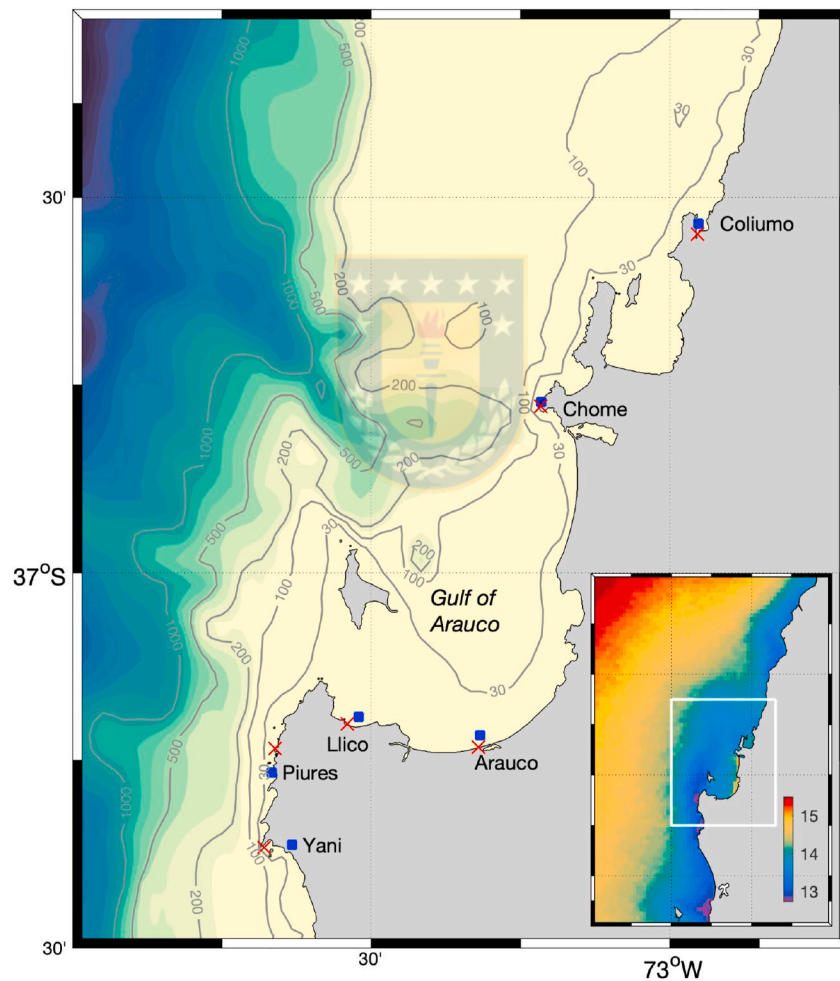


Fig. 1. Geographic location of subtidal sites (red symbols) and points where continuous records of near-bottom temperature and dissolved oxygen were gathered (blue symbols). Coastal bathymetry is shown to emphasize the complexity of coastal geomorphology in the study region. The inset map shows the mean distribution of MODIS-Aqua Sea Surface Temperature (°C) in 2003–2018. The white rectangle indicates the area spanned by our benthic surveys and *in situ* environmental records. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

are closely tied to shoreline complexity and its interaction with wind-driven circulation and water column stratification (Walter et al., 2014). Therefore, the subtidal benthos along an upwelling region with an intricate shoreline may be exposed to a variety of contrasting regimes of hypoxia and near-bottom temperatures, which are expected to modify local community features such as dominant species or species richness. Recently published observational work off the coast of Southern California (Gallo et al., 2020) has revealed that temporal variability in bottom temperature and dissolved oxygen can be greatly underestimated when assessed through low-frequency periodic observations (i.e., seasonal CTD profiles) instead of continuous high-frequency monitoring through moored sensors.

Here we combine continuous records of bottom temperature and dissolved oxygen conditions with data gathered from diving surveys of subtidal benthic communities along the central Chile upwelling region to assess the link between spatial changes in benthic community structure and among-site differences in temporal variability of bottom temperature and dissolved oxygen. We combined a number of multivariate and time-series analysis techniques to test which aspects of temperature and oxygen variability are useful as additional explanatory variables (i.e., in addition to substrate type) for the ordination of sites according to the composition and relative abundance of benthic species.

## 2. Materials and methods

Data on the benthic community structure of megafauna and macrophytes were obtained from surveys conducted at six sites spanning ca. 180 km of shoreline in the central Chile coast (Fig. 1). The spatial and temporal variability of environmental conditions along this region is strongly influenced by wind-driven coastal upwelling, which is most intense in spring-summer months (Sobarzo et al., 2007). However, it leaves a distinct thermal signature in the mean, year-long distribution of satellite-derived surface temperatures (Fig. 1, inset).

All six study sites correspond to coastal management areas known in Chile as AMEBR (Areas for the Management and Exploitation of Benthic Resources), which provide territorial use rights to legally organized artisanal fishers, provided that surveys are conducted periodically (annually or biennially) to assess the abundance of commercially important species and check the state of subtidal benthic communities. At each site, a subtidal survey spanning a depth range of 0–30 m was conducted by scientific divers experienced in identifying benthic species in the field. The six surveys (one per AMEBR) were completed between April 2017 and November 2018 (Table 1). During each survey,

observations were collected at a minimum of 40 geo-referenced sampling units. At each sampling point (i.e., sampling unit), divers surveyed a  $10 \times 2$  m transect from the deepest to the shallowest end, using 0.25 m<sup>2</sup> quadrats (50 cm by 50 cm) arranged every 2 m along the transect.

Depending on the type of benthic species, different measures were used to obtain a dataset that allowed the characterization of distribution patterns for multiple species at the same points in space. For disaggregated species that can be easily counted, such as limpets, urchins, and crabs, their density within each  $10 \times 2$  m transect was recorded. For aggregated species such as mussels, clams, and macroalgae, density estimates obtained from each 0.25 m<sup>2</sup> quadrat were averaged across quadrats within each transect. Finally, for species that are difficult to count individually in the subtidal (e.g., barnacles, ascidians), the percent coverage averaged across quadrats was used as a measure of density at each transect. Relative density was computed for each taxon as its mean density divided by the sum of all densities within a given type of substrate and taxa (e.g., all hard-bottom invertebrates that can be counted).

Divers determined the substrate type by direct observation, estimating the proportion of hard substrates (pebbles, boulders, clay, slab) and soft substrates (shell hash, sand, mud) for each sampling unit. Our analysis used the percentage of rocky substrate averaged across sampling units in each AMEBR as an input variable. Additionally, we included the average depth of the sampling units (Table 1).

Continuous records of near-bottom temperature and dissolved oxygen were obtained from moored sensors deployed at sites near the six AMEBR between February 2018 and February 2019. At each location, a miniDOT logger (PME, USA) was moored ca. 2 m above the bottom, at a nominal depth of 20 m, and programmed to record water temperature and dissolved oxygen at 10 min intervals. Loggers were serviced, and data downloaded every 2–3 months. Data gathered from the loggers were quality controlled and converted into hourly time series. Later, several statistics were computed from each time series to characterize local regimes of temperature and oxygen variability.

Temperature conditions were characterized through the median and the 95th percentile of each temperature distribution; the latter was intended to describe the upper limit for warming events experienced by the benthic community at a given site. Similarly, the oxygen conditions were characterized through the median and 5th percentile of all recorded values, the latter indicating the lowest DO concentration at a given site. The high-frequency variability in temperature and DO was quantified by applying a high-pass Lanczos cosine filter that removed all periods longer than 24 h from each time series, computing the RMS (root mean squared) of these filtered series over the study period, and dividing by the RMS of the raw time series. As for hypoxia, the fraction of measurements with  $DO < 2$  mg/L was computed for each hourly time series. Also, from the duration of all hypoxia events found in each hourly record, the median and 95th percentile were used as descriptors of the typical (i.e., most frequent) and longest exposures of benthic organisms to hypoxic waters, respectively. Hypoxia events were defined as instances of more than two consecutive measurements of  $DO < 2$  mg/L.

In order to visualize the differences in benthic community structure across sites, NMDS ordinations were performed on mean density and coverage data using the metaMDS function of the *vegan* package v2.6-5 (Oksanen et al., 2019) in R, with 500 random starts. The centroids of the species and the site scores were plotted together in a biplot to visualize the associations between species and sites. The statistical significance of relationships between the emerging structure of the NMDS ordination and environmental conditions at each location was tested using PERMANOVA. The different metrics of temperature and oxygen variability and the percentage of rocky substrate were considered independently as factors. This analysis was performed using the *adonis vegan* function, with p-values for the pseudo-F test statistic based on 999 permutations. Factors identified as statistically significant ( $p < 0.05$ ) were then used in a combined PERMANOVA to determine the maximum percentage of variance in the NMDS ordination that they could explain jointly. The

**Table 1**  
General information for each of the six subtidal surveys included in our analysis. Mean Depth and %Rocky Substrate correspond to averages computed across sampling units.

Site	Date	Number of sampling units	Number of Taxa (S)	Mean Depth (m)	%Rocky Substrate
Colitumo	18-Jul-2017	57	17	2.1	75
Chome	26-Mar-2018	69	15	6.1	100
Arauco	13-Apr-2018	45	5	6.5	0
Llico	03-Apr-2017	71	13	2.1	93
Piures	16-Apr-2017	94	20	4.2	100
Yani	17-Jun-2018	40	17	8.1	100

resulting fit of selected environmental metrics to the NMDS ordination was included in the biplots using the *envfit* *vegan* function.

### 3. Results

The six subtidal benthic surveys comprised a total of 381 transects and yielded a database containing 40 taxa (Table 2). The NMDS applied to this entire dataset did not converge (i.e., stress > 0.2). In order to achieve convergence, taxa with relative densities below 0.5% were left out of the analysis, leaving a total of 29 taxa that were finally included in the NMDS (Table 2). The group of 11 taxa removed from the analysis included the starfish *Patiria chilensis* and *Meyenaster gelatinosus*, the sea urchin *Loxechinus albus*, and the crabs *Homalaspis plana*, *Taliepus dentatus*, and *Cancer coronatus*. These species were present in average densities below 0.2 individuals per m<sup>2</sup> and were found mostly at site Coliumo and the southern sites Yani and Piures (see Fig. 1).

The NMDS applied to the remaining 29 taxa produced the ordination shown in Fig. 2, which reached a stress of 0.03 and revealed that site Arauco is segregated from the others due to the presence of the razor clam *Ensis macha*, the carnivorous gastropod *Chorus giganteus*, and the crab *Cancer setosus*. Subtidal benthos at site Llico was characterized by the alga *Mazzaella laminarioides* and the tunicate *Pyura chilensis* and shared with Coliumo the clam *Mulinia edulis* and the alga *Chondracanthus chamissoi*. At the opposite end of the ordination, site Chome was characterized by macroalgae and invertebrates typical of hard-bottom and high-exposure sites, such as the kelps *Lessonia spicata*, *Durvillaea antarctica*, and *Lessonia trabeculata*, the sea urchin *Tetrapygus*

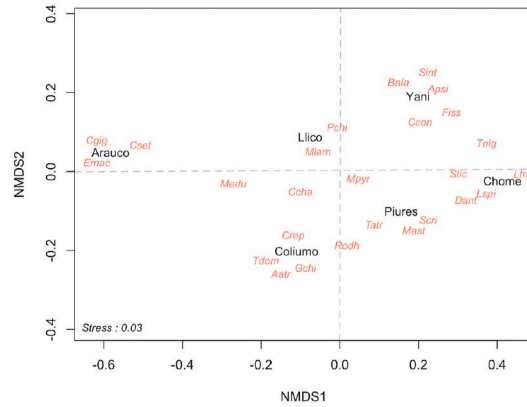


Fig. 2. NMDS-based ordination of the six surveyed sites (black labels) based on the species composition of subtidal benthos. Orange labels are code names for the species (see Table 2). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

*niger*, and the seastar *Stichaster striatus*. At the southern end of our study region, site Yani was characterized by a dominance of the carnivorous gastropod *Concholepas concholepas*, the herbivorous gastropod *Fissurella*

Table 2

Descriptive statistics for the presence and density of each taxon detected in the six subtidal surveys. Crosses indicate the 29 taxa used in the multivariate ordination analysis. Code names given to each taxon are used in Fig. 2. Only species with relative densities >0.5% (shown in boldface) were included in the community analysis.

Type	Taxon	Code	Presence transects	% presence	Mean density	Standard deviation	Relative density
Hard-bottom invertebrates (counted)	<i>Tegula atra</i> +	Tatr	37	9.71	2.58	13.04	<b>39.1</b>
	<i>Crepidula</i> sp. +	Crep	10	2.62	2.33	16.27	<b>35.4</b>
	<i>Astromegabalanus psittacus</i> +	Apsi	14	3.67	0.52	3.72	<b>7.9</b>
	<i>Aulacomya atra</i> +	Aatr	11	2.89	0.48	5.75	<b>7.3</b>
	<i>Chorus giganteus</i> +	Cgig	14	3.67	0.13	0.90	<b>1.9</b>
	<i>Cancer setosus</i> +	Cset	56	14.70	0.10	0.44	<b>1.6</b>
	<i>Tetrapygus niger</i> +	Tnig	25	6.56	0.10	0.46	<b>1.6</b>
	<i>Concholepas concholepas</i> +	Ccon	68	17.85	0.08	0.32	<b>1.2</b>
	<i>Fissurella</i> sp. +	Fiss	55	14.44	0.08	0.30	<b>1.2</b>
	<i>Stichaster striatus</i> +	Stic	37	9.71	0.06	0.28	<b>0.8</b>
	<i>Choromytilus chorus</i>	Ccho	4	1.05	0.02	0.26	0.4
	<i>Patiria chilensis</i>	Pati	4	1.05	0.02	0.17	0.3
	<i>Homalaspis plana</i>	Hpla	28	7.35	0.02	0.07	0.3
	<i>Loxechinus albus</i>	Lalb	12	3.15	0.02	0.20	0.3
	<i>Taliepus dentatus</i>	Tden	16	4.20	0.01	0.08	0.2
	Porifera	Pori	1	0.26	0.01	0.26	0.2
	<i>Cancer coronatus</i>	Ccor	11	2.89	0.00	0.03	0.1
	<i>Meyenaster gelatinosus</i>	Mgel	18	4.72	0.01	0.04	0.1
	<i>Athyonidium chilensis</i>	Achi	1	0.26	0.01	0.10	0.1
	<i>Cancer plebejus</i>	Cple	5	1.31	0.00	0.02	0
Polyplacophora	Poly	3	0.79	0.00	0.04	0	
Hard-bottom (coverage)	<i>Pyura chilensis</i> +	Pchi	46	12.07	1.14	5.87	<b>54.2</b>
	<i>Balanus</i> sp. +	Bala	24	6.30	0.96	5.57	<b>45.8</b>
Soft-bottom invertebrates	<i>Allopetrolisthes punctatus</i> +	Apun	4	1.05	1.38	17.24	<b>30.7</b>
	<i>Mulinia edulis</i> +	Medu	31	8.14	1.33	7.87	<b>29.4</b>
	<i>Ensis macha</i> +	Emac	36	9.45	1.05	3.80	<b>23.3</b>
Kelps	<i>Tagelus dombeii</i> +	Tdom	13	3.41	0.75	10.41	<b>16.5</b>
	<i>Macrocystis pyrifera</i> +	Mpyr	50	13.12	0.66	2.04	<b>34.4</b>
	<i>Lessonia spicata</i> +	Lspi	39	10.24	0.62	1.96	<b>32.1</b>
	<i>Durvillaea antarctica</i> +	Dant	43	11.29	0.57	1.81	<b>29.4</b>
Red and green algae	<i>Lessonia trabeculata</i> +	Ltra	9	2.36	0.08	0.53	4.1
	<i>Chondracanthus chamissoi</i> +	Ccha	54	14.17	4.96	14.74	<b>41.0</b>
	<i>Mazzaella laminarioides</i> +	Mlam	30	7.87	2.22	8.33	<b>18.3</b>
	<i>Sarcothalia crispata</i> +	Sscr	19	4.99	1.39	6.60	<b>11.5</b>
	<i>Stenogramme interrupta</i> +	Ssint	11	2.89	1.35	8.83	<b>11.2</b>
	<i>Pyropia columbina</i> +	Pcol	8	2.10	1.07	8.57	<b>8.8</b>
	<i>Gracilaria chilensis</i> +	Gchi	12	3.15	0.67	5.52	<b>5.5</b>
	<i>Rodhymenia</i> sp. +	Rodh	16	4.20	0.19	1.20	<b>1.6</b>
<i>Ulva</i> sp. +	Ulva	6	1.57	0.15	1.25	<b>1.2</b>	
<i>Mastocarpus latissimus</i> +	Mast	4	1.05	0.10	1.13	<b>0.8</b>	



sp., the barnacles *Balanus* sp. and *Austromegabalanus psittacus*, and the red alga *Stenogramme interrupta* (Fig. 2).

The near-bottom temperature and dissolved oxygen (DO) records revealed local regimes that differed substantially among sites (Fig. 3). There was an apparent difference in the strength of high-frequency variability of both temperature and DO between the most exposed sites (Chome, Piures, Yani) and those that are more protected (Coliumo, Arauco, Llico) (Fig. 3, Table 3). At all sites, fluctuations of bottom temperature and DO were coherent during spring-summer months (February–March 2018, November 2018–January 2019, Fig. 3a–f), following a pattern of variability that is consistent with that expected from coastal upwelling, i.e., drops/increases in DO associated with drops/increases in temperature (Fig. 3a–f). Overall, differences among sites appeared more dramatic for DO than for temperature (Fig. 3g–h). However, higher temperatures were recorded at sites Llico and Arauco, whereas Chome, Piures, and Yani appeared to be more frequently exposed to cooler waters (Fig. 3g). In terms of dissolved oxygen, sites Arauco, Chome, and Coliumo exhibited DO distributions that were skewed towards low values, with medians close to the 2 mg/L level commonly used as a reference level for hypoxia (Fig. 3h). The median DO concentration for sites Llico, Piures, and Yani, on the other hand, were all above 5 mg/L (Fig. 3h and Table 3). In terms of cumulative exposure to hypoxia, sites at the southern end of the study region were the least exposed (Fig. 3h–i and Table 3). As for the duration of hypoxia events, these were longer at sites Arauco and Chome, and secondarily at Coliumo, whereas the southern sites were exposed to substantially shorter events (Fig. 3i and Table 3).

The series of PERMANOVA analyses conducted separately for substrate type and indices of environmental variability as factors explaining the NMDS-based ordination of benthic sites (Table 4) showed that only 4 out of 11 factors considered initially explained a significant fraction of variability in benthic community structure: the upper limit of bottom-water temperatures (T-95), the index of high-frequency fluctuations in water temperature (HF-T), the upper limit of hypoxia event durations (HE-95), and the percentage of rocky substrate (RSub). Each of these four factors explained, by themselves, between 27% and 30% of the total variance in the benthic–community ordination.

A PERMANOVA combining the four variables previously identified as significant (Table 4) revealed that, together, they explain 84% of the total variance in the ordination of benthic sites (Fig. 4). The fit between the NMDS ordination of benthic communities and the environmental

predictors (Fig. 4, blue arrows) highlighted the strong association between some sites and some particular features of environmental variability, as well as the strong negative correlation between the duration of hypoxia events (HE-95) and the percentage of rocky substrate (Rsub). In addition to being the only site with 0% rocky substrate (Table 1), which explains its horizontal position on the ordination (Fig. 4), site Arauco appeared associated with more extreme events of bottom warming (T-95) and more persistent hypoxia events (HE-95). On the other hand, sites Chome, Yani, and Piures are strongly associated with a higher percentage of rocky substrate (RSub), lower incidence of bottom warming and hypoxia events, but stronger high-frequency variability in bottom water temperature (HF-T).

#### 4. Discussion

Our results indicate that considering information on water-column conditions and their temporal variability can substantially improve our understanding of the factors that shape the spatial structure of subtidal benthic communities. While substrate type alone explained 29% of the NMDS ordination of community data from our benthic surveys, adding three features of environmental variability, namely the upper limits for bottom temperatures and duration of hypoxia events, plus the high-frequency variability in temperature, made it possible to explain 84% of the among-site variability in benthic community structure. This is indeed a substantial improvement in the model's explanatory power.

A potentially large fraction of the remaining unexplained variability might be associated with human intervention in these coastal areas, given their use for the commercial exploitation of certain species. Such intervention is likely to increase the spatial variability of population indicators in commercial species (Anderson et al., 2008) and is likely to modify the associated benthic communities (Molina et al., 2014). However, analyzing the extent of such an effect requires data from coastal areas with similar oceanographic characteristics but unaffected by human intervention; unfortunately, there are currently no sites in the region that fit such description.

Eastern boundary upwelling ecosystems are characterized by high primary productivity fueled by the onshore advection of cold, nutrient-rich, and oxygen-deficient waters often associated with oxygen minimum zones (Chavez and Messié 2009). Although upwelling-driven hypoxia has been typically observed and studied at some distance

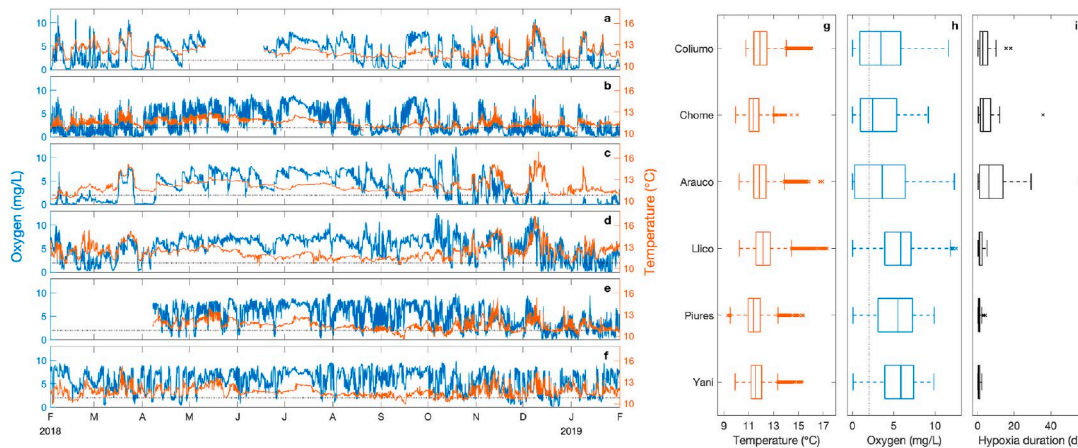


Fig. 3. Records of bottom temperature and dissolved oxygen (DO) used to characterize local environmental regimes at the six study sites. The dotted horizontal lines on panels a through f, and the vertical line in panel h, indicate a DO concentration of 2 mg/L. Panels g through i summarize the distribution of water temperature (g), DO (h), and the duration of hypoxia events (i) detected in the records for each site.

**Table 3**

Statistics from the near-bottom temperature and dissolved oxygen records used to characterize local regimes of environmental variability: median and 95th percentile of temperature (T-50 and T-95), high-frequency variability of temperature (HF-T), median and 5th percentile of dissolved oxygen (DO-50 and DO-5), high-frequency variability of dissolved oxygen (HF-DO), frequency of exposure to hypoxia (FE-H), median and 95th percentile of duration for hypoxia events (HE-50 and HE-95).

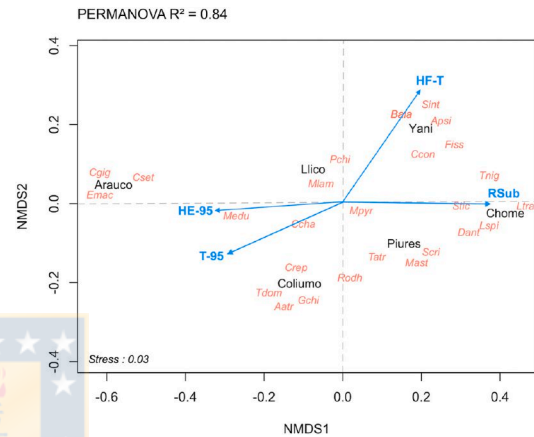
Statistic	Temperature (°C)			DO concentration (mg/L)			Hypoxia events (DO < 2 mg/L)		
	Median	95th ptile	HFvar	Median	5th ptile	HFvar	FrqExp	Median dur (d)	95th ptile (d)
Code	T-50	T-95	HF-T	DO-50	DO-5	HF-DO	F-HE	HE-50	HE-95
Coliumo	11.78	13.88	0.017	2.72	0.13	0.171	0.41	2.83	11.42
Chome	11.28	12.54	0.021	2.14	0.18	0.273	0.51	3.08	10.76
Arauco	11.68	13.86	0.013	2.24	0.01	0.116	0.48	6.21	40.13
Llico	11.99	14.02	0.022	5.40	0.69	0.151	0.13	1.21	3.04
Piures	11.39	13.01	0.023	5.28	1.16	0.185	0.16	0.88	3.67
Yani	11.43	12.85	0.027	5.88	1.68	0.157	0.09	0.67	2.17

**Table 4**

Results of PERMANOVA between the NMDS-based ordination of benthic sites and the environmental indices. df = degrees of freedom, SS = sum of squares, MS = mean squares, F = Fisher's statistic, and R<sup>2</sup> = coefficient of determination. Significant factors (p < 0.05) are shown in boldface.

Source of variability	df	SS	MS	F	p	R <sup>2</sup>
Median temperature (T-50)	1	0.50	0.50	1.39	0.088	0.26
Residuals	4	1.44	0.36			
Total	5	1.94				
<b>95th percentile temperature (T-95)</b>	1	0.58	0.58	1.70	<b>0.036</b>	0.30
Residuals	4	1.36	0.34			
Total	5	1.94				
<b>High-frequency temp variability (HF-T)</b>	1	0.55	0.55	1.58	<b>0.021</b>	0.28
Residuals	4	1.39	0.35			
Total	5	1.94				
Median dissolved oxygen (DO-50)	1	0.42	0.42	1.09	0.278	0.21
Residuals	4	1.53	0.38			
Total	5	1.95				
5th percentile oxygen (DO-5)	1	0.45	0.45	1.20	0.251	0.23
Residuals	4	1.50	0.38			
Total	5	1.95				
High-frequency oxygen variability (HF-O)	1	0.46	0.46	1.26	0.175	0.24
Residuals	4	1.48	0.37			
Total	5	1.94				
Exposure to hypoxia (FE-H)	1	0.41	0.41	1.06	0.321	0.21
Residuals	4	1.54	0.39			
Total	5	1.95				
Median duration hypoxia events (HE-50)	1	0.51	0.51	1.43	0.060	0.26
Residuals	4	1.43	0.36			
Total	5	1.94				
<b>95th percentile event duration (HE-95)</b>	1	0.53	0.53	1.49	<b>0.029</b>	0.27
Residuals	4	1.42	0.36			
Total	5	1.95				
<b>Percentage rocky substrate (RSub)</b>	1	0.56	0.56	1.62	<b>0.008</b>	0.29
Residuals	4	1.38	0.35			
Total	5	1.94				
Average Depth (Depth)	1	0.49	0.49	1.34	0.119	0.25
Residuals	4	1.45	0.36			
Total	5	1.94				

from shore (and depth), it has been shown that, under certain conditions, hypoxic waters can reach shallow coastal habitats (Grantham et al., 2004; Hernández-Miranda et al., 2012), impacting biodiversity, habitat complexity (Fajardo et al., 2018) and, in extreme cases, the survival of local benthic populations (Chu and Tunnicliffe 2015). Sessile benthic species inhabiting coastal upwelling systems have been recurrently exposed to hypoxia for millennia (see Moffitt et al., 2015). Therefore they should be equipped with the array of behavioral and metabolic responses required to withstand hypoxia events within certain margins of periodicity and intensity. An intensification of nearshore hypoxia, in association with more intense coastal upwelling along most



**Fig. 4.** Correspondence between the NMDS-based ordination of sites (black labels) based on the species composition of subtidal benthos (orange labels) and the four indices of environmental variability identified as significant factors through PERMANOVA (blue vectors and labels). Orange labels are code names for the benthic species (Table 2), and boldface blue labels are code names for environmental indices (Table 3). The direction and length of the environmental vectors represent the association and scaled correlation of each factor with the NMDS-based ordination of benthic sites. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Eastern Boundary Upwelling Systems (García-Reyes et al., 2015), may induce changes in the behavior or physiology of some benthic species to the extent that is detrimental for growth, reproduction, and ultimately survival, thus shaping the local structure of benthic communities (Wu 2002; Riedel et al., 2014).

In our case, the site that appeared as the most different in terms of its benthic community (Arauco) is characterized by soft sediments, higher bottom temperatures, and longer hypoxia events. The local dominance of species such as the razor clam *Ensis macha*, the snail *Chorus giganteus*, and the crab *Cancer setosus*, suggests that these infaunal (*E. macha*) and epifaunal species (*C. giganteus* and *C. setosus*) are better adapted for such environmental conditions. On the other hand, sites more strongly associated with rocky substrate and high-frequency variability in bottom temperatures (Chome, Yani, Piures) are dominated by invertebrates (e.g., *Concholepas concholepas*, *Austroragabalanus psittacus*) and macroalgae (e.g., *Durvillaea antarctica*, *Lessonia spicata*) that do better in colder, more fluctuating environments, but with a lower incidence of hypoxia events. The potential structuring role of species found in very low abundance during our surveys and excluded from the NMDS analysis warrants further investigation.

The impact of hypoxia on benthic diversity and abundance has been documented in studies based on long-term monitoring (Seitz et al., 2009) and studies of particular events (Grantham et al., 2004). For instance, a major hypoxia event that took place in south-central Chile during the summer of 2008 (Hernández-Miranda et al., 2012) produced a dramatic loss of biodiversity and resulted in the dominance of carnivorous species (the gastropod *Nassarius* sp.) as well as scavengers (the crab *Cancer coronatus*). In our study, the crab *Cancer setosus* and the carnivorous gastropod *Chorus giganteus* were numerically dominant at site Arauco, which consistently experiences the longest hypoxia events among the studied sites. This finding suggests that this kind of motile, predatory, or scavenging species could be better adapted to future low-oxygen scenarios and, potentially, dominate nearshore benthic communities. However, it is worth noting that some sessile filter-feeding species such as the razor clam *Ensis macha*, which is particularly abundant at site Arauco, also appear to be well adapted to these extreme conditions. Therefore, the differences in benthic community composition between a site like Arauco and the other locations are not only explained in terms of epifaunal species able to escape extreme hypoxia but also by inter-specific differences in physiological tolerance that warrant further study.

The intensification of coastal upwelling expected as a result of climate change (Bakun 1990) may lead to a drop in temperature and oxygen content of nearshore bottom waters (Vaquer-Sunyer and Duarte 2011), as well as to increases in nearshore productivity (Gutiérrez et al., 2011) that further intensify local hypoxia. Although significant progress has been made in understanding how trends in ocean temperature and oxygen content may impact the viability and geographic distribution of marine populations (Deutsch et al., 2015), a good understanding of the community-level effects of coastal hypoxia is still lacking (but see Riedel et al., 2014 and Gallo et al., 2020). Examples of extreme hypoxia events and their often lethal effects on many benthic species can be found in the literature over the past decades (see Levin et al., 2009). However, the structuring role of sublethal effects associated with shorter-term but more repetitive hypoxia stress on coastal benthos is yet to be fully investigated. Understanding how different local regimes of environmental variability modify the spatial structure of benthic communities may provide a starting point towards this goal.

#### CRedit authorship contribution statement

**Aldo Hernández:** Conceptualization, Methodology, Data curation, Formal analysis, Visualization, Writing - original draft. **Fabián J. Tapia:** Conceptualization, Supervision, Formal analysis, Writing - original draft, Writing - review & editing.

#### Declaration of competing interest

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

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### **5.3 Capítulo 3: Harvest rate for a benthic species with highly variable recruitment, the case of the surf clam *Mesodesma donacium* in northern Patagonia, Chile**

Paper submitted to Fisheries Research, May 2021

#### **Abstract**

The exploitation of benthic species in coastal areas managed by artisanal fishers requires a harvest control rule that ensures its sustainability. Defining harvest control rules is particularly important for species with highly variable recruitment. One such case is the fishery for surf clam *Mesodesma donacium* (Lamarck, 1818) in the Cucao management area of northern Patagonia, which is managed through annual quotas determined by applying a constant harvest rate close to 25% of the exploitable stock. We assessed this harvest rate's performance under a scenario of variable recruitment, using data from direct stock assessments to simulate the inter-annual dynamics of a surf clam population at Cucao beach. Our simulations showed that, under variable recruitment, the exploitation rate currently applied to *M. donacium* at Cucao implies an 80% probability of future collapse. In contrast, a 15% harvest rate would ensure fishery sustainability. These results highlight the need to revisit the assumptions implicit in the current management of benthic species, one of which is the regularity of recruitment. Therefore, in addition to annual biomass estimates, harvest control rules should take advantage of direct stock assessment surveys to provide updated information on recruitment success or failure. Sustainable management of this and other benthic fisheries will then be more likely to achieve.

1     **Harvest rate for a benthic species with highly variable recruitment, the**  
2     **case of the surf clam *Mesodesma donacium* in northern Patagonia, Chile.**

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24 **Abstract**

25 The exploitation of benthic species in coastal areas managed by artisanal fishers requires a  
26 harvest rate that ensures sustainability. Defining a harvest rate is particularly important for  
27 species with highly variable recruitment. One such case is the fishery for surf clam  
28 *Mesodesma donacium* in the Cucao management area of northern Patagonia, which is  
29 managed through annual quotas determined by applying a constant harvest rate close to 25%  
30 of the exploitable stock. We used data from direct stock assessments to simulate the surf clam  
31 population dynamics at Cucao beach. The recruitment is estimated considering a sequence  
32 of successes and failures following an underlying Markov chain distribution. Our simulations  
33 showed that, under variable recruitment, the exploitation rate currently applied to *M.*  
34 *donacium* at Cucao implies an 80% probability of future collapse. A 10% harvest rate would  
35 ensure fishery sustainability. These results highlight the need to revisit the assumptions  
36 implicit in the current management of benthic species, one of which is the regularity of  
37 recruitment. Therefore, in addition to annual biomass estimates, harvest rates should take  
38 advantage of direct stock assessment surveys to provide updated recruitment success or  
39 failure information. Sustainable management of this and other benthic fisheries will then be  
40 more likely to achieve.

41 **Keywords:** surf clam, harvest rate, recruitment variability, artisanal fishery, management  
42 areas.

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44

45 **1 Introduction**

46 Benthic marine invertebrates commonly exhibit complex life cycles with a planktonic larval  
47 phase and a sessile adult stage (Roughgarden, 1988). The roles of adult reproduction, larval  
48 survival, and post-settlement success in adult demographics are difficult to unravel (Pineda,  
49 2000; Pineda et al., 2009; Whalan et al., 2015). However, there is consensus that the  
50 distribution of adult stocks depends to a great extent on the existence of successful  
51 recruitment (Defeo, 1996), which is highly variable in benthic species since it depends on  
52 adult biomass, reproductive success, larval abundance and dispersal, settlement success, and  
53 post-settlement survival (Ebert, 2010; Hunt and Scheibling, 1997; Ouréns et al., 2014).

54 The surf clam *Mesodesma donacium* (Lamarck 1818) is among the most highly valued  
55 benthic species in Chile. This species inhabits sandy beaches along the Chilean coast, from  
56 Arica to southern Chiloé (18-43°S), forming dense aggregations at sites with a specific  
57 combination of morpho-dynamic beach features (Jaramillo et al., 1994). The landing records  
58 for surf clam reveal expansion and contraction cycles occurring at mesoscale (Orensanz and  
59 Jamieson, 1998), with significant fluctuations and serial depletion in the populations  
60 distributed along the Chilean coast (Thiel et al., 2007). Initially, in the 1960s and 1970s,  
61 harvesting for this species was concentrated mainly in the northern region (Matamala et al.,  
62 2008), particularly in the sandy banks of Coquimbo. During the late 1980s, banks in the  
63 central-southern zone near Mehuin were under significant extraction pressure. The fishery  
64 practically disappeared in the mid-1990s and started again in 1998 with the simultaneous  
65 harvesting of 10 banks in the southern Los Lagos Region (Rubilar et al., 2001; Stotz, 1997).

66 The surf clam landings come from three sectors of the Chilean coast: a) Coquimbo Region  
67 (29-30°S), with high inter-annual variability in landings at two main coves (Los Choros and



68 Peñuelas, Fig. 1); b) the cove of Quidico in the Biobío Region (38°S), which accounted for  
69 most of the national landings between 2001 and 2004, and subsequently showed a depletion  
70 of the bank; and, c) three coves in the southern Los Lagos Region (42-43°S: Maullín, Mar  
71 Brava, and Cucao) with landings that increased substantially in 2009-2011, and then dropped  
72 to reach a minimum by 2016 (Fig. 1).

73 In Chile, the management of many benthic fisheries is carried out through an administrative  
74 system based on territorial user rights for fisheries (TURF), locally known as “Areas for the  
75 Management and Exploitation of Benthic Resources” (AMEBR). In the AMEBR, sections  
76 of the coast are allocated to artisanal-fisher organizations through temporary rights to harvest  
77 benthic species (Castilla and Fernández, 1998). Fishers must provide baseline information  
78 and a management plan for target benthic species. Private consultants hired by each  
79 organization assess the standing stock biomass of the target species through field surveys.  
80 Based on the estimates of biomass and total allowable catch (TAC) provided by the  
81 consultants, the relevant government agency (Undersecretariat of Fisheries and Aquaculture,  
82 SUBPESCA) authorizes a harvest quota for the target species, seeking to safeguard the  
83 ecosystem’s natural recovery (Aburto and Stotz, 2013; Castilla and Fernández, 1998; Gelcich  
84 et al., 2010; González et al., 2006; Stotz, 1997).

85 At Cucao beach in northern Patagonia, data from direct stock assessments of surf clam are  
86 available annually for the seven years 2011-2017. Different consultants conducted surveys  
87 during this period and provided estimates for the surf clam’s abundance and TAC, which  
88 SUBPESCA reviewed before deciding on harvest limits for this area. For most AMEBR, the  
89 management cycle consists of a) an annual survey of densities, size structure, and length-  
90 weight relationships, which yield estimates of biomass and length composition; b) estimation

91 of proposed annual quotas based on stock biomass; and c) a review of the results by  
92 SUBPESCA, which can authorize or modify the proposed quota, allowing a maximum  
93 harvesting rate of 30% of the estimated stock. This management cycle repeats annually  
94 without considering past surveys and removals of adult biomass, which would be unsuitable  
95 for ensuring the sustainable exploitation of benthic species with highly variable recruitment,  
96 such as the surf clam. Although the constant harvest rate strategy utilized to authorize  
97 harvesting quota for benthic species seems reasonable, the local depletion of surf clam  
98 populations observed in the past along the Chilean coast implies that the species is sensitive  
99 to overexploitation and that an essential element of this species' life cycle has been left out  
100 of the decision process. Although the maximum permitted harvest rate of 30% would be too  
101 high for a species sensitive to overexploitation like the surf clam *M. donacium*, currently, the  
102 management of benthic fisheries in the AMEBR system does not consider biological  
103 reference points.

104 In this study, we used a seven-year data set from stock assessment surveys at Cucao beach  
105 to evaluate various harvest rate scenarios based on a model of population dynamics for surf  
106 clam that simulates interannual variability in recruitment. We analyzed different harvest rates  
107 to establish a total allowable catch that could achieve sustainable exploitation in a scenario  
108 of temporal variability in recruitment.

## 109 **2 Materials and methods**

### 110 *2.1 Study area and data sources*

111 The study area is Cucao beach (24°36'S-74°08'W), located on the western shore of Chiloé  
112 island, in northern Chilean Patagonia (Fig. 1). Over the past decade, Cucao has been one of

113 the main harvesting areas for the surf clam *M. donacium*, with three organizations of artisanal  
114 fishers having territorial use rights since 2015 (Fig. 1).

115 We obtained the data from six stock assessment surveys conducted between 2011 and 2017  
116 (Table 1). Until 2015, the surf clam biomass assessment provided data to establish annual  
117 catch quotas under an administrative measure called “research fishing”, which were based  
118 on direct evaluations from which a catch quota was proposed (Leal et al., 2014). Unlike the  
119 AMERB regime, the quota proposed and subsequently evaluated by SUBPESCA did not  
120 include territorial rights and could be extracted by artisanal fishermen registered in the  
121 fishery. Since 2015, data from the assessments became input information for harvesting surf  
122 clam under the AMEBR system. The approach for setting harvest quota did not change after  
123 2015.

## 124 *2.2 The management cycle and harvest rate*

125 The management cycle for surf clam in the Cucao AMEBR consists of three stages (Figure  
126 2). First, a team of technicians and professional divers carry out annual stock assessment  
127 surveys that comprise population sampling of density, size structure, and the gravimetric  
128 relationship of target species (see Table 1). The survey allows estimating the total abundance  
129 and biomass of target species in the AMEBR. The biomass estimate is size-structured,  
130 allowing the estimation of vulnerable biomass, defined as individuals larger than 50 mm in  
131 length (i.e., the minimum legal size of surf clam). The stock assessment team recommends a  
132 TAC and sends the results of their analysis, along with the data, to the Chilean  
133 Undersecretariat of Fisheries and Aquaculture (SUBPESCA). Currently, the harvest quota  
134 authorized for surf clam fluctuates around 25% of the vulnerable biomass (Table 1). Thus,  
135 the current harvest control rule (HCR) is empirical and uses the estimated vulnerable biomass

136 as a status index. Therefore, the HCR consists of a constant harvest rate of 25% of the  
137 vulnerable biomass:

$$138 \quad 1) \quad Q_i = 0.25B_i$$

139 where  $B_i$  is the vulnerable biomass in the year  $i$ , and  $Q_i$  is the harvest quota of surf clam  
140 authorized by SUBPESCA. Once SUBPESCA approves the quota, fishers can harvest surf  
141 clam from the management area. At the time of harvest, catches are monitored and logged  
142 by the Chilean National Fisheries Service (SERNAPESCA).

143 To compare the current harvest rate ( $\mu = 25$ ), we considered alternative values of  $\mu = 0$ ,  
144  $\mu = 10$ ,  $\mu = 15$ , and  $\mu = 30$  of the vulnerable biomass. The harvest rate  $\mu = 0$  is only a  
145 reference condition to evaluate the population dynamics in the absence of exploitation. The  
146 harvest rate  $\mu = 30$  is the maximum harvest rate allowed by SUBPESCA.

### 147 *2.3 Population dynamics*

#### 148 *2.3.1 Abundance*

149 We conditioned a population dynamics model to known life-history parameters of surf clam.  
150 We used information on total biomass and population size-structure obtained from the direct  
151 stock-assessment surveys (Table 1, 2). The surf clam population dynamics consisted of an  
152 integrative size-structured stock assessment model (Punt et al., 2013; Sullivan et al., 1990),  
153 expressed by

$$154 \quad 4) \quad \mathbf{N}_i = \mathbf{G}\mathbf{N}_{i-1}\mathbf{S}_{i-1} + \mathbf{R}_i$$

155 where  $\mathbf{N}_i$  is a column vector of length  $L$  (number of length classes) containing the population  
156 number-at-length at the beginning of the year ( $i$ ),  $\mathbf{G}$  is a growth transition matrix (dimension

157  $L \times L$ ) determining growth among length-classes (see below). The matrix  $\mathbf{S}_i$  is a diagonal  
 158 square matrix of survival (dimension  $L \times L$ ), with diagonal terms equal to the survival rate  
 159 ( $\exp(-Z_{t-1})$ ) where  $Z$  represents the total mortality rate, i.e.,  $Z=F+M$  (fishing and natural  
 160 mortality, see below). Finally,  $\mathbf{R}_i$  is a column vector of length  $L$  containing the recruitment  
 161 to each length class at the end of the year (or beginning of the next year, see below).

### 162 2.3.2 Mortality

163 The total mortality rate was  $Z = F + M$ , where  $F$  is the fishing mortality and  $M$  is the natural  
 164 mortality rate. We estimated  $M = 0.3 \text{ year}^{-1}$  utilizing the empirical model of Brey and Gage  
 165 (1997) for benthic invertebrates. The fishing mortality rate by length class during a given  
 166 year was

167 5)  $F_{i,l} = s_l F_i$

168 where  $F_i$  is the fishing mortality rate during the year  $i$ , and  $s_l$  is the selectivity at length  $l$ ,  
 169 and defined by

170 6)  $s_l = 0$  if  $l < 50$ ; or  $s_l = 1$  if  $l \geq 50$

171 The selectivity in Eq. 6 is a 'knife-edge' function of minimum legal size ( $l_c = 50$ ) mm.

### 172 2.3.3 Recruitment

173 The recruitment dynamics followed a Beverton-Holt stock-recruitment relationship (SRR)  
 174 impacted multiplicatively by an environmental forcing, and described by

175 7)  $R_i = \frac{4hR_0S_{i-1}}{(1-h)S_0+(5h-1)S_{i-1}} e^{\epsilon_i - 0.5\sigma_R^2} E_i$

176 where  $R_0$  and  $S_0$  are the average unexploited recruitment and spawning biomass,  
 177 respectively. The parameter  $h$  is the steepness of the SRR (Dorn, 2002; Francis, 1992; Lee  
 178 et al., 2012),  $\epsilon_i$  is the annual deviation, which followed a normal distribution  $N(0, \sigma_R)$ , and  
 179  $E_i$  is the multiplicative environmental forcing. We assumed that  $R_0$  was equal to the average  
 180 recruitment during 2011-2017, and  $h$  was set equal to 0.7 considering estimates for the surf  
 181 clam *Spisula solidissima* (Hennen et al., 2018; Powell et al., 2015).

182 In Eq. 7, the environmental forcing ( $E_i$ ) represents a temporal sequence of recruitment  
 183 failures ( $E_i = 0.1$ ) and successes ( $E_i = 1$ ). We generated a sequence of failures (non-  
 184 observed recruitment) and successes (observed recruitment) for seven years according to the  
 185 abundance-at-length lower than 10 mm, i.e., the sequence of events = [Failure, Success,  
 186 Success, Success, Failure, Failure, Success]. Once we established the recruitment sequence,  
 187 we fitted the underlying Markov chain distribution using maximum likelihood with the  
 188 “markovchain” package for R (Spedicato, 2016). Subsequently, we utilized 50 Bootstrap  
 189 replicates to estimate a 2-dimensional discrete Markov Chain, defining the recruitment status  
 190 into failures and successes. We utilized the sequence of recruitment failures and successes to  
 191 conditioning the estimates of recruitment in the population model. We assumed the failures  
 192 occurred at 10% of the expected recruitment and success at 100% of the expected  
 193 recruitment. The failures at 10% is an arbitrary choice, assuming that recruitment failures  
 194 may occur below that percentile.

195 Finally, the annual recruitment was distributed to length classes according to a normal  
 196 probability at length, i.e.,

197 8) 
$$r_l = \int_l^{l+1} \frac{1}{\sqrt{2\pi\sigma^2}} e^{-(l-l_r)^2/2\sigma^2} dl$$

198 where  $l_r$  is the mean length at recruitment,  $l$  is a length class, and  $\sigma^2$  is the variance of length  
199 at recruitment.

#### 200 2.3.4 Observation models

201 The models for observations consisted of the total annual harvest and total biomass in the  
202 surveys. Catch by number was estimated according to the Baranov catch equation, i.e.,

$$203 \quad 9) \quad C_{i,l} = F_{i,l} N_l (1 - e^{-Z_{i,l}}) / Z_{i,l}$$

204 where  $C_{i,l}$  is the catch-at-length in the year  $i$ . The total annual harvest ( $Y_i$ ) was estimated by:

$$205 \quad 10) \quad Y_i = \sum_l W_l C_{i,l}$$

206 where  $W_l$  is the average weight at length class  $l$ .

207 Length composition in the population was estimated by:

$$208 \quad 11) \quad p_{i,l} = N_{i,l} / \sum_l N_{i,l}$$

209 The total biomass ( $TB$ ) at the time of the survey (within the year) followed the expression:

$$210 \quad 12) \quad TB_i = \psi \sum_l W_l N_{i,l} e^{-\tau Z_{i,l}}$$

211 where  $\psi$  is the catchability coefficient and assumed to be equal to 0.99,  $v_l$  is the survey  
212 selectivity at length and assumed to be constant and equal to 1 for all length classes, and  $\tau$  is  
213 the time of year when the stock assessment survey was carried out (Table 1). After that, we  
214 modeled the vulnerable biomass in the direct stock assessment surveys ( $B_i$ ) according to:

$$215 \quad 13) \quad B_i = \psi \sum_l s_l W_l N_{i,l} e^{-\tau Z_{i,l}}$$

216 Total biomass was the sum of products between the abundance and the average weight at  
217 length, and the spawning biomass was

$$218 \quad 14) \quad S_t = \sum_l m_l W_l N_l e^{-T_s Z_{l,t}}$$

219 where  $m_l$  is the female maturity ogive,  $T_s$  is the beginning of the spawning time within a year  
220 (set at 0.81). The model's unknown parameters were estimated by fitting the population  
221 dynamics to the data (Table 1 and 2). The objective function consisted of negative log-  
222 likelihood functions and penalized likelihood (Table 2 and Table 3).

223 We utilized ADMB (Fournier et al., 2012) to implement the estimation procedure, as well as  
224 the projection phase in which we simulated the management cycle over 20 year. The  
225 simulation consisted of a) sampling from the fitted model's posterior through Markov Chain  
226 Monte Carlo (MCMC) and b) simulating a future sequence of recruitment failures and  
227 success utilizing the transition probability of the underlying Markov chain. We utilized 200  
228 MCMC simulations obtained from 10000 samples and saved every 50 using the Metropolis  
229 algorithm implemented in ADMB.

### 230 *2.3.5 Performance of the harvest rates*

231 We summarized the trajectory of simulated recruitment, spawning biomass, and fishing  
232 mortality resulting from each harvest rate with confidence intervals of 95% obtained by  
233 applying a percentile method to all realizations obtained by MCMC. We computed depletion  
234 as the ratio between the spawning biomass in a given year and the average unexploited  
235 spawning biomass. In the absence of explicit target reference points for the surf clam  
236 spawning biomass in the management plan, we considered a default reduction in the  
237 spawning biomass to 40% of the average unexploited scenario, i.e.,  $S_{\text{target}} = 0.4S_0$ .



238 Therefore, exploitation rates generating drops in biomass beyond the target level were  
239 considered unsustainable for the surf clam population. We computed the probability of  
240 keeping the spawning biomass above this target as  $Pr[S_i / S_{\text{target}} > 1]$ . Conversely, the  
241 probability of a collapse was computed by considering reductions in biomass below 50% of  
242 the target reference point, i.e.,  $Pr[S_i / S_{\text{target}} \leq 0.5]$ . We considered “good performance” the  
243 cases where the exploitation rates generated probabilities  $> 50\%$  of achieving the target. In  
244 contrast, cases with a probability of collapse greater than 10% were considered as “bad  
245 performance.”

### 246 **3 Results**

#### 247 *3.1 Surf clam population at Cuaao beach*

248 In 2011 – 2017, the total abundance of surf clam fluctuated between 68 and 385 million  
249 individuals, with a mean of 174.2 million. Total biomass ranged between 1356 and 5407  
250 tons, with a mean of 2994 tons, whereas the vulnerable biomass fluctuated between 1261 and  
251 5399 tons, with a mean of 2716 tons (Table 1).

252 The dispersion statistics (standard deviation, coefficient of variation, and error of the mean)  
253 showed that the variability of densities usually is high, with coefficients of variation ranging  
254 between 30% and 101% of the mean. On the other hand, the mean’s standard error ranged  
255 between 2% and 3% of the mean value, which is related to the representativeness of the  
256 sample size used to estimate population density. Additionally, the bank’s estimated surface  
257 varies widely between years (69 to 120 ha), which is probably related to changes in density  
258 (Table 1).

259 The observed length composition showed clear modal progression for sizes  $>5$  mm, and  
260 recruitment failures in length classes  $< 10$  mm (Fig. 3). The sequence of failures (i.e., no  
261 recruitment observed) and successes (observed recruitment) for size  $< 10$  mm allowed the  
262 estimation of the discrete transition Markov Chain matrix to condition the recruitment state  
263 in the model (Table 4). The matrix contains the probability to move from one state to another.  
264 It implies a probability of 0.375 for recruitment failures and a probability of 0.625 for  
265 recruitment success in the long term.

266 The population model fitted to the data (Tables 1-3) performed well in reproducing the  
267 general trend in surf clam length composition (Fig. 3). According to the model, the mean  
268 length at recruitment ( $l_r$ ) was 8.8 mm (Table 2, last column), with specimens  $<25$  mm  
269 recruiting in 2013, 2014, and 2017 (Fig. 3). This finding suggests that the recruitment process  
270 in the surf clam population of Cucao does not occur regularly on an annual basis, but rather  
271 with pulses of recruitment success to the population followed by periods of failure or  
272 undetected recruitment, approximately every 2-3 years.

273 The population biomass showed a declining trend from 2011 to 2017 (Fig. 4A). A similar  
274 trend was observed for vulnerable biomass, but the spawning biomass was lower due to the  
275 maturity ogive and pre-spawning mortality within the year. The average unexploited  
276 spawning biomass ( $S_0$ ) was estimated at 1343 tons, which is lower than the spawning biomass  
277 estimated for 2011-2017. Hence, the target spawning biomass for management purposes was  
278 estimated at 537 tons. Recruitment was higher in 2011-2017, with above-average values in  
279 2013 and 2014, followed by lower recruitment from 2015 to 2017 (Fig. 4B). The fishing  
280 mortality rate fluctuated with the harvest but was higher in 2017 (Fig. 4C).

281 *3.2 Recruitment simulations and harvest rates performance*

282 The transition Markov chain matrix here obtained (Table 4) allowed generating future  
283 realizations of recruitment state, allowing the simulation of future population dynamics and  
284 the performance of different harvest rate values. Here, we present only one realization of  
285 future recruitment states but 200 equally probable recruitment values due to interannual  
286 variability associated with  $\sigma_R$ . The results were similar for different realizations of  
287 recruitment sequences of failures and success (see Supplementary Results).

288 According to the simulation of a realization of recruitment failures and successes, the  
289 recruitment shows the alternating pattern between higher and lower recruitment (Fig. 5).  
290 However, this feature of recruitment was hidden as represented by the median and confidence  
291 limits of 90% (Fig. 6A).

292 The spawning biomass responded to each exploitation rate (Fig. 6B), as reflected by the  
293 approximately constant fishing mortality (Fig. 6C). Note that a harvest rate of 30% produced  
294 the highest average fishing mortality, close to that estimated in 2017 (Fig. 6C). The current  
295 harvest rate of 25% resulted in a highly depleted spawning biomass at around 20% (Fig. 7),  
296 with a probability of future collapse  $> 80\%$  (Fig. 8). On the other hand, an exploitation rate  
297 of 10% kept the spawning biomass close to the target 40% of the unexploited spawning  
298 biomass (Fig. 7), with probabilities  $> 50\%$  once the biomass was recovered (Fig. 8). Indeed,  
299 an exploitation rate of 10% could revert the declining trend observed in the surf clam  
300 spawning biomass (Fig. 7).

301 **4 Discussion**

302 Recruitment failures and high temporal variability are common features in many species with  
303 short life cycles and can be linked to high rates of natural mortality and greater variability in  
304 growth rates (Bjørkvoll et al., 2012; Defeo, 1996; Pineda and Caswell, 1997). These features  
305 in population dynamics have been described for various surf clam species (Aburto and Stotz,  
306 2013; Lima et al., 2000; Ripley and Caswell, 2006).

307 Infrequent recruitment of surf clams has also been reported previously for the Chilean coast,  
308 possibly in association with environmental factors that affect the release of gametes as well  
309 as oceanographic factors affecting the survival and onshore supply of planktonic larvae  
310 (Thiel et al., 2007). It is common to hear artisanal fishers talk about a “green” surf clam with  
311 lengths of 3-4 cm occasionally found in the exploited banks. This is consistent with the  
312 occasional appearance of juveniles in the annual surveys at Cucao beach, where small  
313 individuals (lengths 2.5-5.0 cm) appeared in large numbers in only one out of seven stock-  
314 assessment surveys (2016). The inconsistent occurrence of juveniles observed in the stock-  
315 assessment surveys was not an artifact of survey mistiming (relative to recruitment), as  
316 indicated by the inter-annual consistency and progression of gaps in the size-structure data  
317 collected during surveys.

318 Recruitment in *Mesodesma donacium* is hard to miss during the stock assessment surveys  
319 since post-settled individuals are easily distinguishable in the field and tend to accumulate in  
320 the swash zone and near the mouth of estuaries or small rivers (Jaramillo et al., 1994), which  
321 represents an advantage over most other benthic species in which the presence of recruits is  
322 less evident. Although the information collected to date does not allow to establish causal  
323 relationships between environmental factors and recruitment success in the surf clam, it is

324 likely that a specific combination of wave and wind conditions, at the right time of year, is  
325 required for competent larvae to reach the shore and settle. The total number of competent  
326 larvae that could reach the shore, in turn, is likely to depend on advective and feeding  
327 conditions in shelf waters during the weeks or months before the recruitment period.

328 Our recruitment estimates for the surf clam in 2011-2017, which conditioned the population  
329 model, showed the alternation of periods with high and low recruitment in the Cucao beach  
330 population, revealing a pattern of failures and successes well described by the Markov chain  
331 matrix. In the long-term, the probability of failures reaches 37.5%, but the surf clam's  
332 estimated lifespan at Cucao was close to 7 years, with cohorts showing a modal progression  
333 in the size structure from 2011 to 2017. The estimated von Bertalanffy growth parameter  
334 ( $K = 0.21 \text{ year}^{-1}$ ) indicates theoretical longevity close to 15 years, i.e.,  $t_{max} \sim 3/K$   
335 (Kenchington, 2014). Thus, the population's age-structure may act as a filter of recruitment  
336 variability, dampening the effects of environmental variability on population renewal and  
337 stock size (Planque et al., 2010).

338 The current management applied in management areas AMEBR in Chile can be viewed as a  
339 "static" or "memory-lacking" process since it does not refer to either past or future  
340 observations. Indeed, annual quotas are computed from the standing stock assessed directly  
341 in the field. In practice, the upper limit for the harvest rate ( $\mu = 30$ ), and even the current  
342 harvest rate of  $\mu = 25$ , is excessive, as demonstrated here. It is advisable to apply a harvest  
343 rate of ( $\mu = 10$ ), which may be low enough to keep the surf clam population's reproductive  
344 potential. Furthermore, it is advisable to implement a harvest control rule in which the harvest  
345 rate declines when the spawning stock declines due to lower recruitment. The ramp-like  
346 harvest control rule could be more effective in ensuring rapid recovery of the spawning

347 biomass, dampening the probability of unobserved or lower recruitments in the future.  
348 Indeed, reducing the harvest rate as the stock declines results in added resilience against  
349 environmental variability (Merino et al., 2019), which appears to be increasing due to climate  
350 change (Roberts et al., 2017).

351 The memory-lacking management procedure is applied to almost all AMEBR in Chile, as  
352 documented in the management and exploitation plan for each target species (Gallardo et al.,  
353 2011). Our analyses revealed that surf clam recruitment does not occur regularly every year.  
354 Instead, 2 to 3 years of low recruitment are followed by one major recruitment episode. The  
355 landing records from other areas where surf clam populations were depleted in previous  
356 decades show that exploitation could be unsustainable when the harvest rate intensity is not  
357 controlled. This behavior is typical in the exploitation of surf clam *M. donacium* along the  
358 Chilean coast (Aburto et al., 2013), as well as for other surf clam species (Fiori and Morsán,  
359 2004; Herrmann et al., 2011; Laudien et al., 2003; Ripley and Caswell, 2006; Weinberg,  
360 1999).

361 For fisheries management, the observed recruitment failures imply that, if recruitment occurs  
362 approximately once every three years, the exploitation rates should be lower than those  
363 recommended by the current harvest rate ( $\mu = 25$ ), and that lower exploitation rates ( $\mu \leq$   
364 10) are needed to ensure sustainable exploitation. Furthermore, the current lack of knowledge  
365 on the spatial-temporal variability of settlement and recruitment in species like the surf clam  
366 brings into question the exploitation strategies currently considered sustainable. The current  
367 approach for AMEBR implicitly assumes the existence of annual recruitments that maintain  
368 populations at sustainable, productive levels, which is not the surf clam case. In this sense,

369 our results raise the need for an even more precautionary approach to commercial  
370 exploitation of benthic species with irregular or non-annual recruitment.

371 The underlying problem is that, in practice, little is known about the intensity and success of  
372 recruitment in most harvested marine populations, which can be attributed to biases  
373 introduced by the extractive activity itself (Punt and Cope, 2019). Sampling from the  
374 commercial catch is usually carried out on landings, which leaves out juvenile fractions. In  
375 the case of benthic species harvested from AMEBRs in Chile, population surveys usually  
376 consider the fraction that can be detected visually by scientific divers or local fishers.  
377 Although this procedure includes individuals under commercial size, it is likely to leave out  
378 newly settled individuals, which are not always visible due to small size, pigmentation, or  
379 behavior. Thus, the quantification of newly established fractions in populations of  
380 commercial species is usually fraught with uncertainty and should be approached through  
381 indirect methods. For management areas where biomass and length composition have been  
382 recorded annually over a long-enough period, it is advisable to implement an integrated  
383 stock-assessment model (Punt et al., 2013; 2011; Smith et al., 2011). Subsequently,  
384 biological reference points should be established to assess the population's status and set a  
385 quota based on population projections. Thereafter, it is advisable to review the AMEBR's  
386 management procedure to keep the exploitation of benthic species within biologically safe  
387 margins.

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Table 1. Summary of the yearly stock assessment surveys of surf clam *Mesodesma donacium* at Cucao beach, used to conditioning the operating model. The observed harvest rate (u) was computed as the ratio between the quota and the vulnerable biomass.

<b>Stock assessment results</b>	<b>2011*</b>	<b>2012*</b>	<b>2013*</b>	<b>2014*</b>	<b>2015**</b>	<b>2017**</b>
Date of the stock assessment	14-Jun	30-Mar	26-Apr	14-Jan	04-Dec	31-Jan
Sampling units (quadrats)	647	1063	328	1116	800	236
Average density (ind/m <sup>2</sup> )	110.5	213.2	441.5	197.5	359.1	78.7
Estimated bank surface (ha)	69.4	112.7	117.2	70.7	108.7	120.6
Abundance (10 <sup>3</sup> individuals)	72,530	221,053	203,711	68,008	385,039	94,972
Biomass (ton)	1,356.2	4,638.8	5,407.2	1,687.1	3,257.5	1,618.3
Vulnerable biomass (ton)	1,261.3	4,459.9	5,398.6	1,646.3	1,992.4	1,539.5
Quota (10 <sup>3</sup> individuals)	16,671	52,173	44,578	8,878	24,628	19,060
Quota (ton)	347	1169	1350	356	450	403
<b>Quota/Vulnerable Biomass</b>	<b>0.275</b>	<b>0.262</b>	<b>0.250</b>	<b>0.216</b>	<b>0.226</b>	<b>0.262</b>
Catch (ton)	199	662	800	304	101	592

\* Data obtained from Fundación Chiquihue (2012)

\*\* Data obtained from Technical Reports of the Undersecretariat of Fisheries and Aquaculture (SUBPESCA). In the operating model, we allocated the sampling in 2015 to the following year 2016.

Table 2. General configuration of the population model for surf clam *Mesodesma donacium* in Cucao beach.

Process	Definition	Parameter or vector	Value	Prior	Penalization or bounded	Estimation
Growth	Asymptotic length of VBGF	$L_\infty$	Fixed	93.4 mm	-	93.4 mm
	Growth coefficient of VBGF	$K$	Estimated	0.25 year <sup>-1</sup>	Eq. T3.1	0.21 year <sup>-1</sup>
	Standard deviation for K penalty	$\sigma_k$	Fixed	0.1	Eq. T3.1	-
	Length at recruitment	$l_r$	Estimated	20 mm	-	8.8 mm
	Standard deviation of $l_r$	$\sigma$	Estimated	1.5 mm	-	2.72 mm
Mortality	Growth increment shape	$\beta_r$	Estimated	0.2	-	0.313
	Natural mortality rate	$M$	Fixed	0.3	-	-
Recruitment	Fishing mortality	$F_t$	Estimated	$\log(F_t)$	$\sim U(-6, 1.39)$	Fig. 3
	Steepness of SRR	$h$	Fixed	0.7	-	-
	Average unexploited recruitment	$\bar{R}$	Estimated	$\log(R_0)$	-	38.5 10 <sup>6</sup>
	Standard deviation of recruitment	$\sigma_R$	Fixed	0.4	-	-
Catchability	Recruitment deviations (log-scale)	$\varepsilon_t$	Estimated	$\varepsilon_t \sim N(0, \sigma_R)$	Eq. T3.2	Fig. 3
	Survey catchability coefficient	$\psi$	Estimated	0.99	Eq. T3.3	0.99
Selectivity	Standard deviation for $\psi$ penalty	$\sigma_\psi$	Fixed	0.1	Eq. T3.3	-
	Fishery selectivity at length	$s_l$	Fixed	-	-	-
Reproduction	Survey selectivity at length	$v_l$	Fixed	-	-	-
	Maturity ogive	$m_l$	Fixed	-	-	-
	Steepness	$h$	Fixed	0.7	-	-
	Spawning time	$T_s$	Fixed	0.81	-	-





Table 3. Penalties ( $\rho_j$ ) and negative log-likelihood functions ( $\ell_j$ ) contributing to the objective function ( $f$ ) in the estimation of unknown parameters ( $\theta_k$ ) for the surf clam operating model. Standard deviations for fitting: Standard deviation for total harvest  $\sigma_Y = 0.01$ , standard deviation for total survey biomass  $\sigma_B = 0.1$ , effective size for multinomial length composition  $\omega_i$ .

Components	Equation	Number
Growth coefficient of VBGF	$\rho_2 = \frac{(\log(\hat{R}/K))^2}{2\sigma_k}$	T3.1
Recruitment deviations (log-scale)	$\rho_1 = \frac{1}{2\sigma_R} \sum_i \varepsilon_i^2$	T3.2
Survey catchability coefficient	$\rho_3 = \frac{(\log(\hat{\psi}/\psi))^2}{2\sigma_\psi}$	T3.3
Total annual harvest	$\ell_1 = \frac{1}{2\sigma_Y^2} \sum_{i=1}^n (\log(\hat{Y}_i/Y_i))^2$	T3.4
Survey biomass	$\ell_2 = \frac{1}{2\sigma_B^2} \sum_{i=1}^n (\log(\hat{TB}_i/TB_i))^2$	T3.5
Survey length composition	$\ell_3 = \omega_i \sum_{i=1}^n \sum_l p_{i,l} \log(\hat{p}_{i,l})$	T3.6
Objective function	$f = \sum_j \ell_j + \sum_j \rho_j$	T3.7

Table 4. Discrete time Markov Chain for the state of surf clam recruitment, obtained by bootstrap. The sequence of events for 2011-2017 was [Failure, Success, Success, Success, Failure, Failure, Success], where “Failure” is the absence of observable recruitment and ‘Success’ is the observed recruitment of surf clam in length composition surveys at Cucao beach. Standard errors are shown in parentheses, and the environmental forcing (E) is the value chosen to affect the recruitment dynamics given the recruitment state (see text).

Recruitment State	Failure	Success	Environmental forcing (E)
Failure	0.245 (0.042)	0.755 (0.042)	0.1
Success	0.453 (0.036)	0.547 (0.036)	1



Figure 1. Principal landing points of surf clam *M. donacium* along the Chilean coast (left), and performance of regional landings from 2000 (right). Source: National

[Click here to access/download;Figure;Figure01.png](#)

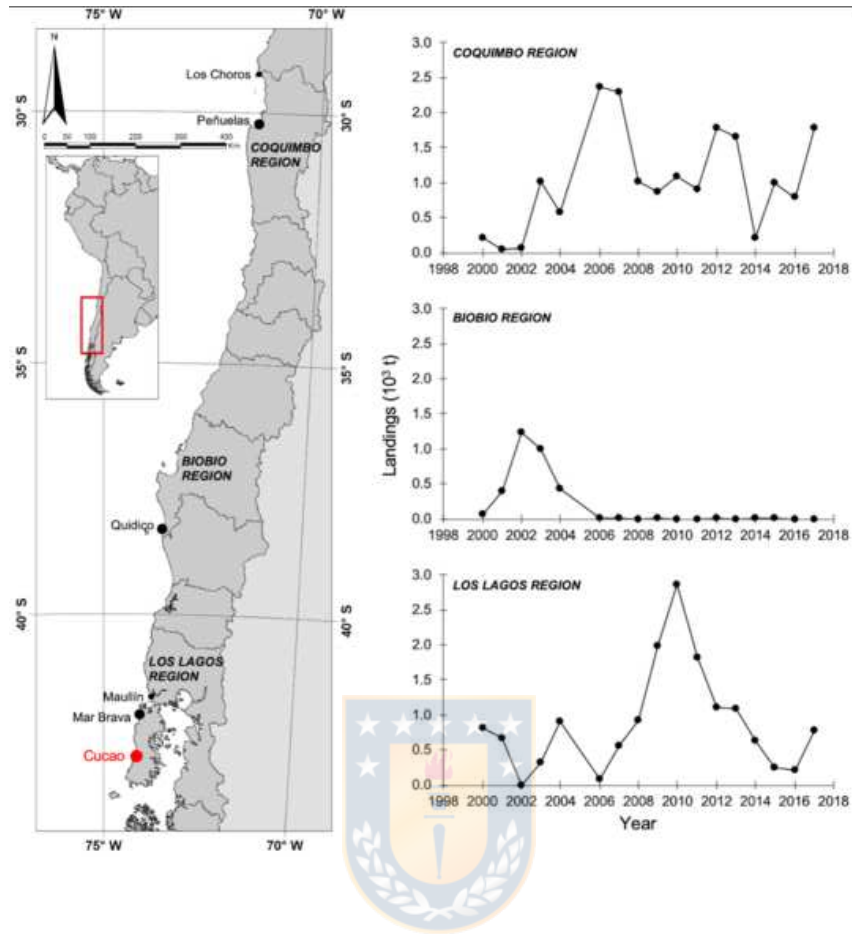


Figure 2. Current assessment procedure for the surf clam *M. donacium* in the AMEBR Cucao.

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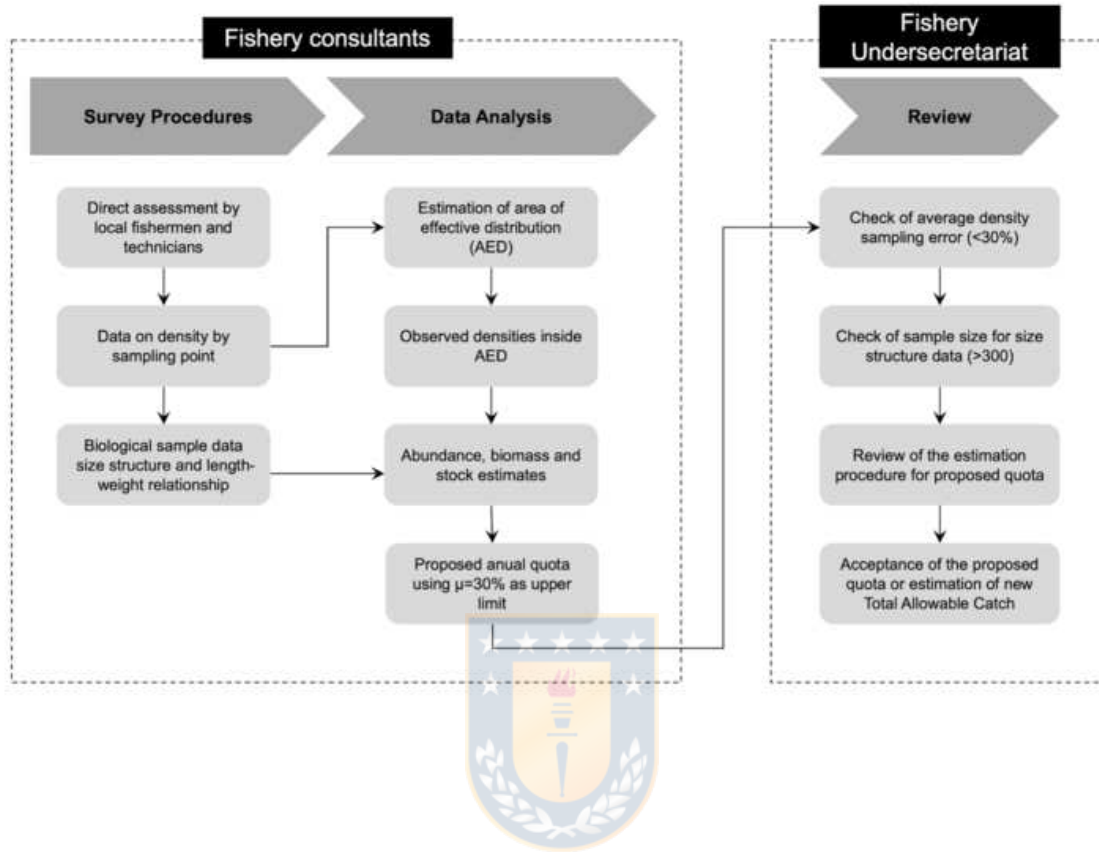


Figure 3. Observed and predicted length composition of surf clam *Mesodesma donacium* at Cucao in 2011-2017. The predicted

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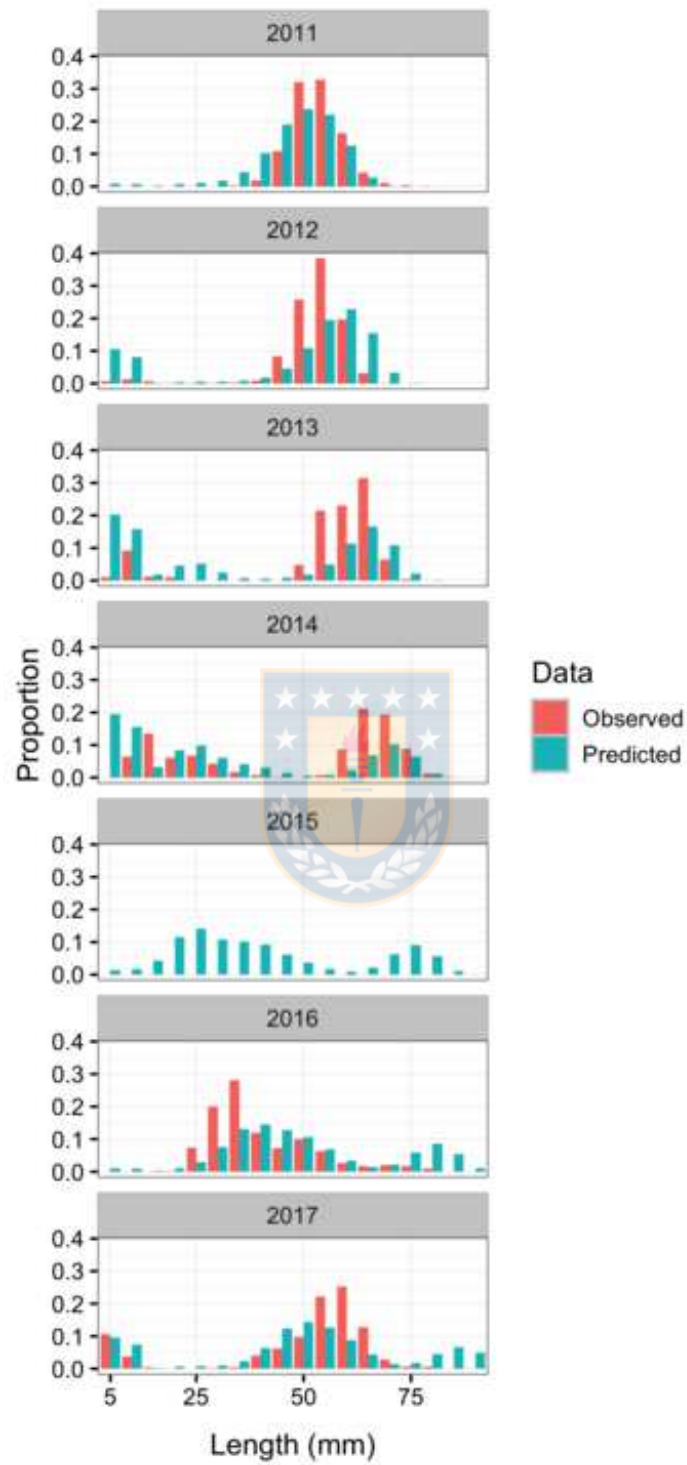


Figure 4. Population biomass and catch (A), annual recruitment (B), and fishing mortality rate (C) of surf clam *Mesodesma donacium* at Cucao during 2011-2017

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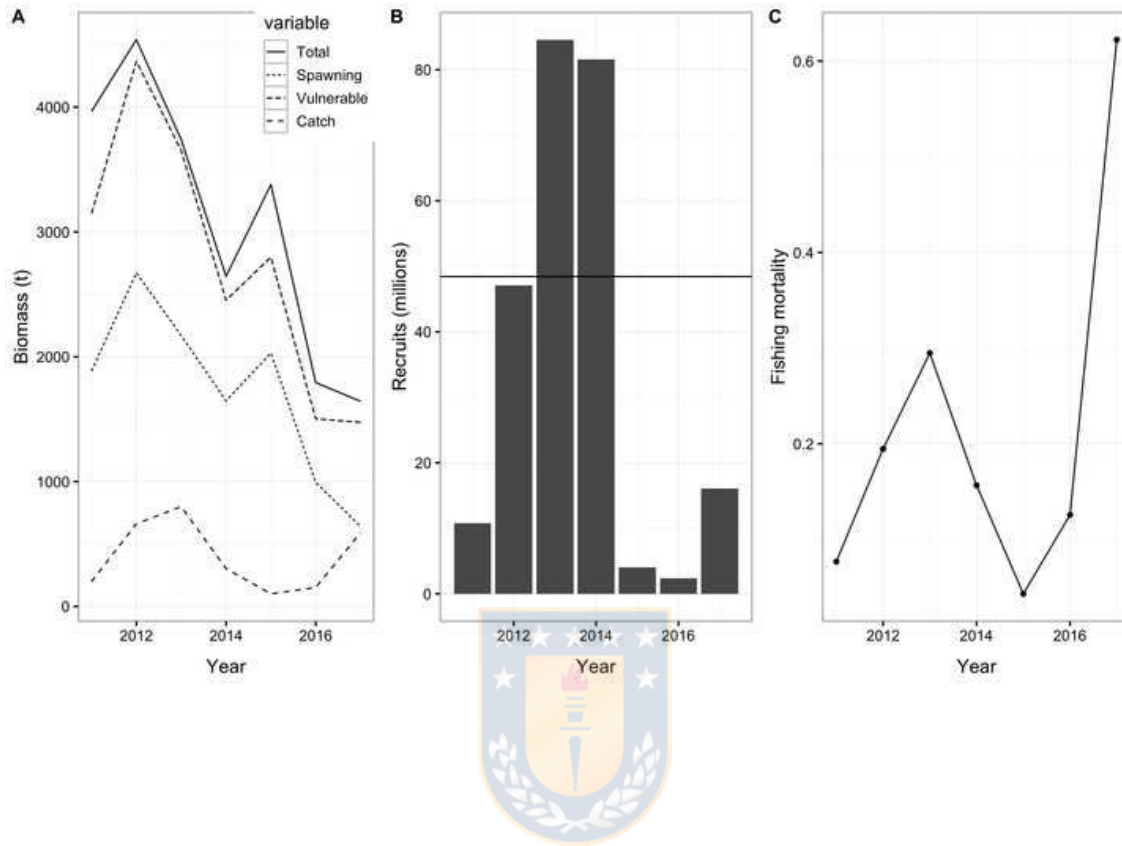


Figure 5. Single realizations of simulated unexploited future recruitment for surf clam *Mesodesma donacium* at Cucao beach, northern Patagonia.

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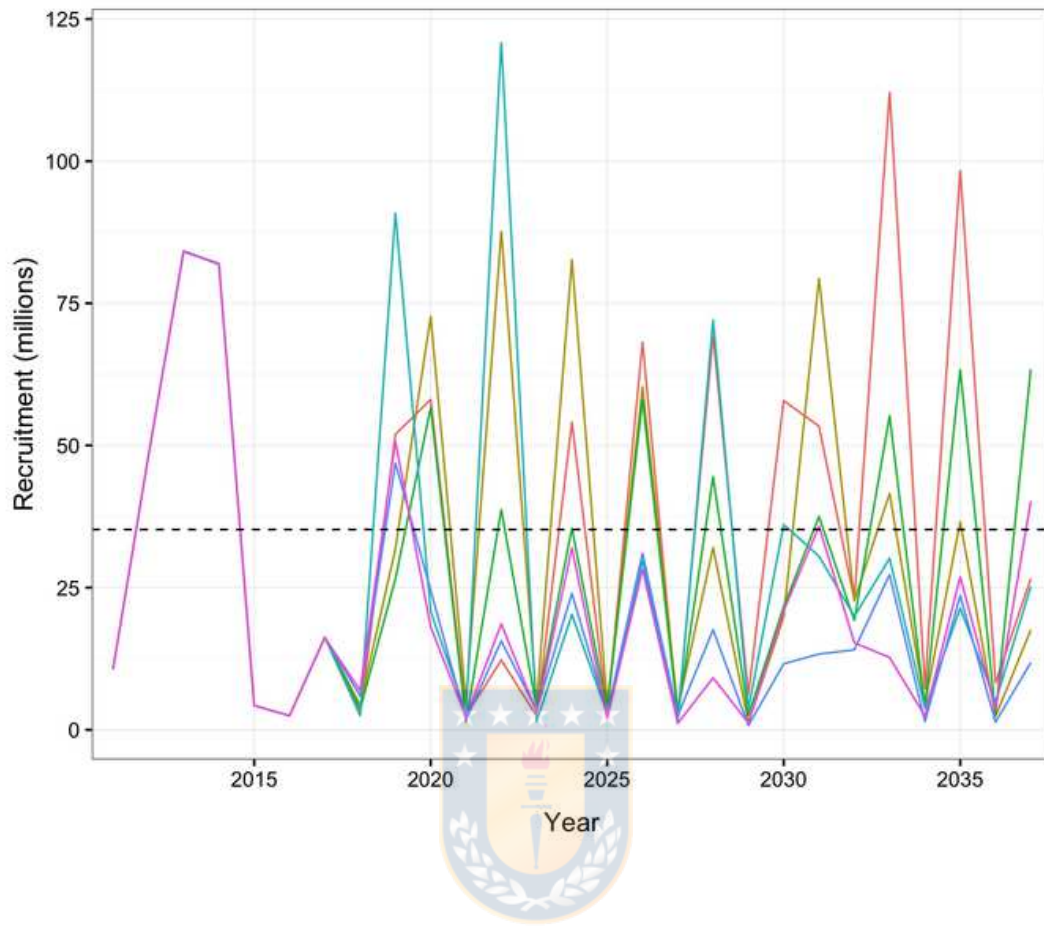


Figure 6. Summary of 200 simulations of projected recruitment (A), and responses in the spawning biomass (B), fishing mortality (C), and catch (D) for the surf clam

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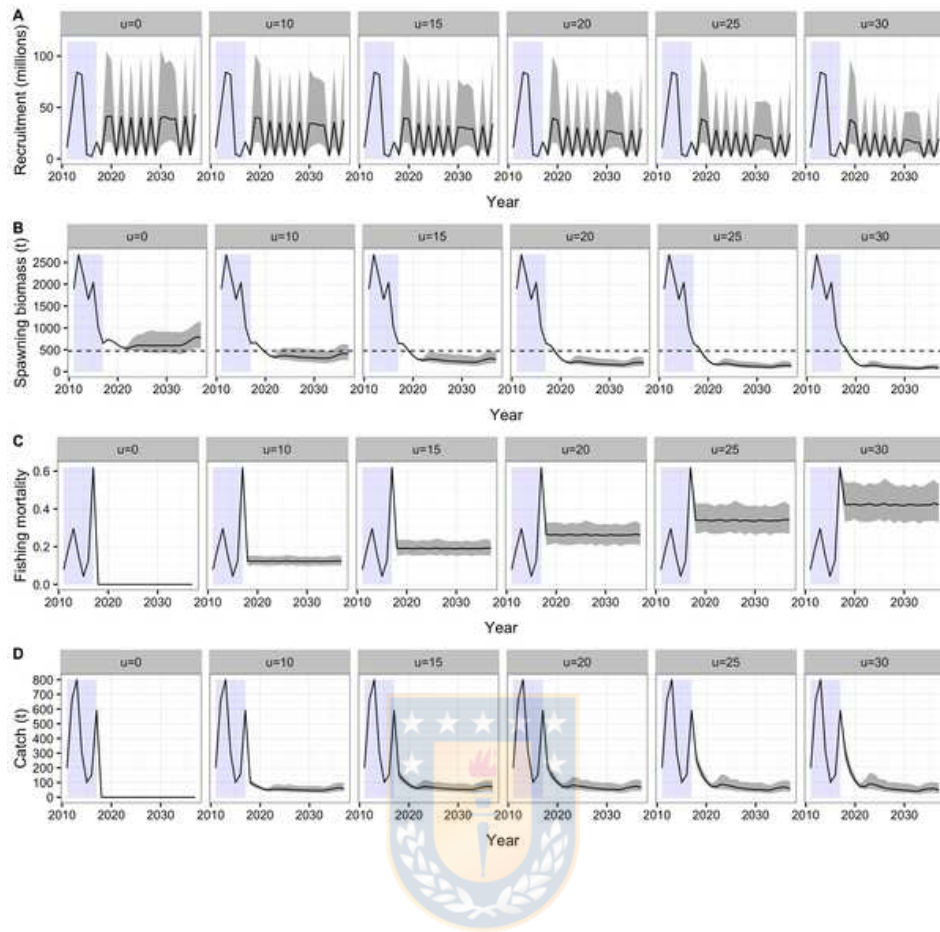




Figure 7. Expected depletion of the spawning biomass of surf clam *Mesodesma donacium* at Cucao beach according to six different harvest rates. Light purple shading

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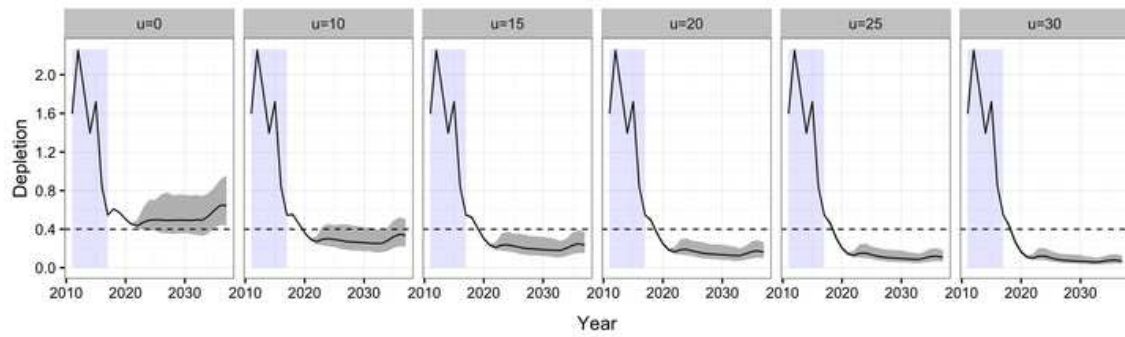
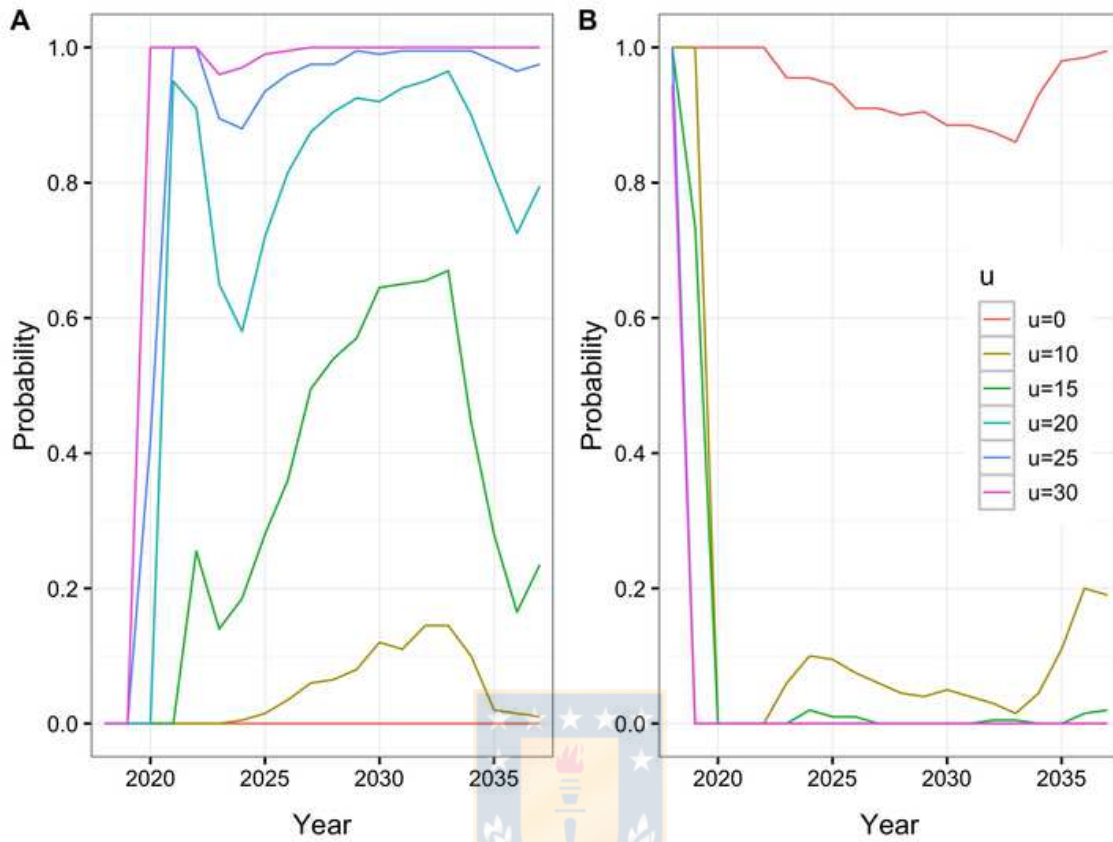


Figure 8. Probability of collapse (A) and the probability of achieving the target surf clam biomass equal to 40% of the spawning biomass (B) at Cucao beach under different

[Click here to access/download;Figure;Fig08\\_Probability.jpg](#)



## 6 DISCUSIÓN

Los resultados obtenidos en los trabajos que componen esta Tesis Doctoral ponen de manifiesto el rol estructurador de la geomorfología costera sobre la variabilidad en las condiciones oceanográficas y el papel de esta variabilidad sobre la estructura de las comunidades bentónicas submareales de la zona costera. Tal variabilidad puede ser utilizada como un predictor del tipo de comunidad o de especie factible de encontrar en un sitio específico, lo que puede ser empleado favorablemente en el manejo de las poblaciones de recursos hidrobiológicos sujetos a explotación a través de la medida AMERB. Adicionalmente, esta variabilidad ambiental afecta el éxito de procesos clave para la sustentabilidad de poblaciones explotadas, como el reclutamiento, lo que afecta directamente la estructura de tamaños y la abundancia poblacional de la fracción adulta.

Al evaluar la relación entre la estructura comunitaria del bentos submareal en 30 AMERB de la Región del Biobío y factores ambientales considerados como potenciales variables explicatorias (Capítulo 1), se confirmó la importancia del grado de exposición de la costa como modulador de las condiciones ambientales a escala local, y se observaron diferencias en cuanto a la conexión entre variables oceanográficas de superficie y las comunidades de fondos duros versus fondos blandos. En efecto, para las comunidades de fondos duros, la presencia de sustrato rocoso parece modular la presencia de algas pardas y foliosas-corticadas, las que a su vez generan condiciones adecuadas para la presencia de filtradores de la epifauna, ramoneadores, depredadores y carroñeros. Por su parte, en las comunidades de fondos blandos, las condiciones de la columna de agua son el principal factor que influye sobre la presencia de filtradores de la infauna y detritívoros. La presencia de zonas de fondo blando en sectores semi-expuestos o protegidos de la costa proporciona condiciones adecuadas para el asentamiento larval de invertebrados propios de estas zonas, sin una influencia significativa de otros grupos taxonómicos en la estructuración de comunidades bentónicas.

A pesar de la asociación bien documentada entre los patrones espaciales en las condiciones oceanográficas superficiales y los cambios en la estructura de las comunidades bentónicas intermareales (e.g., Broitman et al., 2001; Navarrete et al., 2005;

Menge & Menge, 2013), las variables derivadas de sensores satelitales no contribuyeron sustancialmente a la predicción de la estructura comunitaria del bentos submareal, lo que puede deberse a que la mayoría de las mediciones satelitales están restringidas a la capa superficial, que puede no reflejar adecuadamente el efecto de las condiciones del estrato de fondo sobre el bentos. Además, las aguas cercanas a la costa presentan una fuerte variabilidad a escalas temporales más cortas que las capturadas por los compuestos semanales utilizados en este primer estudio. En este sentido, y como se detallará más adelante, los resultados asociados con el segundo objetivo específico de esta Tesis, mostraron una mejora sustancial en cuanto a la captura los patrones en la estructura comunitaria que pueden ser explicados a partir de la variabilidad en las condiciones ambientales.

La inclusión de variables relativas a la actividad extractiva en las AMERB no resultó significativa en ninguno de los casos analizados. Este fue un resultado sorprendente, dado que se espera que la pesca disminuya la densidad y aumente la variabilidad en la abundancia de especies explotadas (Anderson et al., 2008; Stenseth & Rouyer, 2008), afectando a las comunidades del bentos (Molina et al., 2014). En este caso, es posible que los desembarques provenientes de AMERB no hayan aparecido como un factor significativo en la modelación por estar enmascarados por el efecto de la extracción ilegal, que ha tenido un impacto sostenido sobre el desempeño de las AMERB.

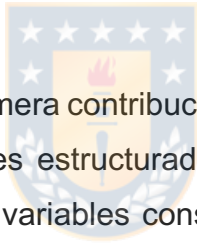
Aunque la extracción ilegal en AMERB constituye un problema transversal a nivel nacional, los estudios que se han abocado a determinar las causas de esta actividad son todavía escasos. En este contexto, es claro que el desempeño del sistema AMERB es diferente del que puede inferirse a partir de las estadísticas oficiales (Oyanedel et al., 2017), con niveles de extracción ilegal altamente variables y que han sido estimados entre un 32% y 68% de los ingresos percibidos por AMERB (Bandin & Quiñones, 2014), hasta niveles que superan el 85% de los desembarques oficiales (Oyanedel et al., 2017). El incremento sostenido en la extracción ilegal puede estar relacionado con que la planificación territorial de las AMERB ha conducido a un incremento en la extracción ilegal, por falta de áreas de libre acceso y zonas de conservación biológica (Gelcich et

al., 2006; Fernández et al., 2020), lo que se asocia con una visión atomizada de la administración de estos espacios costeros, donde el éxito de la medida ha sido evaluado en términos del número de solicitudes de AMERB (Gelcich et al., 2006). Esta realidad, demuestra la necesidad de evaluar el desempeño de las AMERB en una escala espacio-temporal adecuada, considerando no sólo indicadores biológico-pesqueros de las especies comerciales, como es en la actualidad, sino también los cambios socio-económicos y actitudinales que la medida ha producido (Gelcich et al., 2013; Fernández et al., 2020; Franco et al., 2021).

Otro factor que puede explicar la ausencia de respuestas claras de la estructura comunitaria de las AMERB a la presión de pesca, se relaciona con que el análisis de las 30 AMERB se realizó sobre grupos funcionales, mientras que el efecto de la captura es especie-específico. El análisis comunitario basado en grupos funcionales puede verse afectado por la presencia de *redundancia funcional*, la cual puede mantener estables las propiedades agregadas de comunidad, a pesar de que la composición de las especies pueda cambiar con el tiempo (González & Loreau, 2009). Según Mouchet et al. (2010), dos o más especies son redundantes para un proceso en el ecosistema cuando la ausencia de una o más de estas especies no afecta significativamente a este proceso. Por lo tanto, la redundancia funcional puede favorecer la resiliencia del ecosistema a las perturbaciones (Braeckman et al., 2014; Francisco & De la Cueva, 2017). Está demostrado que la intervención pesquera aumenta la variabilidad espacial de indicadores poblacionales en especies sujetas a explotación (Anderson et al., 2008) con efectos sobre las comunidades bentónicas asociadas (Molina et al., 2014). Sin embargo, el análisis del alcance de este efecto requiere contar con datos de zonas costeras con características oceanográficas similares, pero que no hayan sido afectadas por la intervención humana. Desafortunadamente, en la actualidad no hay sitios en la región de estudio que se ajusten a tal descripción.

Los resultados del análisis de ruta demuestran que los factores ambientales pueden combinarse para predecir, hasta cierto punto, el tipo de comunidad bentónica esperada para una localidad determinada, contribuyendo así a la comprensión de los factores que

estructuran espacialmente el bentos submareal, lo que constituye un aporte al manejo asociado a las AMERB y es relevante en el contexto de los desafíos de conservación y del manejo integrado de zonas de costeras (Crowder & Norse, 2008). En efecto, por medio de mediciones simples como la exposición de la costa y el tipo de sustrato, es posible establecer *a priori* y con un grado razonable de certidumbre el tipo de comunidad submareal que puede prosperar naturalmente en una zona determinada y, por lo tanto, el tipo de especies que eventualmente pueden ser cultivadas, consideradas para repoblamiento, o manejadas con mayor éxito. Este tipo de enfoque analítico puede contribuir a la clasificación de las áreas costeras de acuerdo con su aptitud para diferentes usos. Una mejor clasificación de las zonas costeras en atención a la estructura de las comunidades bentónicas, considerando los regímenes ambientales locales, es pertinente en el contexto del desarrollo de enfoques de manejo integrados y en la asignación de derechos territoriales a las comunidades que históricamente han hecho uso de estos sistemas.



Pese a que los resultados de esta primera contribución (Capítulo 1) representan un aporte relevante al conocimiento de factores estructuradores de comunidades bentónicas en AMERB, el poder explicativo de las variables consideradas en el análisis no superó el 60%. Las variables ambientales incluidas correspondieron a las disponibles para la región de estudio y, en particular, para las AMERB analizadas. Probablemente, la inclusión de otras variables ambientales clave en la modulación de la estructura comunitaria, tales como el régimen de oxígeno disuelto (Kordas et al., 2011; Brennan et al., 2016; Fajardo et al., 2018), o la concentración de nutrientes y contaminantes (Grall & Chavaud, 2002; Carrier-Belleau et al., 2021) a escala de las AMERB podrían haber incrementado el desempeño (i.e., la bondad de ajuste) de los modelos ajustados. Por otro lado, el uso de información satelital en la forma de promedios semanales no permitió analizar la variabilidad de mayor frecuencia en condiciones de superficie, ni las características de los estratos sub-superficiales de la columna de agua sobre las comunidades del bentos.

Las limitaciones enunciadas más arriba motivaron el análisis del rol que la variabilidad temporal en las condiciones del agua de fondo podría tener como estructurador de las

comunidades del bentos submareal (Capítulo 2). Los resultados de este análisis mostraron una mejora sustancial en cuanto a explicar la variabilidad de la estructura comunitaria del bentos submareal a partir de la dinámica temporal en las condiciones ambientales. Mientras que el tipo de sustrato explicó el 29% de la ordenación NMDS de los datos comunitarios, la adición de tres índices de variabilidad ambiental (límite superior de la temperatura, variabilidad de alta frecuencia en temperatura, duración máxima de eventos de hipoxia) permitió explicar hasta el 84% de la ordenación de las comunidades bentónicas analizadas. Esta es una mejora sustancial en el poder explicativo del modelo estadístico utilizado.

La localidad que mostró mayores diferencias en la estructura de la comunidad bentónica (Arauco) se caracteriza por ser una zona de fondos blandos, con temperaturas más altas en el agua de fondo, y eventos de hipoxia más largos. El dominio local de especies como el huepo (*Ensis macha*), el caracol trumulco (*Chorus giganteus*) y la jaiba peluda (*Cancer setosus*), sugiere que estas especies de la infauna (*E. macha*) y epifauna (*C. giganteus* y *C. setosus*) estarían mejor adaptadas para tales condiciones ambientales. Por otro lado, sitios con mayor presencia de sustrato rocoso, asociados con temperaturas de fondo en promedio más bajas pero con una mayor variabilidad de alta frecuencia (Chome, Yani, Piures) están dominados por invertebrados de la epifauna (e.g., *Concholepas concholepas*, *Austromegabalanus psittacus*) y macroalgas (e.g., *Durvillaea antarctica*, *Lessonia spicata*) que se desempeñan mejor en ambientes más fríos y fluctuantes, pero con una menor incidencia de eventos de hipoxia de larga duración.

En ecosistemas de surgencia, la alta productividad primaria sustentada por el afloramiento de aguas ricas en nutrientes pero deficientes en oxígeno, contribuye a la generación de condiciones hipóxicas tanto en la columna de agua como en los sedimentos (Chávez & Messie, 2009; Levin et al., 2009; Sobarzo et al., 2007; Veas et al., 2012; Kampf & Chapman, 2016). Aunque la hipoxia impulsada por la surgencia ha sido estudiada típicamente a cierta distancia de la costa (y en profundidad), se ha demostrado que, bajo ciertas condiciones, las aguas hipóxicas pueden alcanzar hábitats costeros someros (Grantham et al., 2004; Hernández-Miranda et al., 2012, 2017), impactando la

biodiversidad (Fajardo et al., 2018) y, en casos extremos, la supervivencia de las poblaciones bentónicas locales (Chu & Tunnicliffe, 2015; Hernández-Miranda et al., 2012; Veas et al., 2012). Las especies bentónicas sésiles que habitan en los sistemas de surgencia han estado expuestas a la hipoxia durante milenios (véase Moffitt et al., 2015). Por lo tanto, están equipadas con una gama de respuestas conductuales y metabólicas necesarias para resistir eventos de hipoxia, dentro de ciertos márgenes de periodicidad e intensidad (González & Quiñones, 2000). No obstante, una intensificación de la hipoxia cercana a la costa, en asociación con una surgencia costera más intensa (García-Reyes et al., 2015; Jacob et al., 2018), puede inducir cambios en el comportamiento o fisiología de algunas especies bentónicas, afectando el crecimiento y la sobrevivencia (Díaz & Rosenberg, 2008; Rabalais et al., 2014), y modificando la estructura local de las comunidades bentónicas (Wu, 2002; Veas et al., 2012; Riedel et al., 2014).

El impacto de la hipoxia sobre la diversidad en zonas costeras se ha documentado en estudios basados en monitoreos de largo plazo (Seitz et al., 2009), en el contraste de condiciones ambientales divergentes (Gallardo et al., 2004; Sellanes et al., 2007) y en el análisis de eventos particulares de corta duración (Grantham et al., 2004; Hernández-Miranda et al., 2012). A nivel nacional, varios estudios han abordado el efecto de las condiciones de hipoxia sobre las comunidades de la macrofauna de fondos blandos (Carrasco & Gallardo, 1983; Oyarzún et al., 1987; Carrasco et al., 1988; Gallardo et al., 2004; Palma et al., 2005; Veas et al., 2012). En el caso de las zonas costeras de la Región del Biobío, Veas et al. (2012) señalan la existencia de un alto grado de estabilidad de mesoescala en la composición de las comunidades de la macrofauna de fondos blandos, con un ensamble de especies dominado por organismos tolerantes a las condiciones de hipoxia, siendo la intrusión estacional de AESS uno de los principales factores moduladores de estas comunidades.

No obstante, a nivel de la megafauna, y en particular en el caso de comunidades bentónicas costeras sometidas a actividades de extracción pesquera, como es el caso de las AMERB, el nivel de conocimiento en cuanto a los efectos de las condiciones ambientales sobre la estructura comunitaria, es mucho menor. Dentro de la zona de



estudio, Hernández-Miranda et al. (2012) analizaron los efectos de un evento de hipoxia que tuvo lugar en el verano de 2008, que produjo una pérdida dramática de biodiversidad y resultó en el dominio de especies carnívoras (el gastrópodo *Nassarius sp.*) y carroñeras (la jaiba *Cancer coronatus*). El análisis desarrollado en esta tesis (Capítulo 2) reveló el dominio numérico de la jaiba *Cancer setosus* y el gastrópodo *Chorus giganteus* en la localidad de Arauco, que resultó ser la que experimenta los eventos de hipoxia más largos entre las seis localidades estudiadas. Este hallazgo sugiere que este tipo de especies móviles, depredadoras o carroñeras podrían adaptarse mejor a futuros escenarios de bajo oxígeno y, potencialmente, dominar las comunidades bentónicas cercanas a la costa. Sin embargo, vale la pena señalar que algunas especies filtradoras sésiles como *Ensis macha*, particularmente abundante en la localidad Arauco, parecen estar bien adaptadas a estas condiciones extremas. Por lo tanto, las diferencias en la composición de la comunidad bentónica entre un sitio como Arauco y los demás sitios analizados, no sólo se explican en términos de especies de la epifauna capaces de escapar de la hipoxia extrema, sino también por diferencias inter-específicas en la tolerancia fisiológica, lo que justifica estudios posteriores.

La intensificación de la surgencia costera que se predijo hace tres décadas como resultado del cambio climático (Bakun, 1990), y que se ha documentado para la mayoría de las regiones de borde oriental (Bakun et al., 2015; Di-Lorenzo, 2015; Kampf & Chapman, 2016), conducirá a un descenso en la temperatura y contenido de oxígeno de las aguas cercanas a la costa (Vaquer-Sunyer & Duarte, 2011), así como a aumentos en la productividad costera (Gutiérrez et al., 2011), lo que puede intensificar aún más la hipoxia local. Aunque se ha avanzado significativamente en la comprensión sobre cómo las tendencias en la temperatura de los océanos y el contenido de oxígeno pueden afectar la viabilidad y la distribución geográfica de las poblaciones marinas (e.g. Deutsch et al., 2015), todavía está pendiente la comprensión de los efectos a nivel comunitario de la hipoxia costera (e.g. Riedel et al., 2014; Gallo et al., 2020). Ejemplos de eventos extremos de hipoxia y sus efectos a menudo letales en muchas especies bentónicas se pueden encontrar en la literatura en las últimas décadas (véase Levin et al., 2009). Sin embargo, aún no se ha investigado en detalle el papel de los efectos subletales asociados con el

estrés de hipoxia a corto plazo, pero de alta frecuencia. Comprender cómo diferentes regímenes locales de variabilidad ambiental modifican la estructura espacial de las comunidades bentónicas puede proporcionar un punto de partida hacia este objetivo.

A nivel poblacional, la variabilidad ambiental en el océano costero afecta directamente el éxito de procesos clave en el ciclo de vida de especies bentónicas, como el transporte larval, asentamiento y reclutamiento, traspasando esta variabilidad a la dinámica poblacional y a la biomasa adulta, particularmente en el caso de especies con ciclos de vida cortos (Defeo, 1996; Pineda & Caswell, 1997; Bjørkvoll et al., 2012). Los complejos mecanismos que conectan la reproducción con el reclutamiento están modulados por la interacción entre el comportamiento larval y el forzamiento ambiental, que determina la supervivencia y dispersión larval, así como el posterior asentamiento (Pineda, 1991; Cushing, 1995). Adicionalmente, factores denso-dependientes que operan a diferentes escalas espaciales (Hixon et al., 2012) limitan el éxito del reclutamiento y la supervivencia de los adultos (Stephens, 1999), cuya densidad puede afectar positiva o negativamente el éxito reproductivo y la disponibilidad de propágulos (Jenkins et al., 2009). Ambos tipos de factores (ambientales y poblacionales) no son excluyentes, sino que interactúan a través de diferentes escalas para determinar las densidades poblacionales en el bentos.

Como una forma de evaluar el efecto de la variabilidad temporal en el reclutamiento sobre la biomasa de poblaciones bentónicas explotadas, se analizó la dinámica poblacional de la macha *Mesodesma donacium* en la AMERB de playa Cucao, Región de Los Lagos (Capítulo 3), utilizando información proveniente de evaluaciones directas realizadas en el contexto de pescas de investigación y estudios de AMERB entre los años 2011 y 2017. *M. donacium* se caracteriza por habitar playas de arena expuestas al oleaje, entre Bahía Sechura, al norte de Perú, y el extremo sur de Chiloé (5°S-43°S), formando agregaciones cuyas densidades dependen de aspectos morfodinámicos tales como la granulometría, pendiente y perfil de la playa (Osorio & Bahamonde 1970; Jaramillo et al., 1994). Sus poblaciones muestran una clara segregación entre adultos y juveniles, con los adultos ubicados preferentemente en el submareal y los recién asentados en la zona intermareal, normalmente asociados a desembocaduras de esteros, donde la salinidad disminuye

(Jaramillo et al., 1994; Ariz et al., 1994; Rubilar et al., 2001). Esta especie constituye un recurso comercial que genera importantes ingresos directos para las comunidades pesqueras artesanales (Castilla & Defeo, 2001), gracias a su alto valor de mercado.

Los resultados de la modelación de la dinámica poblacional de *M. donacium* revelaron una alternancia de períodos con altos y bajos reclutamientos, con un patrón de fallas y éxitos en el reclutamiento que fue bien descrito a través de la cadena Markov y que no es explicado directamente por el modelo stock-recluta. A largo plazo, la probabilidad de fallas estimada alcanza el 37,5%, con una edad máxima cercana a los 7 años y con cohortes que mostraron una progresión modal en la estructura de tamaños entre 2011 y 2017. La presencia de fallas en los reclutamientos de macha ha sido observada en la zona centro-sur (Stotz et al., 2004) y se ha asociado con factores ambientales que afectan la liberación de gametos, la supervivencia y el suministro de larvas (Thiel et al., 2007). Adicionalmente, se ha sugerido que procesos de escala interanual son claves en la regulación de la biomasa de la especie. Por ejemplo, se ha vinculado el colapso de la población de machas en Huasco (28°30'S) y de la desaparición de machas en Coquimbo (29°58'S) con inundaciones costeras debidas al exceso de precipitaciones durante El Niño de 1997-1998 (Aburto & Stotz, 2003; Jerez et al., 2009). En Perú, una alta mortalidad de machas se atribuyó al aumento de temperatura causado por El Niño de 1982-1983 (Arntz et al., 1987) y se ha sugerido que la recuperación de los bancos agotados de machas puede llevar más de 20 años (Arntz et al., 2006), lo que ha sido evidenciado en la zona centro-sur, donde la pesquería no se ha recuperado tras el agotamiento del banco de machas de Quidico (38°15'S) entre los años 2000 y 2005 (Hernández et al., 2006).

Dentro de la zona de estudio, es común escuchar a los pescadores artesanales hablar de la "macha verde", con longitudes de 3-4 cm y que ocasionalmente se encuentra en los bancos explotados, como una buena señal en términos de la abundancia futura del recurso. Esta percepción es coherente con la aparición ocasional de tallas menores en las evaluaciones anuales en la playa de Cucao, donde los individuos juveniles (i.e., longitudes de 2,5-5,0 cm) aparecieron en grandes cantidades en sólo una de las siete evaluaciones directas (2016). La alta variabilidad en la ocurrencia de juveniles observada

durante las evaluaciones directas no es un artefacto de fallas en la evaluación en relación con el reclutamiento, ya que para esta especie es improbable no observar el asentamiento durante las evaluaciones directas. Esto debido a que los individuos post-asentados son fácilmente distinguibles y tienden a acumularse en la zona de lavado y cerca de las desembocaduras de estuarios o pequeños ríos (Jaramillo et al., 1994), lo que representa una ventaja sobre la mayoría de las otras especies bentónicas en las que la presencia de fracciones tempranas es menos evidente.

Aunque la información recopilada hasta la fecha no permite establecer relaciones causales entre los factores ambientales y el éxito de reclutamiento en la macha, es probable que se requiera una combinación específica de condiciones de oleaje y viento, en la época correcta del año, para que las larvas competentes lleguen a la costa y se asienten (Fuchs et al., 2007; Navarrete et al., 2015). El número total de larvas competentes que podrían llegar a la costa, a su vez, es dependiente de las condiciones advectivas y de la presencia de alimento en la zona costera durante las semanas o meses previos al reclutamiento, lo que puede explicar la alta variabilidad observada en el reclutamiento, que también se ha descrito en otras latitudes y para otras especies de macha (Lima et al., 2000; Ripley & Caswell, 2006; Thiel et al., 2007; Aburto et al., 2013).

La estrategia actualmente aplicada en el manejo de la pesquería de machas en AMERB puede ser vista como un proceso “estático” o “carente de memoria”, ya que no considera la información de evaluaciones pasadas en la toma de decisiones. De hecho, las cuotas anuales se calculan a partir del stock presente evaluado directamente en terreno. En la práctica, y como ha sido demostrado, el límite superior recomendado para la tasa captura en AMERB ( $\mu = 30\%$ ), e incluso una tasa de captura más precautoria, como la utilizada en el caso del AMERB Cucao ( $\mu = 25\%$ ) es excesiva. Nuestros resultados indican que es recomendable aplicar una tasa de cosecha máxima de  $\mu = 15\%$ , que puede ser lo suficientemente baja como para mantener el potencial reproductivo de la población de machas dada la incertidumbre en el reclutamiento. Adicionalmente, es aconsejable implementar una regla de control de la cosecha, en la que la tasa de cosecha disminuya cuando el stock desovante disminuya debido a reclutamientos bajos o ausencia de éstos.

Una regla de control de la cosecha del tipo rampa podría ser más eficaz para garantizar una recuperación de la biomasa desovante bajo condiciones de incertidumbre (Kritzer et al., 2019). De hecho, la reducción de la tasa de cosecha a medida que las poblaciones disminuyen se traduce en una mayor resiliencia frente a la variabilidad ambiental (Merino et al., 2019), que claramente está aumentando debido al cambio climático (Roberts et al., 2017).

El procedimiento de manejo estático recién descrito se aplica a casi todas las AMERB en Chile, y está asociado al Plan de Manejo y Explotación de cada especie objetivo (Gallardo et al., 2011). Nuestros análisis (Capítulo 3) indicaron que el reclutamiento de macha no se produce regularmente todos los años, sino que cada 2 a 3 años de bajos reclutamientos hay un episodio de reclutamiento importante. Los registros de desembarque de otras áreas donde las poblaciones de macha se agotaron en décadas anteriores muestran que la explotación pesquera podría ser insostenible cuando no se controla la intensidad de la tasa de cosecha. Este comportamiento es típico en la explotación de *M. donacium* a lo largo de la costa chilena (e.g., Aburto & Stotz, 2013), y ha sido observado en otras especies de machas globalmente (Weinberg, 1999; Laudien et al., 2003; Fiori & Morsán, 2004; Ripley & Caswell, 2006; Herrmann et al., 2011).

El problema subyacente es que, en la práctica, el conocimiento sobre la intensidad y el éxito del reclutamiento en la mayoría de las poblaciones sometidas a explotación es escaso, lo que puede atribuirse a sesgos introducidos por la propia actividad extractiva (e.g., Punt & Cope, 2019). El muestreo de la captura comercial se realiza generalmente en los desembarques, lo que deja fuera las fracciones juveniles. En el caso de las especies bentónicas cosechadas desde AMERB, los estudios poblacionales suelen considerar la fracción que puede ser detectada visualmente por buzos científicos o pescadores locales. Aunque este procedimiento incluye individuos bajo el tamaño comercial, es probable que deje fuera a los individuos recién asentados, que normalmente no son visibles debido a su pequeño tamaño, pigmentación y/o comportamiento. Por lo tanto, la cuantificación de fracciones recién asentadas en

poblaciones de especies comerciales suele estar sujeta a incertidumbre y debe abordarse a través de métodos indirectos.

Para las áreas de manejo en que la biomasa y composición de tallas se han registrado anualmente durante un período lo suficientemente largo, es aconsejable implementar un modelo integrado de evaluación de stock (Punt et al., 2013, 2011; Smith et al., 2009). Posteriormente, deben establecerse puntos de referencia biológicos para evaluar el estado de la población y establecer una cuota basada en proyecciones poblacionales. De lo anterior, se deriva que es necesario revisar el procedimiento de administración de las AMERB, con una mirada conducente a mantener la explotación de especies bentónicas dentro de márgenes biológicamente seguros. Para el manejo de la pesquería de macha, en particular, las fallas en el reclutamiento implican que, si el reclutamiento se produce aproximadamente una vez cada tres años, las tasas de explotación deben ser inferiores a las recomendadas por el procedimiento actual ( $\mu = 25\%$ ), requiriéndose tasas de explotación bajo el 15% para garantizar una explotación sostenible de esta especie.

De esta forma, los resultados obtenidos dan sustento a la hipótesis central de esta Tesis, habiéndose demostrado que tanto la geomorfología costera como la variabilidad en las condiciones ambientales permiten explicar y, hasta cierto punto, predecir la estructura de las comunidades del bentos submareal en AMERB. La exposición de la costa, el tipo de sustrato, la variabilidad de alta frecuencia y valor máximo en la temperatura del agua de fondo, y la duración máxima de los eventos de hipoxia aparecen como los predictores más relevantes. Por otra parte, el análisis de la dinámica poblacional de *Mesodesma donacium* permite sugerir que la variabilidad interanual en el reclutamiento está asociada a la variabilidad en las condiciones ambientales, que genera un proceso de fallas y éxitos, con una probabilidad de falla cercana al 37%. Esta variabilidad tiene efectos significativos sobre la estructura poblacional adulta, y fuertes implicancias en relación a las tasas de captura precautorias aplicables en el contexto del manejo de la especie.

Las AMERB fueron las unidades de estudio en que se basó esta Tesis. Esta herramienta de administración ha mostrado hasta ahora beneficios para las comunidades costeras,

pero resulta evidente que el análisis de su desempeño requiere de una mirada a una escala que va más allá de los límites individuales de cada una de estas unidades. En este sentido, los resultados presentados señalan la importancia de entender los procesos que explican la estructura y dinámica de las comunidades bentónicas de AMERB desde una escala espacial adecuada y no sólo desde una perspectiva atomizada, como es el caso en la actualidad. Una perspectiva más amplia, que considere la dinámica de procesos oceanográficos relevantes, tales como la surgencia costera y los regímenes de hipoxia asociados, posibilita entender el rol de los procesos ambientales como reguladores del tipo de comunidad presente en cada sector. Al mismo tiempo, permite identificar las especies que se verían más favorecidas por acciones orientadas a incrementar o restaurar la productividad natural de estos sitios. En un escenario de cambio climático, entender qué tipo de comunidad bentónica o de especies pueden ser más tolerantes a la variabilidad ambiental observada y pronosticada resulta relevante, especialmente si se considera el rol social de las AMERB para las comunidades costeras. El análisis de la dinámica poblacional de machas reveló la existencia de fallas en los reclutamientos anuales, que afectan la dinámica poblacional y plantean la necesidad de revisar los criterios de explotación que actualmente son considerados como sustentables por la autoridad administrativa. Es importante destacar que actualmente se desconoce si estas fallas en el reclutamiento están ocurriendo en otras especies relevantes para las AMERB, como el loco, siendo aconsejable implementar modelos integrados de evaluación de stock, que permitan analizar la data disponible desde una perspectiva temporal y espacial adecuada.

## 7 CONCLUSIONES

La estructura funcional de las comunidades bentónicas submareales en AMERB de Chile central, y específicamente de la Región del Biobío, responde a la variabilidad en atributos físicos tales como la exposición de la costa, la temperatura superficial del mar y concentración de clorofila-a.

Para las comunidades de fondos duros, la presencia de filtradores, herbívoros, depredadores y carroñeros se correlacionaron significativamente con la presencia de algas foliosas y corticadas, las que a su vez se correlacionaron significativamente con el grado de exposición de la costa. En las comunidades de fondos blandos, la presencia de filtradores de la infauna y los detritívoros de la epifauna se correlacionó positivamente con una menor variabilidad temporal en la temperatura y mayores concentraciones medias de clorofila-a.

Desde la perspectiva de la administración pesquera, estos resultados indican que en ambientes de fondos blandos con mayor productividad y más estabilidad térmica sería factible que las AMERB implementen sistemas de producción o acciones de manejo para filtradores de la epifauna e infauna (e.g., mejillones y almejas). En AMERB de fondos duros expuestas a una mayor variabilidad ambiental serían más adecuados sistemas productivos de macroalgas, filtradores epifaunales, herbívoros y carnívoros.

Al utilizar registros continuos de temperatura y oxígeno disuelto en las aguas del fondo para explicar la estructura de comunidades de 6 AMERB ubicadas en zonas con condiciones contrastantes, los índices: variabilidad de alta frecuencia en la temperatura, percentil 95 de la temperatura y duración de los eventos de hipoxia, explicaron individualmente un porcentaje de variabilidad similar al tipo de sustrato (aproximadamente 30%) sobre la estructura de la comunidad bentónica. Cuando se combinan estas variables en un solo análisis, los cuatro factores explican el 84% de la varianza total de la estructura comunitaria.



Las especies de fondo blando como *Ensis macha*, *Chorus giganteus* y *Cancer setosus*, podrían ser fisiológicamente más tolerantes a condiciones más rigurosas en términos de temperaturas más altas y eventos de hipoxia más prolongados. Especies de fondo duro como los gastrópodos *Concholepas concholepas* y *Fissurella* sp. y el cirripedio *Austromegabalanus psittacus*, estarían mejor adaptados a ambientes donde la temperatura es más baja en promedio, pero más variable, y donde las condiciones hipóxicas son intensas pero más intermitentes.

Estos hallazgos destacan el papel estructurador de la variabilidad y la ocurrencia de condiciones extremas de temperatura y oxígeno disuelto, en lugar de los niveles promedio. Estas dos propiedades están estrechamente entrelazadas en esta y otras regiones de surgencia costera, y son susceptibles de sufrir cambios importantes en escenarios climáticos futuros.

A nivel poblacional, el análisis de la variabilidad en el reclutamiento de macha (*Mesodesma donacium*) sobre las tasas de captura propuestas para el AMERB Cucao, demostró que, bajo las condiciones de reclutamientos altamente variables observadas a lo largo de 7 años de evaluaciones directas, la tasa de explotación que se aplica actualmente a la macha ( $\mu=25\%$ ) implica un 80% de probabilidad de colapso futuro. Una tasa de captura del 15% del stock permitiría garantizar la sostenibilidad de la actividad extractiva frente a eventuales fallas en el reclutamiento.

El análisis de la variabilidad en el reclutamiento de macha, destaca la necesidad de revisar los supuestos y criterios sobre los cuales se basa el manejo actual de especies comerciales en AMERB, uno de los cuales es la regularidad o consistencia interanual del reclutamiento. Para las áreas de manejo en las que la biomasa y la composición de la longitud se han registrado anualmente durante un período lo suficientemente largo, es aconsejable implementar modelos integrados de evaluación de stock y establecer puntos de referencia biológicos que permitan evaluar el estado de la población y establecer una cuota de captura basada en proyecciones obtenidas bajo incertidumbre, especialmente

considerando las actuales tendencias climáticas y los cambios que han generado en la dinámica física y biológica del océano costero.

Los resultados obtenidos dan sustento a la hipótesis central de esta Tesis, habiéndose demostrado que la variabilidad en las condiciones oceanográficas y la geomorfología costera determinan la estructura de las comunidades del bentos submareal en AMERB de manera predecible. En el caso de *Mesodesma donacium*, esta variabilidad ambiental influye sobre el éxito del reclutamiento, traspasando esta variabilidad a la estructura poblacional, lo que influye sobre la vulnerabilidad de la especie a la sobreexplotación.



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