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**EFFECTO DE LA PESQUERÍA ARTESANAL EN LAS REDES TRÓFICAS DEL
SUBMAREAL E INTERMAREAL DE CHILE CENTRAL**

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RESUMEN

La sobreexplotación de especies por parte de la pesca es la principal causa de pérdida de biodiversidad marina y del colapso de los stocks pesqueros a nivel global. Ante esta situación amenazante, es necesario realizar manejos más integrales. Sumado a lo anterior, el manejo pesquero tradicionalmente se basa en modelos de una sola especie, los cuales no consideran que las especies que son cosechadas por la pesca son parte de redes complejas de interacción. En consecuencia, incluso cuando una sola especie está "bien administrada", existe una gran incertidumbre sobre los impactos que dicha explotación tiene en el resto del ecosistema. A lo largo de cuatro capítulos, en esta tesis se utilizó análisis de redes y un modelo bioenergético de múltiples especies para evaluar la naturaleza y magnitud de los impactos que la pesca puede tener sobre los patrones de estructura de dos redes tróficas que son fuertemente explotadas por la pesca artesanal, la red del intermareal rocoso y submareal somero de Chile central.

En el primer capítulo se desarrolló el código de análisis *NetworkExtinction* en R para evaluar, a través de enfoques 'estáticos' (basado en presencia-ausencia de nodos e interacciones, sin dinámica poblacional) la estructura y robustez de redes tróficas frente a la pérdida de especies. Se desarrollaron tres funciones para simular la extinción de especies en función de: a) un ordenado, definido por el investigador, b) desde la más a la menos conectada, y c) una secuencia aleatoria. Además, se desarrollaron otras dos funciones. Una para comparar los índices que resumen la topología de las redes entre las secuencias de extinción aleatorias y no aleatorias. La otra, para visualizar el cambio de las métricas a lo largo de la secuencia de extinción de interés. El paquete *NetworkExtinction* fue aplicado en el segundo capítulo de la tesis.

En el segundo capítulo, se evaluó la importancia relativa de la pesca artesanal sobre la estructura de la red trófica intermareal. Usando la topología de esta red, una de las mejores resueltas en el mundo, se usó un enfoque estático para evaluar el impacto de extinguir a todas las especies cosechadas por pesquería en comparación con el impacto de extinguir especies en forma aleatoria de la red a través de un enfoque estático. Además, se evaluó la importancia relativa de la pesca artesanal sobre la persistencia de la red trófica intermareal, comparando el impacto de extinguir a todas las especies cosechadas por pesquería con el impacto de extinguir a especies que tienen un alto índice de centralidad y en forma aleatoria de la red. Para esto se utilizó el enfoque estático, pero además se desarrolló un enfoque dinámico con intensidades de interacción variables y nodos dinámicos (dinámica poblacional). Para el enfoque dinámico se utilizó el modelo bioenergético alométrico de redes tróficas (ATN, por sus siglas en inglés), el cual se parametrizó con datos empíricos de tamaños corporales de las especies que conforman la red del intermareal y aplicamos reglas de escalamiento alométrico en el uso de energía para definir intensidades de interacción. Esta aproximación cuantitativa y dinámica permite incorporar el impacto de las pesquerías sobre la biomasa de las especies explotadas y no solamente como un agente de extinción de esas especies, y a su vez examinar los impactos sobre la abundancia de las especies en el resto de la red. Este capítulo también tuvo como objetivo comprender la importancia de la pesca como una forzante que genera cascadas tróficas “top-down”, en comparación con forzantes “bottom-up”, como cambios en productividad primaria. Usando el modelo ATN, evaluamos el efecto independiente y combinado de la pesca artesanal y el de cambios positivos y negativos en la productividad del plancton. Los resultados utilizando el enfoque estático señalan que el impacto del escenario de extinción de todas las especies de importancia comercial es mayor en la estructura de la red que el de la extinción de especies en

forma aleatoria. Sin embargo, los resultados utilizando el enfoque estático y dinámico señalan que la estructura de interacciones de la red del intermareal es altamente robusta al escenario de extinción de todas las especies de importancia comercial pero altamente sensible al escenario de extinguir especies con una alta centralidad, ya que se produjeron cero y muchas extinciones secundarias, respectivamente. El análisis además mostró que la pesca como una forzante “top-down” genera efectos positivos sobre la biomasa de todas las especies que no son cosechadas por la pesca; mientras que la perturbación de la productividad del plancton como una forzante “bottom-up” generó efectos tanto positivos como negativos. Estas dos fuerzas interactuaron entre ellas, ya que la pesquería compensa el impacto negativo de la perturbación de la productividad del plancton en las especies no cosechadas, mientras que la perturbación de la productividad del plancton intensificó el efecto negativo de la pesca en las especies cosechadas. Por lo tanto, los ecosistemas costeros son vulnerables a las pesquerías, y su impacto sobre las especies podría verse magnificado debido a cambios en la productividad de los océanos.

En el tercer capítulo, se usó el modelo ATN para simular la presión de la pesca sobre todas las especies que actualmente son capturadas por las pesquerías artesanales de la red del intermareal rocoso y submareal somero de Chile central, bajo diez escenarios de explotación diferentes. Después de cada escenario de explotación, evaluamos el efecto de la pesca sobre el cambio de biomasa a largo plazo de cada una de las especies que componen las redes, con respecto a un nivel basal sin pesca. En ambas redes y en todos los escenarios de explotación, la pesca indirectamente produjo efectos positivos en la biomasa de casi todas las especies no cosechadas. En la red del intermareal, los herbívoros fueron los que más aumentaron en biomasa como respuesta a la pesca; mientras que en la red del submareal fueron los filtradores, carnívoros y depredadores tope. Entre las especies de importancia comercial, en ambas redes, las macroalgas

(incluidos los kelps) fueron las más sensibles a la pesca. Finalmente se encontró que las especies cosechadas del submareal (donde se concentra la mayor parte de la pesca artesanal) fue en promedio 1.8 veces más sensible a la pesca que las del intermareal. Por lo tanto, este capítulo entrega resultados generales que pueden ser relevantes para futuros planes de manejo y resalta la necesidad de planes de manejo para las macroalgas que son altamente explotadas, tal como los kelps.

Las redes tróficas que fueron estudiadas en esta tesis representan a ecosistemas bentónicos, en los cuales el espacio es uno de los recursos más limitantes y la competencia por este recurso es una de las interacciones no tróficas que más contribuye a la dinámica de estas redes. Como la aproximación de redes tróficas solamente incluye interacción de competencia producido por consumo compartido de especies presa, la interferencia por uso de espacio no está capturada en estas aproximaciones. Por este motivo, en el cuarto capítulo se evaluó el cambio en dinámica de las redes al incorporar competencia por el espacio entre especies sésiles y se estudiaron los efectos de la pesca artesanal en la red del intermareal en comparación a los resultados anteriores. A través del modelo ATN se simuló la dinámica de la red del intermareal con y sin competencia por el espacio entre las especies sésiles, que incluyen tanto a macroalgas como filtradores sésiles (cirripedios y mitílidos). En todos los casos, se simuló la presión de la pesca sobre todas las especies que actualmente son capturadas por las pesquerías artesanales, bajo diez escenarios de explotación diferentes. La inclusión de competencia por espacio tuvo efectos cuali- y cuantitativos sobre la dinámica de la red explotada. En comparación a los escenarios sin competencia por el espacio, con la competencia por el espacio se encontraron resultados opuestos en los efectos que la pesca artesanal tiene sobre las especies no cosechadas que pertenecen a los niveles tróficos superiores. En el resto de las especies no cosechadas, la

competencia por el espacio intensificó los efectos positivos de la pesca con respecto a escenarios sin competencia por el espacio. Entre las especies de importancia comercial, las macroalgas continuaron siendo las especies más sensibles a la pesca. Sin embargo, al considerar la competencia por el espacio, la sensibilidad a la pesca de los carnívoros disminuyó; mientras que la de los omnívoros y herbívoros aumentó. Por lo tanto, nuestros resultados sugieren que la competencia por el espacio, cuando ocurre y es importante en los niveles basales de una red, resulta muy importante para comprender los impactos de las pesquerías en los ecosistemas bentónicos.

A través de los enfoques de múltiples especies esta tesis contribuye a iluminar patrones y tendencias generales sobre cómo se propagan los efectos de la pesca en los ecosistemas bentónicos costeros de Chile central, las cuales son fuertemente explotados por las pesquerías artesanales. Estos patrones generales pueden ser de gran utilidad para complementar la información que actualmente deriva de modelos de una sola especie y los modelos construidos representan una plataforma base interesante para avanzar hacia estrategias de manejo multi-específicos.

ABSTRACT

Overexploitation of species by fisheries is the main cause of the global biodiversity loss and the collapse of fish stocks. Faced with this threatening situation, it is necessary to carry out more comprehensive management. Additionally, fisheries management is traditionally based on single-species models, which do not consider that harvested species are part of complex interaction networks. Consequently, even when a single species is “well-managed”, there is large uncertainty about the impacts that such exploitation has on the rest of the ecosystem. Throughout four chapters, in this thesis I used network analysis and a multi-species bioenergetic model to evaluate the nature and magnitude of the impacts that fishing can have on the patterns of the structure of two food-webs that are strongly exploited by artisanal fishing, the rocky intertidal and shallow subtidal food-web of central Chile.

In the first chapter, we developed the code *NetworkExtinction* in R to evaluate through a static approach (based on presence-absence of nodes and interactions, without considering population dynamics) the structure and robustness of food-webs to species loss. We developed three functions to simulate the sequential extinction of species based on: a) a given order, defined by the researcher, b) from most to least connected, and c) a random sequence. Moreover, we developed other two functions. One to compare topological indices summarizing the food-web topology between random and non-random extinction sequences. The other, to visualize the change of the metrics throughout the extinction sequence of interest. The *NetworkExtinction* package was applied in the second chapter of the thesis.

In the second chapter of the thesis, we evaluate the relative importance of artisanal fishing for the structure of the intertidal food-web. Using the topology of this network, one of the best

resolved in the world, we use a static approach to assess the impact of extinction of all harvested species from the food-web compared to random species removals in the food-web. We also evaluated the relative importance of artisanal fishing for the persistence of the intertidal food-web, we assessed the impact of extinction of all harvested species from the food-web compared to the extinction of species with a high centrality index and to random species removals. For this we use the static approach, but we also develop a dynamic approach with variable interaction strengths and dynamic nodes (population dynamics). For the approach we used the allometric trophic network allometric (ATN) bioenergetic model, which we parameterize with empirical data of body sizes of the species in the intertidal food-web and we apply allometric scaling rules in the use of energy to define interaction strength. This quantitative and dynamic approach allows us to incorporate the impact of the fisheries on the biomass of the harvested species and not only as an extinction agent of those species, and in turn, allow us to examine impacts on the abundance of the species in the rest of the food-web. This chapter also aimed to understand the importance of fishing as a forcing that generates “top-down” trophic cascades, and to compare with “bottom-up” forcing, as changes in primary productivity. Using the ATN model, we evaluated the independent and combined effect of fisheries and changes in plankton productivity. Our results using the static approach indicate that the impact of the extinction scenario of all harvested species is greater on the food-web structure than the random extinction of species. However, our results using the static and dynamic approach indicate that interaction structure of the intertidal food-web is robust to the extinction scenario of all harvested species but sensitive to the scenario of extinction of species with high centrality, since that zero and many secondary extinctions occurred, respectively.

The dynamic analysis also showed that fishing as a "top-down" forcing generates positive effects on the biomass of all non-harvested species; while changes of plankton productivity as a "bottom-up" forcing generates both positive and negative effects on the species biomass. These two forces interact with fisheries dampening the negative impact of plankton productivity perturbation on non-harvested species, and plankton productivity perturbation intensifying the negative effect of fishing on harvested species. Therefore, coastal ecosystems are vulnerable to fisheries, and their impact on species could be magnified due to changes in the productivity of the oceans.

In the third chapter, we use the ATN model to simulate the fishing pressure on all currently harvested species by the artisanal fisheries in the intertidal rocky-shore and subtidal food-web, under ten different exploitation scenarios. After each exploitation scenario, we evaluated the effect of fishing over the long-term biomass change of each species in the food-web, with respect to a no-fisheries basal level. Under all exploitation scenarios, and in both food-webs, fishing indirectly produced positive effects on the biomass of most non-harvested species. In the intertidal food-web, herbivores increased the most in biomass after fishing; while in the subtidal food-web, were the filter feeders, carnivores and top predators. Among harvested species, macroalgae (including kelps) were the most sensitive to harvesting pressure in both food-webs. Finally, we found that the harvested species of the subtidal food-web - where most of the artisanal fisheries concentrates- were on average 1.8 times more sensitive to exploitation pressure than intertidal harvested species. Therefore, we highlight the need for management plans for highly exploited macroalgae, such as kelps.

The food-web studied in this thesis represent benthic ecosystems, in which space is one of the most limiting resources and competition for this resource is one of the non-trophic interactions that most contributes to the dynamics of these food-webs. As the food-web approach only includes competition interaction produced by the consumption of shared prey, the interference by space use is not captured in these approaches. For this reason, in the fourth chapter we evaluate the change in the food-web dynamic by incorporating competition for space among sessile species and studied the effects of artisanal fishing on the intertidal food-web compared to previous results. Through the ATN model, we simulate the food-web dynamics with and without competition for the space between sessile species, which include both macroalgae and sessile filter-feeders (barnacles and mussels). In all cases, we simulate the fishing pressure on all the species that are currently caught by artisanal fisheries, under ten different exploitation scenarios. The inclusion of competition for space had qualitative and quantitative effects on the dynamics of exploited food-web. Compared to the scenarios without competition for space, with competition for space we find opposite results in the effects that artisanal fishing has on non-harvested species that belong to the higher trophic levels. In the rest of the non-harvested species, competition for space only intensified the positive effects of fishing that were found without competition for space. Among the harvested species, macroalgae continued to be the most sensitive species to fishing. However, when considering competition for space, the sensitivity of carnivores to fishing decreased; while that of omnivores and herbivores increased. Therefore, our results suggest that competition for space, when it occurs and is important at the basal levels of a food-web, is very important for understanding the impacts of fisheries on benthic ecosystems.

Through multi-species approaches, this thesis contributes to illuminate general patterns and trends on how the effects of fishing are propagated in the coastal benthic ecosystems of central Chile, which are heavily exploited by artisanal fisheries. These general patterns can be very useful to complement the information that is currently derived from single-species models and the constructed models represent an interesting base platform for moving towards multi-specific management strategies.

INTRODUCCIÓN GENERAL

Los ecosistemas marinos son extremadamente importantes para el bienestar, trabajo, economía y seguridad alimentaria de la población humana (FAO, 2018). Lamentablemente, como sociedad hemos sido incapaces de manejar los recursos marinos de una forma eficiente, y hoy en día, es una importante preocupación. La sobreexplotación de especies es un problema global (Costello et al., 2016; Defeo and Castilla, 2005; Pauly, 1998; Pauly and Zeller, 2016; Worm, 2016), y es la principal causa de la pérdida de la biodiversidad de peces y del colapso de los stocks pesqueros (WWF, 2018). En el 2010, alrededor del 50% de los stocks pesqueros se encontraban colapsados (Worm et al., 2006), hasta la fecha estos han seguido declinando (FAO, 2018), y se espera que estas cifras aumenten a más del 90% en el 2050 (Costello et al., 2016). En consecuencia, los ecosistemas marinos se han transformado en sistemas menos productivos, menos predecibles y en donde la recuperación de la pesquería es más difícil (Kuparinen et al., 2016; Travis et al., 2014). En este contexto, es urgente desarrollar una mejor comprensión del funcionamiento de los ecosistemas marinos y del manejo de los recursos naturales.

Tradicionalmente, el manejo de las pesquerías se enfoca en modelos poblacionales de una sola especie e ignoran que las especies que son objetivo de pesca son componentes de diversas y complejas comunidades ecológicas (Collie et al., 2016; Dunn et al., 2017; Garcia, 2003; Pikitch, 2004; Skern-Mauritzen et al., 2016). Además, los modelos de una sola especie no consideran que las pesquerías cosechan múltiples especies en forma simultánea, las que a su vez pueden ser recursos y / o depredadores de otras especies que pueden o no ser objetivo de pesca (Ávila-Thieme et al., unpublsh; Christensen & Walters, 2004; Fulton et al., 2001; Gómez-Canchong et al., 2013; Kuparinen et al., 2016; Neira et al., 2004; Ortiz et al., 2015; Pérez-Matus et al., 2017; Yodzis, 2001). Entonces, la cosecha de una sola especie puede afectar a otras

especies interactuantes y alterar sus abundancias y las características de las comunidades ecológicas (Pauly, 1998). Por lo tanto, el uso de enfoques más holísticos, como lo son los de múltiples especies, son necesarios para entender los impactos que la explotación pesquera produce en los ecosistemas y para mejorar las actuales estrategias de manejo (Collie et al., 2016; Christensen & Walters, 2004, Garcia, 2003; Plagányi, 2007).

Una forma de abordar el estudio y / o entendimiento del efecto de la pesca desde un punto de vista de múltiples especies es a través del estudio de redes tróficas (Boit et al., 2012; Gomez et al., 2017; Kuparinen et al., 2016; Ortiz et al., 2015; A Pérez-Matus et al., 2017), marco conceptual que ha contribuido en la comprensión de la estructura y la dinámica de los ecosistemas naturales, y ha proporcionado conceptos y potentes métodos para analizar comunidades biológicas complejas (Glaum et al., 2019; Pascual and Dunne, 2006). A diferencia de otros enfoques que comúnmente se usan, tal como Ecopath con Ecosim (EwE) (Colléter et al. 2015) el cual ha sido altamente criticado por su naturaleza de caja negra y por el alto número de parámetros que tienen que ser parametrizados a partir de datos empíricos (Plagányi and Butterworth, 2004), el estudio de redes tróficas permite desarrollar una teoría más fundamental y ampliamente aplicable porque los modelos de redes pueden ejecutarse en una variedad de configuraciones ecológicas, tanto empíricas como generadas de manera realista, al parametrizar el metabolismo y las interacciones de las especies a través de reglas alométricas (Glaum et al., 2019). A pesar de estos avances y de que existe un reconocimiento en la importancia de usar enfoques de múltiples especies en pesquerías (García, 2003; Plagányi, 2007), aún existe un desacople entre cómo los sistemas naturales funcionan y cómo los estudiamos. Si se compara el número de trabajos publicados en los que se evalúa el efecto de las pesquerías a nivel de poblaciones versus a nivel de múltiples especies, se aprecia que aún existe un déficit en el

conocimiento de cuáles son y cómo se propagan los efectos de las pesquerías a través de las comunidades (Skern-Mauritzen et al., 2016) (Fig. 1 para ver el contraste de número de trabajos publicados). Por lo tanto, entender las consecuencias de las pesquerías en los recursos y la biodiversidad, desde un punto de vista de múltiples especies es aún un desafío en ecología (Glaum et al., 2019; Sutherland et al., 2013; Travis et al., 2014).

En esta tesis se usaron enfoques de multi-especies provenientes de teoría de redes y de tramas tróficas para comprender los impactos de la pesca en ecosistemas marinos. Los modelos de estudio de esta tesis fueron las redes tróficas del intermareal rocoso (Kéfi et al., 2015) y submareal somero (Pérez-Matus et al., 2017) de Chile central. Ambas redes representan las interacciones tróficas de más de 100 especies que ocurren en la zona central de Chile, alrededor de 600 millas de costa. Ambos sistemas son explotados intensivamente por la pesca artesanal que es de naturaleza multi-específica. En ambas redes ya se ha descrito la topología (Kéfi et al., 2015; Pérez-Matus et al., 2017) y en el caso de la red Intermareal, su variación espacial (Lurgi et al., 2020) así como también algunos aspectos dinámicos que incluyen otros tipos de interacción (Kéfi et al., 2016). Solamente en la red del submareal se ha incorporado la pesca artesanal como un nodo dentro de la red y se ha evaluado su importancia solamente en término del número de interacciones (Pérez-Matus et al. 2017). En ninguna de estas redes se ha evaluado de qué manera se propaga el efecto de la pesca a través de ellas y cuán sensibles son a estas perturbaciones, tanto las especies explotadas como las no explotadas en la pesquería. En este contexto, en esta tesis, en primer lugar se desarrolló un paquete en R para realizar simulaciones de extinción de especies en redes de interacción (capítulo I) y así, entender cuán robustas son estas redes ante el potencial colapso (extinción) de las especies de importancia comercial (capítulo II). Además, se desarrolló un modelo dinámico con intensidades de interacción

variables y nodos dinámicos (dinámica poblacional) de enfoques dinámicos para evaluar la importancia relativa de la pesquería como una forzante descendente o “top-down” en comparación a la perturbación de la productividad de plancton como una forzante ascendente o “bottom-up” en la red del intermareal y sus impactos sobre la abundancia de las especies en el resto de la red (capítulo II). En el tercer capítulo, se analizó cómo los impactos que genera la actividad pesquera se propagan y alteran la dinámica y abundancia de las especies que componen ambas redes. Además, se reconocieron a las especies más sensibles a la pesca. Las dos redes tróficas analizadas en esta tesis representan a ecosistemas bentónicos, en los que el espacio es un recurso limitante que promueve la competencia entre especies sésiles (Connell, 1961). Esta competencia, es una de las interacciones no tróficas que más influye en la estructura (Castilla, 1999) y estabilidad de las redes tróficas (Miele et al., 2019). Por lo tanto, en el cuarto capítulo, nos preguntamos cuál es el rol de la competencia por el espacio para entender los efectos de la pesca artesanal en la red del intermareal.

CAPÍTULO 1.

NETWORKEXTINCTION: AN R PACKAGE TO EXPLORE THE PROPAGATION OF EXTINCTIONS THROUGH COMPLEX ECOLOGICAL NETWORKS

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Abstract

1. Biodiversity loss is one of the major drivers of global changes in the Anthropocene, which is profoundly impacting ecosystem resilience. To study this connection, different measures and tools (e.g., simulations of extinction events) have been created to analyze the structure of ecological systems and their stability under biodiversity loss, especially in complex settings conformed by multiple interacting species, such as food webs. However, there remains the need for tools that facilitate the assessment of food web resilience to species loss and the impacts on food webs structure under different scenarios. Here, we develop an R package to explore the propagation of species extinctions through food webs, measured as secondary extinctions, according to user-defined node removal sequences.

2. In the *NetworkExtinction* package, we seek the integration between network theory and computational simulations by developing six functions to analyze and visualize the structure

and robustness of networks. Three functions to simulate the sequential extinction of species, one function to compare food web metrics between random and non-random extinction sequences, one function to visualize the change in a given network metric along with the steps of sequential species extinction. The sixth function allows the user to fit and visualize the degree distribution of the network, fitting linear and non-linear regressions. We illustrate the package use and outputs by analysing a Chilean coastal marine food web.

3. By using the *NetworkExtinction* package, the user can estimate the food web robustness after performing species' extinction routines based on several algorithms. Moreover, the user can compare the number of simulated secondary extinctions against a null model of random extinctions. The visualizations allow to graph any topological index that the deletion sequences functions calculate as a function of each removal step. Finally, the user can fit the degree distribution of the food web.

4. The *NetworkExtinction* R package is a compact and easy-to-use package to visualize and assess the food web structure (degree distribution) and robustness to different sequences of species loss. Therefore, this package is particularly useful to evaluate the ecosystem response to anthropogenic and environmental perturbations that produce non-random species extinctions. In that way, it also allows to assess the contribution of central nodes to food webs stability.

Keywords: network science, food webs, extinction analysis, R package

Introduction

Biological systems can be represented as complex networks of interactions through which information, matter, and energy flow in a structured way (Benedek et al., 2007; Pascual and Dunne, 2006; Proulx et al., 2005). A myriad of perturbations, however, can substantially alter these fluxes at different temporal and spatial scales (Donohue et al., 2016; Radchuk et al., 2019; Venter et al., 2016), modifying either the network components, by adding or removing species from the network, or the interactions among them, re-wiring pathways of connection and changing interaction strengths. Hence, the relationship between topology and the propagation of such disturbances through the main system offers useful avenues in the understanding of entangled biological phenomena (Gao et al., 2016).

Ecological networks, species represent nodes and their interactions vertices or links between nodes, are currently subject to particularly strong perturbations produced by climate change and/or human activities which in many cases lead to local or global extinction of species, or to drastic reduction in their abundance (e.g. total biomass) (Barnosky et al., 2011; Costello et al., 2016; May et al., 1995; Pimm et al., 2019; Scheffer et al., 2001; Vitousek et al., 1997). As a consequence of this, beyond the directly affected species, the extinction of other species in the network can take place with significant impacts, or not, on the stability and resilience of the main system (Dunne et al., 2002b). Whether cascading effects are observed or not following removal or addition of a node depends, to some extent, on the complex structural attributes that define the network. Since, the extinction of species and/or the modification of their interactions may directly induce degradation of ecosystem services, thus impacting human well-being, anticipating the potential propagation of these effects is of great practical importance (Barnosky et al., 2011; Dirzo and Raven, 2003). Therefore, the understanding of ecosystem stability and

resilience to different perturbations has received considerable attention (Allesina and Pascual, 2009; Curtsdotter et al., 2011; Dunne et al., 2002a; Hastings et al., 2016; Jordán, 2009; Pimm et al., 2019; Ramos-Jiliberto et al., 2012; Valdovinos et al., 2009).

On topological properties shaping the stability of complex networks.

The complexity of biological networks imposes some challenges to develop an integrated framework and tools to study these systems. Some general attributes that characterize most empirically constructed ecological networks do exist, however. For instance, the number of connections that each node in the network has, i.e., the degree distribution, usually follows a fat tail degree distribution (Bascompte, 2009; Dunne et al., 2008). Theoretical models show that the degree distribution of the network is strongly associated with its robustness to species loss (Sole and Montoya, 2001) and, therefore, linking degree distribution to resilience and robustness of different types of ecological networks seems to be a promissory research venue (de Santana et al., 2013). For instance, power-law degree distributions, where superconnected nodes are more common, are more vulnerable to the removal of the most connected nodes (de Santana et al., 2013; Dunne et al., 2002; Estrada, 2007; Sole and Montoya, 2001). More generally, a directed attack to the nodes with higher degree, can have larger whole-sale consequences in the network (Albert and Barabási, 2002; Albert et al., 2000). Similarly, the role of diversity and connectance has been emphasized as providing robustness to food webs, to the extent that increasing number of species and connectance among them seem to delay the onset of a cascade of secondary extinctions Dunne et al. (2002b).

Assessing what is the model that best describes an empirical degree distribution has been an active research area and is a common task in the analysis of ecological networks.

Different statistical approaches have been proposed to fit the degree distribution, such as maximum likelihood (Clauset et al., 2009), ordinary least squares (OLS), or linear and non-linear regression (Xiao et al., 2011). As in other fields, the use of linear and non-linear regressions has been controversial (Xiao et al., 2011). Some have suggested that the linearization using logarithmic scale is flawed and that instead, the analysis should be conducted on the original scale of measurement using non-linear regression methods (Xiao et al., 2011). In part this is because when using linear regressions (LR) on log-transformed data the error distribution may not conform to model assumptions needed to statistically compare across different models. The second group of approaches considers the use of non-linear regression using general least squares, in combination with Akaike's information criteria to select the best model that fits the degree distribution.

Other topological measures are relevant to the persistence of ecological networks. For example, several studies have evaluated the importance of species traits (Binzer et al., 2011; Curtsdotter et al., 2011), species centrality (Albert and Barabási, 2002; Allesina and Pascual, 2009; Dunne et al., 2002; Jordán, 2009) or species vulnerability to environmental conditions (Berg et al., 2015). In particular, *in silico* experiments suggest that species' degree and species centrality are key to food webs persistence. The assessment of the importance of species on food web persistence is typically carried out by performing a sequence of node (species) removals followed by the evaluation on food web robustness measured as the number of secondary extinctions. Several indices have been proposed to define the importance of species in this context, and a variety of open source R packages have been created to visualize and analyze the topology and the energy flows occurring within of networks (Table S1).

But despite the recent diversification of analytical tools, we still lack with a way to efficiently assess food web robustness to a 'user-defined' sequence of species loss implemented in an open source platform, such as R. Simulating food web responses to an extinction sequence involve a number of computationally demanding steps following the removal of the target nodes, which can be challenging and time consuming for researchers without experience in programming. Some node metrics (e.g. node degree) are dynamically changing through the process and they must be calculated after each removal step. Assigning the next species to the extinction sequence depends on the calculations made after the previous one was removed. Similarly, to calculate other metrics, such as node richness or network connectance, it is necessary to remove all secondarily-extinct and totally isolated nodes (which are assumed extinct by definition). Our goal here is to develop an open-source free-access package aiming to facilitate the exploration of network resilience and changes in attributes following the removal or extinction of nodes in complex food webs. Here, we present the R package *NetworkExtinction*, which carries out the statistical analysis and visualization of the degree distribution of a network and summarizes their topological changes to the simulated extinction of focal species.

Description and use of the package

1. The *NetworkExtinction* R package

The *NetworkExtinction* package analyzes food webs represented solely by unweighted nodes (e.g. all the same biomass) and their connections through a similar type of interaction, which in the case of food webs is consumption of biomass). Species biomass and variation in interaction strengths between nodes are not considered. Thus, the input adjacency matrix

describing the networks contains 1s (connected through consumption) and 0s (no connected through consumption) as element.

1.1 Network representation in R and empirical example

NetworkExtinction package interacts with other R-packages, especially with the network package (Butts et al., 2008). From network, *NetworkExtinction* inherits the network class of the starting object, which allows the use of some functions to perform network analysis.

To represent and analyze the networks with the *NetworkExtinction* package, is necessary to start with a network object (Butts et al., 2008).

To show how the *NetworkExtinction* package works and its outputs, we will use an empirical marine intertidal rocky shore food web (hereafter, "chilean_intertidal") which has 107 species, 1381 trophic interactions, connectance of 0.12 and a mean trophic level of 1.64 (Kéfi et al., 2015).

1.2 The package, functions, and outputs

Let us begin by installing and loading the *NetworkExtinction* package into the R environment:

```
R> install.packages(NetworkExtinction)
```

```
R> library("NetworkExtinction")
```

We developed three functions to measure the food web topology and robustness after performing specific species' deletion sequences. These sequences are based on species' degree (*Mostconnected*), a user-defined order (*ExtinctionOrder*) and a random sequence

(*RandomExtinctions*). A fourth function, *Comparison*, compares the number of secondary extinctions produced by any of the first two options against the random deletion sequence. A fifth function, *ExtinctionPlot*, allows to visualize the changes in any of the network statistics that the deletion sequence generates after calculate at each removal step. Finally, a sixth function fits the degree distribution of the food web using two approaches, the linear (on log-transformed data) and the non-linear regression (*degree_distribution*).

1.2.1 Extinction functions

-The *Mostconnected* function.

This function begins by sorting the species from the most to the least connected node, considering their total degree (in-degrees plus out-degrees), and storing the information in a vector. Then, the function calculates the species richness, number of links and network connectance, as topological indices. Then, it removes the most connected node in the network, simulating its extinction (primary extinction), recalculating the topological indexes of the network and counting the secondary extinctions, i.e., how many species, except primary producers, results with an in-degree = 0 after the primary extinction. All the extinct species are removed from the network. After that removal, the algorithm recalculates the degree ranking, iterating the process until the number of links in the network is zero (Dunne and Williams, 2009; Dunne et al., 2002; Solé and Montoya, 2001).

To run the *Mostconnected* function is necessary the following arguments:

– *Network*: Network class. The name of the network object to analyze

```
R> data("chilean_intertidal")
```

```
R> Mostconnected(Network = chilean_intertidal)
```

This function returns a data frame with the metrics of the network after every step of species removal (Table 1). The first column shows the vertex position of the removed species in the vector (Spp). From the second to the fifth column, we represent the following topological indexes of the food web: nodes richness (S), number of links (L), food web connectance ($C = L/S^2$) and link density ($\text{Link_density} = L/S$). The sixth column indicates the number of secondary extinctions produced after each removal step (SecExt), which was quantified as the number of nodes (except for the basal nodes) that results with an indegree = 0 after producing a primary extinction. The seventh column represents the number of species that were released from predation after each removal step (Pred_release), which was quantified as the number of nodes resulting with zero predators (outdegree) after a primary extinction. The predation release index does not consider the initial top predators in their calculation. Finally, from the 8th to the 11th columns, we represent the number of nodes the result with a total degree = 0 (Iso_nodes), the accumulative number of secondary extinctions (AccSecExt), the accumulative number of primary removals (NumExt) and the total number of extinctions ($\text{TotalExt} = \text{NumExt} + \text{AccSecExt}$).

Table 1. Summarized results of the *Mostconnected* function for the intertidal food web, showing the first and last three rows.

Spp	S	L	C	Link_density	SecExt	Pred_release	Iso_nodes	AccSecExt	NumExt	TotalExt
15	106	1314	0.12	12.40	0	0	0	0	1	1
13	105	1252	0.11	11.92	0	0	0	0	2	2
4	104	1192	0.11	11.46	0	0	0	0	3	3
.
.
.
67	57	10	0.00	0.18	8	41	47	23	35	58
107	48	1	0.00	0.02	1	46	46	24	36	60
33	46	0	0.00	0.00	1	45	46	25	37	62

Spp: node position of the extinct species, S: richness, L: number of links, C: connectance, Link_density: link density (L/S), SecExt: secondary extinctions, Pred_release: predation release, Iso_nodes: isolated nodes, AccSecExt: accumulative secondary extinctions, NumExt: number of primary extinctions, TotalExt: number of total extinctions

-The *ExtinctionOrder* function.

The *ExtinctionOrder* function removes nodes using an user-defined order. Then, it calculates the secondary extinctions and the same topological network indexes are calculated by the *Mostconnected* function. This function requires the following arguments:

– *Network*: Network class. The name of the network to analyze.

– *Order*: Numeric vector. The removal sequence of interest with the node position of the species sorted in order of interest.

In our example, the customized order is a vector with the species ordered by vulnerability, from the most to the least vulnerable according the number of predators.

```
R> data("chilean_intertidal")
```

```
R> ExtinctionOrder (Network = chilean_intertidal, Order = c(67,37,69,...,97,106,107))
```

In this case, the function returns a data frame with the metrics of the food web after each removal step (Table 2) and a graph with the accumulated secondary extinctions after each removal step (Fig. 1). The nomenclature of this table is the same as the nomenclature of the table 1. In the data frame, the last species removed was the species in the position 27. This is because the extinction functions stop when the network reaches a zero number of links.

Table 2. Summarized results of the *ExtinctionOrder* function for the intertidal food web, showing the first and last three rows of the original data frame.

Spp	S	L	C	SecExt	Pred_release	AccSecExt	NumExt	TotalExt
67	106	1345	0.12	0	0	0	1	1
37	105	1309	0.12	0	0	0	2	2
69	104	1275	0.12	0	0	0	3	3
.
.
.
1	6	7	0.19	0	0	37	80	117
4	5	2	0.08	3	1	40	81	121
27	2	0	0.00	1	1	41	82	123

Spp: node position of the extinct species, S: richness, L: number of links, C: connectance, SecExt: secondary extinctions, Pred_release: predation release, Iso_nodes: isolated nodes, AccSecExt: accumulative secondary extinctions, NumExt: number of primary extinctions, TotalExt: number of total extinctions

When we look at the results of the plot in the Fig. 1, the figure represents the cumulative secondary extinctions (y-axis) that were produced after each removal step (x-axis).

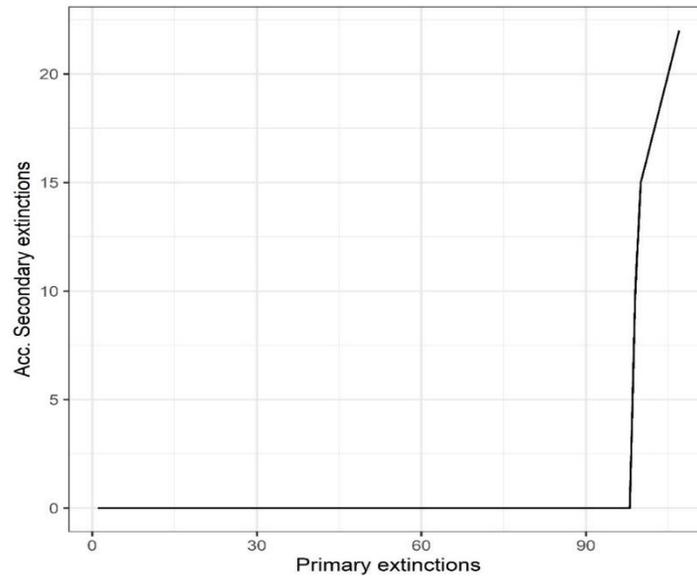


Figure 1. Accumulative secondary extinctions after each removal step (Primary extinctions) using the *ExtinctionOrder* function for the intertidal food web.

-The *RandomExtinction* function.

The *RandomExtinctions* function generates *nsim* independent random extinction sequences using bootstrapping method. Each trajectory in *nsim* runs until all species are extinct. After all the trajectories were simulated, the function calculates the average and standard deviation of the number of secondary extinctions through *nsim* for each removal step.

To run the *RandomExtinctions* function the following arguments are necessary:

- *Network*: Network class. The name of the network to analyze.
- *nsim*: is number of random extinction sequences chosen by the user.

– *parallel*: is an optional argument to run the simulation in parallel through different cores to decrease the running time. If it is TRUE, it will use parallel processing, if FALSE (default) it will run sequentially.

– *ncores*: number of cores to use if using parallel processing. To calculate the number of cores you can run this code:

```
R> ceiling(parallel::detectCores())
```

```
R> data("chilean_intertidal")
```

```
R> RandomExtinctions (Network= chilean_intertidal, nsim= 500, parallel = TRUE, ncores = 4)
```

The function returns a data frame and a plot with the mean of secondary extinctions for each removal step averaged through all the simulations.

When we look at the results of the data frame in the Table 3, the resulting data frame contains three columns. The first column incorporates the cumulative number of species removed (NumExt). The second column shows the cumulative average of the secondary extinctions among all the simulations performed. The third column presents the cumulative standard deviation of the secondary extinctions among all the simulations performed.

Table 3. Summarized results of the *RandomExtinction* function for the intertidal food web, showing the first and last three rows.

NumExt	AccSecExt sd	AccSecExt mean
1	1.90	0.25
2	2.22	0.33
3	2.46	0.42
.	.	.
.	.	.
.	.	.
104	5.12	8.92
105	5.26	9.31
106	5.24	9.86

Now, when we look at the results of the plot in the Fig. 2, the resulting plot contains a graph with the accumulative average number of secondary extinctions (\pm sd) along with the number of primary extinctions.

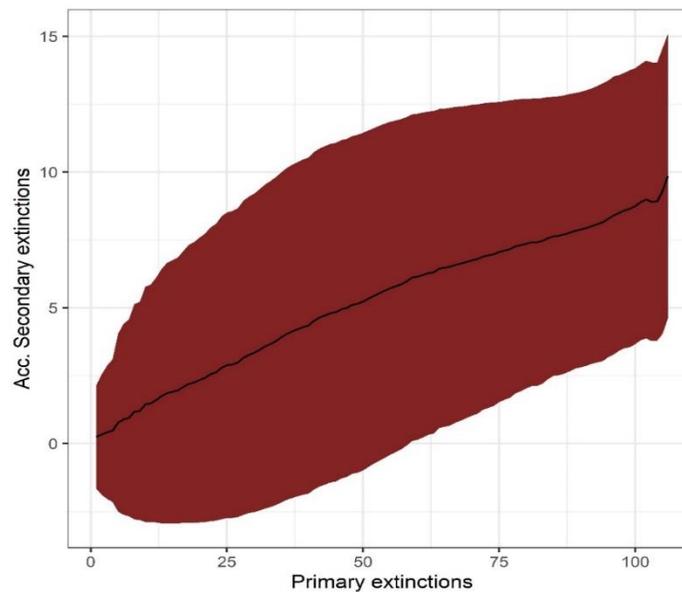


Figure 2. Accumulative secondary extinctions (Acc. Secondary extinctions) after each removal (Primary extinctions) step using the *RandomExtinction* function for the intertidal food web.

-The *CompareExtinction* function.

The *CompareExtinctions* function compares the accumulative observed extinction generated by the *ExtinctionOrder* function or by the *Mostconnected* function against a null model of the expected accumulative secondary extinctions developed by the *RandomExtinctions* function.

To run the *CompareExtinctions* function is necessary the following arguments:

– *Nullmodel*: A data frame. The object returned by the *RandomExtinctions* function.

– *Hypothesis*: A data frame. The object returned by the *Mostconnected* function or the *ExtinctionOrder* function.

In this case, we compared the secondary extinctions produced by the *random* deletion sequence with the extinctions produced by the *Mostconnected* deletion sequence.

```
R> data("chilean_intertidal")
```

```
R> Random <- RandomExtinctions(Network= chilean_intertidal, nsim= 500, parallel = TRUE,
ncores = 4) (see RandomExtinctions function to arguments information)
```

```
R> MC <- Mostconnected(Network = chilean_intertidal) (see Mostconnected function to
arguments information)
```

```
R> CompareExtinctions(Nullmodel = Random, Hypothesis = MC)
```

This function returns a data frame with the goodness of fit statistics of the comparison between the observed and the expected null secondary extinctions (Person's χ^2 test) (Table 4) and a figure comparing the number of secondary extinctions between the two deletion sequenced performed (Fig. 3).

The resulting data frame (Table 4) contains four columns. The first column shows the value of the χ^2 statistic (statistic). The second column shows the p-value for the test. The third column shows the degrees of freedom of the approximate chi-squared distribution of the test statistic (parameter). The last column shows the name of the test that was performed (method)

Table 4. Results of the comparison test

statistic	p.value	parameter	method
74.98	1.31E-09	16	Pearson's χ^2 test

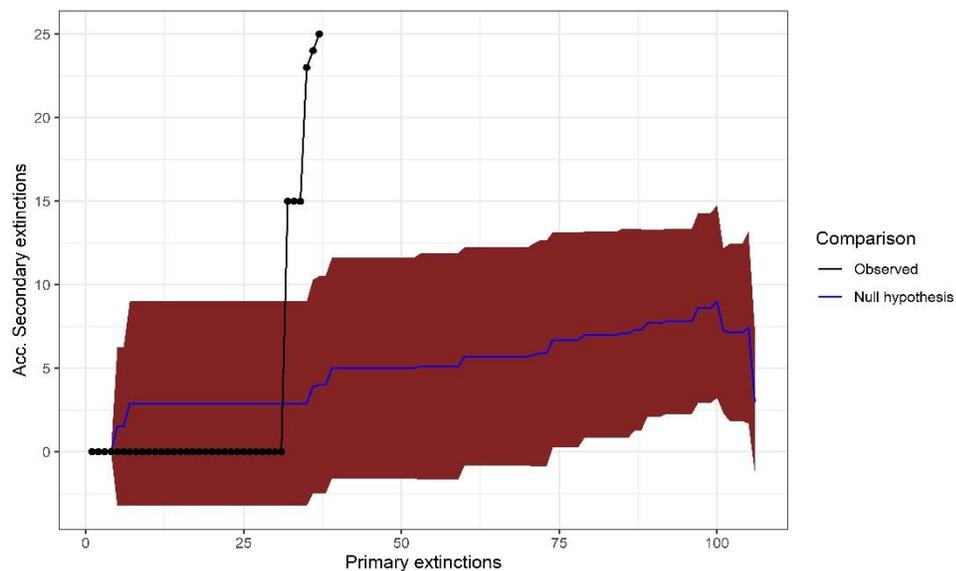


Figure 3. Comparison of the accumulative secondary extinctions (Acc. Secondary Extinctions) after each removal step (Primary extinctions) between the random (Null hypothesis) and Mostconnected (Observed) deletion sequence in the intertidal food web using the *CompareExtinctions* function. The solid blue line is the average (\pm sd) of secondary extinctions of the null model and the solid black line, the secondary extinctions of the observed model.

-The *Extinctionplot* function.

The *ExtinctionPlot* function takes an output data frame from any of the extinction functions and plots the indicator of interest after each primary extinction step. By default, this function plots the number of accumulated secondary extinctions after every primary extinction, but any of the indices (e.g., link density, or predation release) can be plotted with the function by changing the *Variable* argument.

To run the *ExtinctionPlot* function is necessary the following arguments:

- *History*: A data frame. The object returned by the *Mostconnected* function or the *ExtinctionOrder* function.
- *Variable*: is the name of the dependent variable of interest to be plotted against the number of extinctions.

As an example, we plot the density of the intertidal food web at each removal using the *Mostconnected* function (Fig. 4)

```
R> data("chilean_intertidal")
```

```
R> MC <- Mostconnected(Network = chilean_intertidal)
```

```
R> ExtinctionPlot(History = MC, Variable = "Link_density")
```

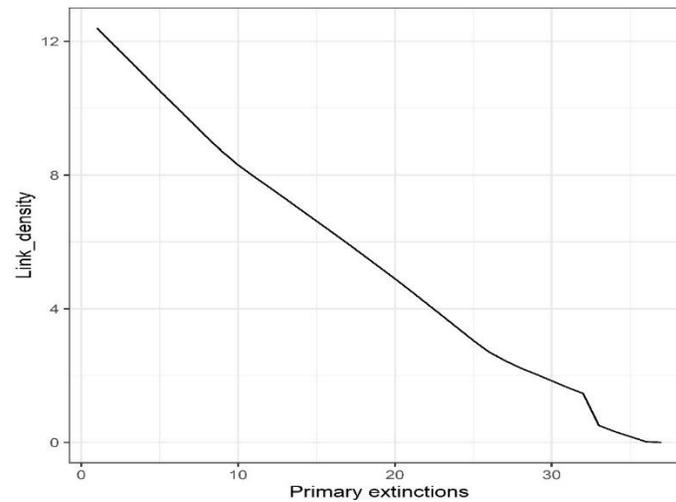


Figure 4. Links density (Link density) after each removal step (Primary extinctions) in the intertidal food web using the *ExtinctionPlot* function.

-The *degree_distribution* function

The *degree_distribution* function computes the degree distribution of a network, calculating $P(k)$, i.e, the probability that a node in the network is connected to k other nodes (Estrada, 2007). Then, the observed distribution is fitted to the exponential and power-law models using two different approaches, non-linear least squares (Godfrey et al., 1998), and linear models on log-transformed data (Xiao et al., 2011). We do not incorporate a complete set of model fitting techniques (Clauset et al., 2009) as such a complete package (see *powerLaw* R package) already exist (Clauset et al., 2009).

We used a two-step model selection approach between the two models fitted to the network degree distribution. Firstly, it select the best way of fitting the models (non-linear, NLR vs log-transformed linear approach, LR) in terms of providing good estimates of precision for hypothesis testing, and secondly, after one approach has been selected for the exponential and the power-law distribution, it is selected to which distribution form the data fits better. To select

the method for fitting each distribution, exponential or power-law, we fit each the model of each distribution using both methods (LR and NLR) (Table 5). Since we want to compare different distributions, it is important to obtain estimates of precision and, therefore, we tested the assumption that residuals have an approximately normal distribution. Hence, following (Xiao et al., 2011), we used maximum likelihood fitting for testing the normal distribution of residuals, and calculated $AICc$ values for each method. To do that, we compared the $\Delta AICc$ between both methods (LR and NLR) to each distribution model. If, the $\Delta AICc$ between LR and LNR is larger than 2 (like it is in example below), we used that method as the best for fitting the distribution, otherwise, a model average is used between both methods using Akaike weights following (Burnham and Anderson, 2002).

After the linearized or non-linear approach has been selected, a comparison is made between the selected approaches of the exponential vs the power-law distributions using AIC comparison (Burnham and Anderson, 2002). By doing this, we only select the best model describing the degree distribution, since there is no way of doing model averaging between both models (for more details about the model selection see (Xiao et al., 2011)).

Table 5. Formulas for the different distributions

Distribution	Non-linear Model	Linear Model
Power-law	$P(k) = ck\beta$	$\log P_{(k)} = \beta \log k + c$
Exponential	$P_{(k)} = e\lambda k+c$	$\log P_{(k)} = \lambda k + c$

To run the *degree_distribution* function is necessary the following arguments:

- *Network*: Network class. The name of the network to analyze.
- *scale*: a character stating if the graph is on a log-log scale (“LogLog”) or arithmetic scale (“arithmetic”)

Here, we will exemplify using a log-log scale. Thus,

```
R> data("chilean_intertidal")
R> degree_distribution(chilean_intertidal, scale = "LogLog")
```

The results of this function are three data frames (*models*, *params*, and *DDvalues*) with:

- *models*: The comparison of the AIC and normal distribution of the residual assumption test between the different distribution tested (Table 6)
- *params*: The statistical parameters of each model (Table 7).
- *DDvalues*: The degree distribution with the observed values and the value of each fitted model.

To recognize which model better fits the observed data, it is necessary to analyze the data frame *models* (Table 6). The data frame contains six columns with the fitted model information in the rows ordered by descending AIC, that is, from the best to the least agreement between data and model. The first column shows the relative likelihood of the error structure.

The second and third column shows the AIC and BIC information criteria measures. The fourth column indicates the best model of each distribution that was selected (LR or NLR of each family distribution). The fifth column indicates whether or not the normal distribution of the errors and log-normal errors assumptions is met. The last column represent the family distribution of the model fitted to data.

Table 6. Models parameters and normal distribution assumption testing

logLik	AIC	BIC	model	Normal.Resid	family
83.15	-160.30	-153.64	Exp	No	Exponential
13.39	-20.77	-14.20	Power	No	PowerLaw

In our example, the best model is the exponential degree distribution obtained from NLR with a AIC = -160.30. If we calculate the difference between the AIC value obtained from NLR (Exp model) with the AIC value obtained from LR (LogExp) ($-160.30 - 60.96 = -221.26$), it is < -2 , which means that we proceed with the results obtained from NLR. Thus, the intertidal food web follows an exponential degree distribution (Fig. 5).

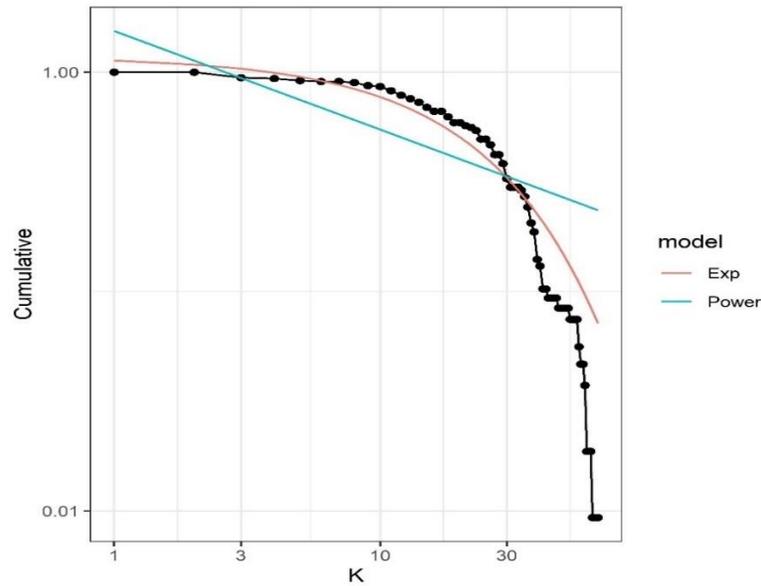


Figure 5. Cumulative probability distribution (Cumulative) for a given degree (k) using the *degree_distribution* function. The plot shows two different model fits (lines) note that since the fitted lines are regression models, their predicted values can sometimes start in values over one. Dots are the observed values.

Finally, the statistical parameters of the models are presented in Table 7. The data frame contains the parameters of the power-law and exponential models and their log-transformed versions. The first column represents the term of the models presented in Table 5. From the second to the fourth columns are the statistical parameters obtained with Kolmogorov Smirnov test. The sixth column indicate the model that is been represented.

Table 7. Statistical parameters of the models

term	estimate	std.error	statistic	p.value	model
y	-0.45	0.04	-11.17	0	Power
a	1.54	0.15	10.27	0	Power
lambda	-0.04	0.00	-26.98	0	Exp
c	0.16	0.02	6.63	0	Exp

Manuals and vignette

Additional information concerning this package and each function can be found in the R vignette and in the project webpage (<https://derek-corcoran-barrios.github.io/NetworkExtinction>). To download future package updates insert the following code in R:

```
R> devtools::install_github("derek-corcoran-barrios/NetworkExtinction")
```

Data availability

The code is available at <https://rdrr.io/cran/NetworkExtinction/man/>

Literature cited

Albert, R., and A.-L. Barabási. 2002. Statistical mechanics of complex networks. *Reviews of modern physics* 74:47.

Albert, R., H. Jeong, and A.-L. Barabási. 2000. Error and attack tolerance of complex networks. *Nature* 406:378.

Allesina, S., and M. Pascual. 2009. Googling food webs: can an eigenvector measure species' importance for coextinctions?. *PLoS computational biology* 5:e1000494.

- Barnosky, A. D., N. Matzke, S. Tomiya, G. O. Wogan, B. Swartz, T. B. Quental, C. Marshall, J. L. McGuire, E. L. Lindsey, K. C. Maguire, et al. 2011. Has the earth's sixth mass extinction already arrived?. *Nature* 471:51.
- Bascompte, J. 2009. Disentangling the web of life. *Science* 325:416–419.
- Benedek, Z., F. Jordán, and A. Báldi. 2007. Topological keystone species complexes in ecological interaction networks. *Community Ecology* 8:1–7.
- Berg, S., A. Pimenov, C. Palmer, M. Emmerson, and T. Jonsson. 2015. Ecological communities are vulnerable to realistic extinction sequences. *Oikos* 124:486–496.
- Binzer, A., U. Brose, A. Curtsdotter, A. Eklöf, B. C. Rall, J. O. Riede, and F. de Castro. 2011. The susceptibility of species to extinctions in model communities. *Basic and Applied Ecology* 12:590–599.
- Burnham, K. P., and D. R. Anderson. 2002. A practical information-theoretic approach. *Model selection and multimodel inference*, 2nd ed. Springer, New York.
- Butts, C. T., et al. 2008. network: a package for managing relational data in r. *Journal of Statistical Software* 24:1–36.
- Clauset, A., C. R. Shalizi, and M. E. Newman. 2009. Power-law distributions in empirical data. *SIAM review* 51:661–703.
- Costello, C., D. Ovando, T. Clavelle, C. K. Strauss, R. Hilborn, M. C. Melnychuk, T. A. Branch, S. D. Gaines, C. S. Szuwalski, R. B. Cabral, et al. 2016. Global fishery prospects under contrasting management regimes. *Proceedings of the national academy of sciences* 113:5125–5129.
- Curtsdotter, A., A. Binzer, U. Brose, F. de Castro, B. Ebenman, A. Eklöf, J. O. Riede, A. Thierry, and B. C. Rall. 2011. Robustness to secondary extinctions: comparing trait-based sequential deletions in static and dynamic food webs. *Basic and Applied Ecology* 12:571–580.
- de Santana, C. N., A. F. Rozenfeld, P. A. Marquet, and C. M. Duarte. 2013. Topological properties of polar food webs. *Marine ecology progress series* 474:15–26.
- Dirzo, R., and P. H. Raven. 2003. Global state of biodiversity and loss. *Annual review of Environment and Resources* 28.
- Donohue, I., H. Hillebrand, J. M. Montoya, O. L. Petchey, S. L. Pimm, M. S. Fowler, K. Healy, A. L. Jackson, M. Lurgi, D. McClean, et al. 2016. Navigating the complexity of ecological stability. *Ecology Letters* 19:1172–1185.
- Dunne, J. A., and R. J. Williams. 2009. Cascading extinctions and community collapse in model food webs. *Philosophical Transactions of the Royal Society B: Biological Sciences* 364:1711–1723.

- Dunne, J. A., R. J. Williams, and N. D. Martínez. 2002. Food-web structure and network theory: the role of connectance and size. *Proceedings of the National Academy of Sciences* 99:12917–12922.
- Dunne, J. A., R. J. Williams, N. D. Martínez, R. A. Wood, and D. H. Erwin. 2008. Compilation and network analyses of cambrian food webs. *PLoS biology* 6:e102.
- Estrada, E. 2007. Food webs robustness to biodiversity loss: the roles of connectance, expansibility and degree distribution. *Journal of theoretical biology* 244:296–307.
- Gao, J., B. Barzel, and A.-L. Barabási. 2016. Universal resilience patterns in complex networks. *Nature* 530:307–312.
- Godfrey, K. R., P. Tanswell, R. A. Bates, M. J. Chappell, and F. N. Madden. 1998. Nonlinear pharmacokinetics of tissue-type plasminogen activator in three animal species: a comparison 338 of mathematical models. *Biopharmaceutics & drug disposition* 19:131–140.
- Hastings, A., K. S. McCann, and P. C. de Ruiter. 2016. Introduction to the special issue: theory of food webs. *Theoretical Ecology* 9:1–2.
- Jordán, F. 2009. Keystone species and food webs. *Philosophical Transactions of the Royal Society B: Biological Sciences* 364:1733–1741.
- Kéfi, S., E. L. Berlow, E. A. Wieters, L. N. Joppa, S. A. Wood, U. Brose, and S. A. Navarrete. 2015. Network structure beyond food webs: mapping non-trophic and trophic interactions on chilean rocky shores. *Ecology* 96:291–303.
- May, R. M., J. H. Lawton, and N. E. Stork. 1995. Assessing extinction rates. *Extinction rates* 1:13–14.
- Pascual, M., and J. A. Dunne. 2006. *Ecological networks: linking structure to dynamics in food webs*. Oxford University Press.
- Pimm, S. L., I. Donohue, J. M. Montoya, and M. Loreau. 2019. Measuring resilience is essential to understand it. *Nature Sustainability* 2:895–897.
- Proulx, S. R., D. E. Promislow, and P. C. Phillips. 2005. Network thinking in ecology and evolution. *Trends in ecology & evolution* 20:345–353.
- Radchuk, V., F. D. Laender, J. S. Cabral, I. Boulangeat, M. Crawford, F. Bohn, J. D. Raedt, C. Scherer, J.-C. Svenning, K. Thonicke, et al. 2019. The dimensionality of stability depends on disturbance type. *Ecology letters* 22:674–684.
- Ramos-Jiliberto, R., F. S. Valdovinos, P. M. de Espanés, and J. D. Flores. 2012. Topological plasticity increases robustness of mutualistic networks. *Journal of Animal Ecology* 81:896–904.
- Scheffer, M., S. Carpenter, J. A. Foley, C. Folke, and B. Walker. 2001. Catastrophic shifts in ecosystems. *Nature* 413:591.
- Solé, R. V., and M. Montoya. 2001. Complexity and fragility in ecological networks. *Proceedings of the Royal Society of London B: Biological Sciences* 268:2039–2045.

- Valdovinos, F. S., R. Ramos-Jiliberto, J. D. Flores, C. Espinoza, and G. López. 2009. Structure and dynamics of pollination networks: the role of alien plants. *Oikos* 118:1190–1200.
- Venter, O., E. W. Sanderson, A. Magrath, J. R. Allan, J. Beher, K. R. Jones, H. P. Possingham, W. F. Laurance, P. Wood, B. M. Fekete, et al. 2016. Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. *Nature Communications* 7:12558.
- Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997. Human domination of earth's ecosystems. *Science* 277:494–499.
- Xiao, X., E. P. White, M. B. Hooten, and S. L. Durham. 2011. On the use of log-transformation vs. nonlinear regression for analyzing biological power laws. *Ecology* 92:1887–1894

INFORMACIÓN SUPPLEMENTARIA (CAPÍTULO 1)

Table S1. Comparison of the package properties between the most common package that analyze food webs with the *NetworkExtinction* package. We compare three categories according to the food web attributes that accept, the network metrics that calculates and the type of network analysis that performs. PP: primary producers. * The connectance order could be generated using a particular order function.

Food web attributes	Igraph	FoodWeb	Network	Cheddar	PowerLaw	NetworkExtinction	enaR
Non directed networks	X		X				
Directed networks	X	X	X	X		X	X
Weighted networks	X		X	X			X
Accept other node attributes (e.g. abundance, body size)			X	X			X
Accept environmental factors				X			
<hr/>							
Food web metrics							
<hr/>							
Calculate Number of nodes	X	X	X	X		X	X
Calculate Numbers of Links	X	X	X	X		X	X
Calculate Density of links		X	X	X		X	X
Calculate Connectance		X		X		X	
Calculate other ecological index (e.g. Trophic level, omnivory level)		X		X			
<hr/>							

Food web analysis				
Removal of nodes	X	X	X	X
Remove a sequence of nodes with particular order			X	X
Remove nodes sequentially in order of degree			*	X
When the most connected node are removed, recalculate the new most connected node of the network				X
Remove nodes in a random order				X
Remove the secondary extinctic nodes				X
When secondary removals occur, it is never in the pp				X
Quantifies the secondary extinctions of the network			X	X
Visualization of removal analysis				X
Statistic comparison between different removal analysis				X

Calculate degree distribution	X	X	X
Plot degree distribution analysis	X	X	X
Adjust the best model of degree distribution		X	X
Use different statistical methods to adjust degree distribution			X

CAPÍTULO 2.

VARIATION IN COASTAL PRODUCTIVITY INCREASES SENSIBILITY TO FISHERIES IN MARINE FOOD WEBS

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Abstract

Top-down and bottom-up forces determine ecosystem function and dynamics. Fisheries as a top-down force can shorten and destabilize food-webs, while climate-change driven effects can alter the bottom-up force of coastal productivity. We use network analyses to study these two global change drivers in a marine intertidal rocky-shore food-web off the coast of central Chile. First, we quantify the relative importance of small-scale artisanal fisheries as another predator species by assessing the impact of losing all harvested species on the food-web. Second, we parameterized the Allometric Trophic Network model with empirical data of this food-web and assess the independent and combined effects of fisheries and climate change through plankton productivity perturbation. We found that the extinction of all harvested species causes

null secondary extinctions, but the perturbation of plankton productivity causes many secondary extinctions. These two forces interact with fisheries dampening the negative impact of plankton productivity perturbation on non-harvested species, and plankton productivity perturbation intensifying the negative effect of fishing on harvested species. Our results suggest that small-scale artisanal fisheries in the Central Coast of Chile acts as a keystone species similar to human-gatherers in the North Pacific.

INTRODUCTION

Direct human impacts and the full suite of drivers of global change are the main cause of species extinctions in Anthropocene ecosystems^{1,2}, with important impacts on ecosystem functioning and the services that benefit human societies^{3,4}. Predicting the consequences of species extinctions pose important challenges because species are part of complex and diverse ecological communities of strongly and weakly interacting species, which generates a myriad of lagged, non-linear, and unexpected propagation of effects on the community or local food-webs⁵. Consequently, species extinctions can affect the persistence and dynamics of other interacting species and trigger cascades of secondary extinctions^{6–9} that are difficult or impossible to anticipate from information on interacting pairs of species. Therefore, the ongoing environmental crisis urges us to understand and generate scenarios for the potential impacts of species extinctions on entire ecosystems^{10–12}. The present work advances in that direction by using an empirically-constructed food-web to evaluate the effects of artisanal fisheries and climate-induced changes in primary productivity on a marine rocky-shore community.

Ecological networks have advanced our understanding of the structure and dynamics of ecosystems by providing powerful concepts and methods to analyze complex biological

communities^{12,13}. Previous studies have used this framework to assess food-web robustness against species extinctions (i.e., the fraction of initial species that remain present in the ecosystem after a primary extinction) ^{6,14–18}. Through the use of static and dynamic approaches, these studies have shown the relevance of highly connected species^{6,15,19,20}, basal species¹⁴ and highly connected species that trophically support other highly connected species¹⁷ for food-web persistence. The static approach stems from network theory and analyzes the impacts of structural changes on food-webs represented by nodes (species) and links (interactions) that connect nodes, but ignores interaction strengths and population dynamics of interacting species⁶. In this approach, a non-basal species is considered extinct after a perturbation (defined here as a secondary extinction) if all its resource species (food) go extinct. Basal species are assumed to be autotrophs or otherwise obtain resources from outside the modeled web, e.g. through subsidies from other ecosystems and, therefore, do not experience extinctions unless directly removed (defined here as a primary extinctions). Thus, the static approach only considers extinctions produced by direct bottom-up effects. A dynamic approach considers not only the structure and intensity of interactions in a food-web, but also the changes in species abundances through time and the indirect and dynamic effects that these changes have on the abundances of other species^{14–16,21,22}. A species is then considered to be secondarily extinct when its abundance drops below a threshold as a consequence of its population losses being higher than its population gains. Therefore, a dynamic approach can take into account both bottom-up and top-down effects of perturbations on the system, and both forces can contribute to produce secondary extinctions¹⁴. We use both the static network-based approach and a dynamic approach based on energy-transfer to evaluate the impacts of artisanal fisheries and changes in primary productivity on a marine rocky-shore community.

The world fisheries crisis cuts across fishing strategies, oceanic regions, species attributes and types of fisheries (subsistence, artisanal, industrial) and includes countries that have little regulation and those that have implemented rights-based co-management strategies to reduce overharvesting^{23–26}. Chile has been one of the countries implementing Territorial Use Rights (TURFs²⁷) over an unprecedented geographic scale to manage the diverse coastal benthic resources using a co-management strategy^{28,29}. Over 60 coastal benthic species form part of these artisanal fisheries²⁸, with species that are extracted from intertidal and shallow subtidal habitats^{30,31}. The Chilean TURFs system brought significant improvements in sustainability of this complex socio-ecological system, helping to rebuild benthic fish stocks^{28,29}, improving fishers' perception towards sustainability and increasing compliance²⁷, as well as showing positive ancillary effects on conservation of biodiversity^{32,33}. However, the situation of most artisanal fisheries is still far from sustainable, and many fish stocks and coastal ecosystems show signs of over exploitation and ecosystem degradation, a consequence of the low levels of cooperation and low enforcement of TURF regulations, which leads to high levels of free-riding and illegal fishing^{34–36}. Thus, it is imperative to improve our understanding of the effects of these multi-species fisheries which simultaneously harvest species at all trophic levels, from kelp primary producers to top carnivores^{31,37}.

To compound things, removal of biomass from the ocean occurs simultaneously with multiple other stressors associated to climate change that compromise the individuals' capacity to respond to perturbations^{38–40}. Besides sea surface temperature (SST), climate change also affects many other physical-chemical characteristics of marine coastal waters (stratification, acidification, ventilation, among others)^{41,42}, as well as the wind regimes that control surface water productivity along the productive coastal upwelling ecosystems^{43–47}. Changes in the

productivity of the oceans are reflected in changes of plankton biomass, which contributes approximately half of the global primary production, supports the productivity of marine food-webs, and influences the biogeochemical process in the ocean and strongly affects commercial fisheries^{48–50}. Indeed, an overall decrease in marine plankton productivity is expected over global scales^{42,48,51}. Along extensive regions of the Humboldt upwelling ecosystem off Chile, long-term increases and decreases in plankton productivity have already occurred over the past two decades^{52,53} and are expected to propagate up the pelagic and benthic food webs. We therefore analyzed the bottom-up impact of fluctuations in plankton productivity in combination with fisheries exploitation of these food-webs.

Ever since the bioenergetic allometric approach of Yodzis and Innes ⁵⁴ became widely used to analyze the dynamics of consumer-resource systems, its extension to larger food-webs (i.e., Allometric Trophic Network, ATN⁵⁵, model) has been useful for answering a variety of questions about food-web dynamics and stability. For example, the ATN model has been used to evaluate the potential effects of fisheries on food-webs of the Sanak Archipelago in Alaska⁵⁶, and of the Lake Constance at the northern foot of the European Alps⁹. Other studies have used the ATN model to analyze the potential effects of climate change (specifically global warming) on the dynamics of generic food-webs, by altering the body size of organisms and accelerating their metabolism^{40,57}. Thus, the ATN provides an appropriate modeling framework to explore the independent and interactive effects of fisheries and altered productivity on these complex food webs⁵⁸.

In this contribution, we explore (1) the importance of the pattern of trophic interactions of harvested species on the structure and persistence of the intertidal food-web by simulating a

scenario of over-exploitation-driven extinction of all harvested species. We then evaluate (2) the robustness of this food-web to the extinction of species harvested by artisanal fisheries in comparison to three commonly used extinctions sequences (see below), and (3) the effect of three fisheries scenarios on other species abundance, persistence and food-web dynamics. We finally (4) analyze the independent and combined effects of fisheries and plankton productivity changes on the food-web dynamics through altering plankton subsidy. Our study differs from previous work using network approaches in that it assumes the food-web is subsidized by an external source, by including a subsidy in the plankton node that is considered to be controlled by advective processes unaffected by local benthic consumption. This represents well the situation of most marine benthic ecosystems⁵⁹. We also note that, to our knowledge, the ATN model we develop here is the largest empirical dynamic food-web model ever parameterized (our intertidal food-web contains 107 species), which by itself represents an advancement in food web modeling. Moreover, the added realism of plankton subsidy allows us to simulate the effect of climate-change driven effects described above as the alteration of such subsidy.

RESULTS

1. Food-web description and the relative importance of harvested species to the food-web structure

The highly omnivorous fisheries node (F node in Fig. 1A) contributed 22 links, from basal kelp species to top carnivores (Fig. 1A). Among the species harvested by the artisanal fisheries, 10 belong to the 30 most connected species of the food-web (Fig. 1A, and Supplementary Table S1). Moreover, these fisheries exploit at least one species that is a

resource or a consumer of about 70% of the species (harvested and non-harvested species) in the intertidal food-web (Fig. 1B). With the static approach we found that the removal of all 22 species (see methods) negatively affected the structural properties of the food-web, specially, reduces the overall number of trophic interactions by 48%. This loss represents, on average, 100 more links lost than that expected from randomly removing 22 species from the food-web (see supplementary Table S3 and supplementary material for more detailed results).

2.1. Food-web robustness to species extinctions

Following previous work^{6,14–16}, we evaluated the robustness of the intertidal food-web to species extinction by sequentially removing species and counting the subsequent secondary extinctions, if any. We counted the secondary extinctions caused by the four deletion sequences (harvesting, random, most-connected, supporting-basal) using both static and dynamic approaches (see methods). Both approaches found that the intertidal food web is highly robust to the loss of all harvested species, as null secondary extinctions were observed after removing all harvested species (Fig. 2). The robustness of the intertidal food-web was further demonstrated by the sequential deletion of the most connected species, which showed that over 30% of those species must be removed before any secondary extinctions occur (Fig. 2). As expected from previous work, the loss of supporting-basal species produced the most secondary extinctions (Fig. 2). Both approaches showed similar trends (Fig. 2A and B), but our dynamic approach presented relatively lower food-web robustness (Supplementary Fig. S1).

Although the plankton node (“species”) was directly connected only to filter-feeders, it proved to be the most important in the supporting-basal deletion sequence for both static and

dynamic approaches, as its removal caused 15 and 29 secondary extinctions, respectively. The species that went extinct included not only sessile filter-feeders, but also four harvested species important for the fisheries: the Chilean muricid whelk *Concholepas concholepas*, the giant barnacle *Austromegabalanus psittacus*, the sea squirt *Pyura chilensis* and the whelk *Acanthina monodon*. These results suggest that while the intertidal food-web is robust to harvest-driven extinctions, it can be sensitive to a drastic decrease in plankton productivity.

2.2 Impacts of artisanal fisheries on food-web dynamics

We assessed the impacts of fisheries on the biomass of every species in the food-web using the ATN model. Fig. 3 illustrates with a simplified diagram our results shown in Supplementary Fig. S2. The three fisheries scenarios, in which we simultaneously reduced the biomass of the 22 harvested species by 50%, 80% and 100% (see Methods), highlight/reveal how fishing effects can propagate throughout the entire web (Fig. 3B). The decrease in biomass of harvested species led to an increase in the biomass of most non-harvested species at all trophic levels, especially in basal and herbivorous species (Fig. 3B). On average, 82-86% of non-harvested species increased their biomass by 5-25% after 50-100% fishing impacts on biomass stocks (Supplementary Fig. S2). This biomass increase is explained by two mechanisms: i) decreasing the biomass of harvested species that are consumers reduces the predation intensity on their resources (note that fisheries harvest more species in higher than lower trophic levels, compare Supplementary Figs. 1D and 1C), and (ii) decreasing the biomass of harvested basal species reduces their competitive effects on the non-harvested basal species, allowing them to grow (Supplementary Fig. S3).

The positive effect of artisanal fisheries on the biomass of non-harvested species was qualitatively similar across the different fishing scenarios, becoming larger with an increase in

fishing intensity (Supplementary Fig. S2). The exceptions were top predators, which had opposite responses between the weakest and strongest fishing scenarios. A 50% reduction in harvested species biomass caused a slight decrease in non-harvested top predators' biomass, while 80% and 100% reductions caused an increase in their biomass. This suggests that artisanal fisheries negatively impact top predators by extracting their prey species but, when the exploitation rates are stronger, the indirect positive effects of fisheries on the biomass of the non-harvested species become strong enough to dampen those effects.

2.3. Impacts of plankton subsidy alteration on food-web dynamics

We considered a subsidy term to plankton as an external-controlled subsidy of plankton productivity. We both decreased (Fig. 3C) and increased (Fig. 3D) the plankton subsidy in 50%, 80%, and 100% to simulate the alteration of plankton productivity expected as a response of climate change (see Methods). All biomass changes can be found in Supplementary Fig. S4. Both decreasing (Fig. 3C) and increasing (Fig. 3D) plankton subsidy can deeply alter food web dynamics. The magnitude of plankton subsidy increases or decreases (i.e., 50%, 80%, 100%) only quantitatively affected the food-web patterns shown in Figs. 3C and 3E, becoming more intense with an increasing alteration of the plankton subsidy. Decreasing plankton subsidy had larger impacts on the species biomasses than increasing plankton subsidy in the same magnitude, even causing species extinctions (i.e., -1 in Supplementary Fig. S4E) when the subsidy was removed (i.e., decreased in 100%). The number of total extinctions that occurred after completely removing the plankton subsidy was 29 species, highlighting the bottom-up propagation of effects through the web (Supplementary Fig. S4E).

A drastic decrease in plankton subsidy (100%) resulted in the extinction of all filter-feeder species (specialist consumers of plankton) and decreased the biomass of carnivores and top predators by 99% (Fig. 3C). The biomass reduction in carnivores and top predators, in turn, released predation pressure on omnivores and herbivores, which consequently increased their biomass by 30% and 110%, respectively. The increased biomass of herbivores and omnivores, in turn, increased consumption pressure on basal species, but we found that the biomass of basal species slightly increased by 4% (Fig. 3C). This suggests that the reduction in plankton subsidy positively affects basal species by releasing pressure on the community level carrying capacity (see Methods). Conversely, a 100% increase in plankton subsidy (Fig. 3D) increased the total biomass of filters, carnivores, and top predators by 76%, 107%, and 105%, respectively. As a consequence, the increased predation pressure from higher trophic levels decreased the total biomass of omnivores, herbivores, and basal species by 2%, 20%, and 3%, respectively. Carnivore species were the most vulnerable to the reduction of plankton productivity, going extinct with a reduction of 80% in plankton subsidy (Supplementary Fig. S4C), followed by filter-feeders and top predators, which went extinct with a 100% of subsidy reduction (Supplementary Fig. S4E). Regarding harvested species, 18% of them strongly decreased their biomass when plankton subsidy decreased, while 81% of them slightly decreased their biomass when plankton subsidy increased (compare panels A, C, E with B, D, E of Supplementary Fig. S4).

2.4. Interacting effects of fisheries and plankton-subsidy alteration on food-web dynamics

We evaluated the combined effects of the biomass extraction by fisheries and the alteration of plankton subsidy on the food-web dynamics using a full factorial design that maintains the same fishing and subsidy levels used in each of the last two sections (Methods).

We found that regardless of the fishing scenario, all non-harvested trophic levels persisted when the plankton subsidy increased or decreased (Fig. 4A and B) by 50%. Conversely, when the plankton subsidy decreased in 80%, carnivores went extinct under all fishing scenarios (Supplementary Fig. S5C and D) as well as the top-predators and filter-feeders when the plankton subsidy decreased in 100% (Fig. 4C and D).

The level of plankton subsidy affected the impact of fishing on the biomass of harvested species. Decreasing plankton subsidy decreased the biomass of harvested carnivores and filter-feeders, intensifying the negative effect of fishing on their biomasses (see black arrows pointing down to such result for “Harvested Carnivores” in panels A and C of Fig. 4). The reverse occurred when increasing plankton subsidy, which dampened the effect of fishing on the biomass of harvested carnivores and filter-feeders. Interestingly, decreasing plankton subsidy also increased the biomass of harvested and non-harvested omnivores and herbivores (see results of subsection 2.3), which therefore dampened slightly the negative effect of fisheries on harvested omnivores and herbivores (Fig. 4 A and C).

Fisheries also affected the impacts of perturbing plankton subsidy on species biomasses. Increasing fishing increased the biomass of non-harvested species (see results of subsection 2.2) and, therefore, dampened the negative effects of altering plankton subsidy on the biomass of these species while intensifying the positive effects of altering plankton subsidy in those species (compare panels A and C with B and D of Fig. 4). Specifically, fisheries reversed the negative effect of increasing plankton subsidy on the biomass of non-harvested herbivores (see 4 black arrows pointing down to such result in panels A-C).

DISCUSSION

Fisheries are commonly associated with negative impacts on ecosystems, especially on the food-web structure, total biomass, and species recovery^{9,60,61}. The present study shows that these effects are not necessarily general at a food-web scale. We found that in a rocky-shore intertidal food-web, the simulated extinction of all harvested species caused null secondary extinctions. This despite artisanal fisheries harvesting on more than 20% of the food-web species, which are also highly connected species. In addition, we found that this food-web was highly vulnerable to the decrease of plankton productivity, which is one of the outcomes expected to happen as consequence of climate change^{42,48,51,52}. Finally, we found that artisanal fisheries might contribute to dampening the negative consequences of plankton-productivity decrease by increasing the biomass of non-harvested species. In the following paragraphs, we expand on these results and contextualize them with prior literature.

The impact on the food-web structure of all harvested species going extinct (i.e., food-web shortened and connectance decreased, Supplementary Table S3) caused null secondary extinctions. This suggests that harvested species are embedded in redundant⁶² trophic interactions. In addition, the high food-web robustness suggests that the exploitative competition between artisanal fisheries with harvested and non-harvested species for common resources (Supplementary Fig. 1C) might be weak, as consumers have wider diets that can buffer the loss of harvested species. The high redundancy of trophic interactions is explained by its high levels of omnivory³², generalist consumers⁶³, and a high proportion of transient and weak links⁶⁴. These attributes confer food-webs alternative routes of energy and stability^{22,65}. These results, however, do not imply that local fisher communities will be similarly tolerant to the extinction of harvested species. The socio-economic system in which fishers are embedded

will be directly impacted⁶⁶ if resource management by local TURFs fails and drive the harvested species extinct. Fishers would need to harvest on new species as alternative resources to maintain their livelihood. In our analysis, the loss of harvested species caused the loss of an important amount of redundant links (Table S3). Therefore, fishers exploiting new species will impact the food-web in ways we did not explore here.

Our results also highlight the vulnerability of basal species to fishing. We found that basal species went extinct with an extraction above 0.3% of their available biomass. Harvested basal species are consumed by 2.5 more species than harvested consumers, and their intrinsic growth rate is 3 times lower than that of non-harvested basal species because they are the macroalgae that have the largest body size. Among the harvested basal species is kelp, which plays an important ecological and economical role. Kelp promotes the biodiversity of coastal ecosystems⁶⁷ and has high commercial value, with Chile being one of the main exploiters of its natural populations⁶⁸. Kelp extraction in Chile is managed but hardly supervised⁶⁸. Therefore, kelp's high demand, high value, and low control, leave these algae prone to illegal fishing. In this context, we highlight the urgency of increasing supervision of kelp fisheries and enforcing their compliance with management plans.

A concerning effect of climate change is the alteration of plankton productivity. This can be caused by the physicochemical changes in coastal waters triggered by warmer waters⁴² and by an intensification of upwelling-favorable winds^{53,69}, accompanied with a decrease (or increase) of nutrients given by an intensification of the warm (or cold) phase of ENSO⁷⁰⁻⁷². The importance of plankton is well-known as the energy supply of food-webs, as well as essential for sustaining fisheries⁵⁰. We found that plankton is the most important food-web

component for species persistence. Plankton is consumed by filter-feeders and any alteration of plankton subsidy affects the biomass of all the species in the food-web. On the one hand, a decrease in plankton subsidy caused the intertidal food-web to shorten, with strong impacts on fisheries because of the biomass reduction of harvested species. Similar results were found when climate change effects were simulated as an increase of biological rates^{40,73} caused by temperature raises, which suggests that our results will be magnified if we were to consider the alteration of biological rates. In addition, a reduction in plankton productivity may reduce the recruitment of species (as plankton composition also include larvae of several species⁷⁴), which might cause more secondary extinctions than we found here. On the other hand, an increase in plankton subsidy negatively impacted the biomass of a higher number of species but in smaller magnitude than the decrease of plankton subsidy. Moreover, an enrichment of nutrients can increase the arrival of new species⁷⁵ or the recurrence of harmful algal blooms with a devastating effect on local food-webs⁷⁶. Thus, if we consider these factors, we would expect an intensification in the negative consequences observed in this study.

Finally, artisanal fisheries can enhance the persistence of non-harvested species by harvesting more on their predator than prey species (Supplementary Figs. S1B and C, respectively), and by relaxing the competition for nutrients between basal species by harvesting on primary producers. These mechanisms became evident when fisheries dampened the negative impacts of plankton subsidy alteration on non-harvested species. Ours is not the first study showing the positive effects of fisheries on ecosystems. Previous work⁵⁶ shows that human-gatherers enhance the species persistence of coastal marine ecosystems in the North Pacific. This suggests that, at least in the intertidal food-web studied here, small-

scale artisanal fisheries play a similar role as human-gatherers in the North Pacific, that is, as keystone species to non-harvested species into the food-web.

Limitations of our research mostly consist of factors not included in our modeling approach. For example, artisanal fisheries harvest kelp which plays an important non-trophic role by providing habitat structure and shelter to many species³⁰. Other factors not considered in this study are local spatial features such as the enclosed bay with internal circulation and larval retention⁷⁷ as well as upwelling zones⁷⁸, which can affect species recruitment and affect our results. Similarly, temporal variability and other stochasticity sources associated with global change (e.g., invasive species, pathogens spread, habitat degradation, and several climatic stressors^{1,2}) can also change the relative importance of species in food-webs, making an open-system approach²¹ to ecological networks an important next step in the area. For example, the extinction of all harvested species might release several ecological niches and, consequently, fisheries might increase the species invasion. Moreover, as invasive species are characterized by generalist foraging habits and lacking predators⁷⁹, we might find negative consequences in the abundance of local non-harvested species. Thus, our results should be interpreted with care, and the positive effects of fisheries do not mean that fisheries can indiscriminately exploit these ecosystems. These effects might depend on adaptive prey-switching behavior (mechanism not considered here), allowing them to use alternative or new resources in response to changes in abundances of other species in the community, and with that rewire food-web⁸⁰ and stabilize populations dynamics⁸¹.

In the rocky intertidal ecosystems we studied in this work, artisanal fishermen obtain their resources through hand-picking and use them for self-subsistence²⁴. Therefore, resource

availability in intertidal ecosystems plays an important role for the poorest fishermen. Artisanal fishers with more means apply most of their fishing gears (e.g., diving, spearing, and pot trapping) in subtidal-shallow ecosystems²⁴, from where they harvest ~20% of species in the food-web (Supplementary Fig. S6A). For the above, we repeated our static extinction analysis in the shallow-subtidal marine food-web and found that, as in the intertidal food-web, the subtidal food-web is robust to the loss of all harvested species (Supplementary Fig. S6B). This suggests that similar mechanisms explaining the high food-web robustness of the intertidal ecosystem against the extinction of harvested species, explain the high food-web robustness of the subtidal. Moreover, as in the intertidal food-web, we found that plankton was the most important group (node) for the subtidal food-web persistence. Analyzing the effect of artisanal fisheries on the subtidal food-web with a dynamic approach seems an important next step to understand how anthropogenic activities as well as bottom-up and top-down forces affect coastal food-webs.

Our study shows that the effects of climate change threaten the biodiversity of marine intertidal rocky-shore ecosystems as well as the services they provide, and emphasize the relevance of understanding and predicting the population dynamics of plankton and their impacts on entire food-webs. New strategies for these new scenarios caused by climate change are needed to also protect the economy and wellbeing of the local communities dependent on these coastal ecosystems.

METHODS

1. Food-web description and the relative importance of harvested species to the food-web structure

We studied a well-resolved food-web of the intertidal rocky shore communities of the central coast of Chile³⁰, which is harvested exclusively by small scale artisanal fisheries²⁹. The web represents all species that are found to co-occur on wave exposed rocky platforms of central Chile, from the very low to the highest intertidal and is composed of 107 species (including a fisheries node), with 44% of its species corresponding to primary producers, 53% to invertebrates, and 3% to endotherm vertebrates. In the food-web, we consider as basal level all species of benthic primary producers plus plankton (phytoplankton + zooplankton, single node). Therefore, we represented filter-feeders (sessile filter-feeders + porcellanidae crabs) as specialist consumers of plankton and not as basal species (see detailed description of the food-web in Supplementary Material).

Species harvested by artisanal fisheries were identified using information from the Chilean national fishing service (www.sernapesca.cl) and previous work³¹. A high diversity of species distributed across all trophic levels are harvested by artisanal fisheries (red nodes in Fig. 1), including numerous species of macroalgae (n= 7), filter-feeders (n= 2), herbivores and omnivorous (n= 11), and carnivores (n= 2), totaling 22 species. Using the static approach (without population dynamics), we compared the structure of the food-web with and without the harvested species to the distribution of 1000 food-web structures produced by randomly removing the same amount of harvested species (see more details about this method in supplementary materials).

2. The dynamic model

The Allometric Trophic Network (ATN) model⁸² consists of two basic sets of equations, one set describing the biomass changes of primary producers (eq. 1) and the other describing that of consumers (eq. 2), where \mathbf{B} is the biomass vector with the biomasses of

every species population in the food-web and B_i is the biomass of the population of species i , as follows:

$$\frac{dB_i}{dt} = \overbrace{r_i B_i G_i(\mathbf{B})}^{\text{Autotrophic growth gain}} - \sum_j \overbrace{\frac{x_j y_{ji} B_j F_{ji}(\mathbf{B})}{e_{ji}}}_{\text{Herbivory loss}} - \overbrace{F_{\max i} B_i}_{\text{Fisheries loss}} \quad (\text{eq. 1})$$

$$\frac{dB_i}{dt} = \overbrace{f_a x_i B_i \sum_j y_{ij} F_{ij}(\mathbf{B})}_{\text{Resources consumption gain}} - \overbrace{f_m x_i B_i}_{\text{Maintenance loss}} - \sum_j \overbrace{\frac{x_j y_{ji} B_j F_{ji}(\mathbf{B})}{e_{ji}}}_{\text{Predation loss}} - \overbrace{F_{\max i} B_i}_{\text{Fisheries loss}} \quad (\text{eq. 2})$$

The biomass of producer i changes according to the balance of autotrophic growth gain and losses due to predation. The net autotrophic growth is determined by the logistic growth function $G_i(B) = 1 - (\sum_{j=\text{productores}} c_{ij} B_j)/K$, where r_i is the intrinsic growth rate of producer i , c_{ij} is the inter-specific competition coefficient between producer i and j , and K is the total carrying capacity of primary producers in the system. The biomass loss of producer i by herbivory (caused by herbivores or omnivores) increases with the mass-specific metabolic (x_j) and attack (y_j) rates of consumer i , and decreases with the assimilation efficiency of consumer i for resource j (e_{ji}). The consumers' population dynamics (eq. 2) depend on their mass-specific metabolic rates (x_j) and on the balance between biomass gains by resource consumption, biomass loss by metabolic maintenance, and biomass loss to predation. From the total amount of resources ingested by the consumer population i , $\sum_j y_{ij} F_{ij}(\mathbf{B})$, only a fraction f_a is assimilated into consumer available energy for maintenance and biomass growth. The functional response $F_{ij}(\mathbf{B})$ determines the consumption rate of each consumer i for each resource j , defined by:

$$F_{ij}(\mathbf{B}) = \frac{\omega_{ij} B_j^q}{B_0^q + d_i B_i B_0 + \sum_{l=\text{resources}} \omega_{il} B_l^q} \quad (\text{eq. 3})$$

where ω_{ij} is the relative preference of consumer i for resource j , q controls the shape of eq. 3 which becomes an intermediate functional response between type II and type III when $q=1.2$ ⁸³. $B0_{ij}$ is the biomass of resource j at which the consumer i achieves half of its maximum consumption rate on resource j , and d_i is the intra-specific interference of consumer i when it forages resource j . In Eq. 2, f_m defines the fraction of the consumer biomass that is respired for maintenance of basal metabolism. F_{max} defines the fraction of biomass i that is removed by small-scale artisanal fisheries. In the case of non-harvested species $F_{max} = 0$

The biological rates of production, R , metabolism, X , and maximum consumption, Y , follow a negative power law with the species body size, with an exponent -1.4[55]:

$$R_P = a_r M_P^{-0.25} \quad (\text{eq. 4})$$

$$X_C = a_x M_C^{-0.25} \quad (\text{eq. 5})$$

$$Y_c = a_y M_C^{-0.25} \quad (\text{eq. 6})$$

Where a_r , a_x , and a_y are allometric constants and the subscripts P and C denote producers and consumers, respectively. The timescale to examine the dynamics of the system is defined based on the primary producer with the highest mass-specific growth rate (reference species). The mass-specific growth rate and the metabolic rate of each species were normalized by the growth rate of the reference species, and the maximum consumption rate was normalized by each species' metabolic rate⁵⁵. These normalizations translate to the following expressions of intrinsic growth rate (r_i), metabolic rate (x_i), and maximum consumption rate (y_i) of each species i :

$$r_i = \frac{R_P}{R_{Pref}} = 1 \left(\frac{M_P}{M_{Pref}} \right)^{-0.25} \quad (\text{eq. 7})$$

$$x_i = \frac{X_C}{R_{Pref}} = \frac{a_x}{a_r} \left(\frac{M_C}{M_{Pref}} \right)^{-0.25} \quad (\text{eq. 8})$$

$$y_i = \frac{Y_C}{X_C} = \frac{a_y}{a_x} \quad (\text{eq. 9})$$

Since most benthic marine communities are characterized by the presence of sessile filter-feeders at the bottom, these communities are heavily ‘subsidized’ by the pelagic phytoplankton, which is captured by filter-feeders and transferred up the benthic food web⁵⁹. In general, phytoplankton dynamics is thought to vary primarily due to ‘external processes’ (e.g. water advection, nutrient loadings, etc.), including climate fluctuations⁵². To account for this phenomenon, our implementation of the ATN model assumed that the intertidal community is permanently subsidized by plankton biomass. Therefore, we modeled plankton dynamic as a primary producer (eq. 1) and following [75, 76] we incorporated a constant subsidy s into the plankton dynamics as:

$$\frac{dB_i}{dt} = d_{local} + s, \quad (\text{eq. 10})$$

where d_{local} represents plankton local dynamics (i.e., right hand of eq. 1).

2.1. Food-web robustness to species extinctions

Using the static and dynamic approaches (see the model above), we evaluated the food-web robustness to species extinctions using four deletion sequences. First, we evaluated the food-web robustness to the extinction of harvested species by removing them in descending order of total catch amount (hereafter “harvesting” deletion sequence), according to the Chilean national fishing service (www.sernapesca.cl). Second, we performed three additional deletion sequences: (1) randomly (hereafter “random” deletion sequence), (2) from the most to the least

connected species (hereafter “most-connected” deletion sequence^{6,16}), and (3) from the most connected species that trophically support highly connected species to the least connected species supporting low connected species¹⁷. This last sequence causes the fastest route of collapse¹⁷ by first deleting the basal species that support most of the species in the food-web (hereafter “supporting-basal” deletion sequence). These last three deletion sequences allow us to compare the food-web sensitivity to the extinction of harvested species with that to the extinction of other species, and to identify the most important species for food-web persistence. For the harvesting deletion sequence, species were removed until all the harvested species were deleted, while for all other sequences the procedure was repeated until all species were removed (including the harvested species). In the case of species with an equal number of interactions, the removed species was chosen at random¹⁵.

To compare the food-web robustness across the different patterns of species deletion, except the “harvesting” deletion sequence, we use the R_{50} index⁶. For the harvesting deletion sequence, only the number of secondary extinctions was registered. The R_{50} index represents the proportion of species that have to be removed to cause the extinction of 50% of the species in the network (including primary and secondary extinctions). The highest and lowest possible values of R_{50} are 0.5 and $1/S$, respectively (S is the number of species in the network), which are reached when no secondary extinctions are caused by species deletions and when only one primary species deletion is needed to cause the extinction of 50% of species, respectively. Thus, larger values of R_{50} mean higher robustness. The static approach was simulated using the R package *NetworkExtinction*⁸⁴, while the dynamical model was simulated using ODE45 in MATLAB.

For the dynamic approach, we first ran the dynamic model for 3650 time-steps which corresponds to 10 years, and ensures that the food-web reached a dynamic equilibrium. Then, we started the removal simulations. In each removal step, the number of extinct species was recorded after 10 years, when the system had reached, again, a steady state. A species was considered extinct if its biomass diminished to less than 10^{-6} [85]. Note that in all deletion sequences we removed the nodes from the food-web, so in the harvesting deletion sequence the F_{\max} parameter in the ATN model is zero to all harvested species.

2.2 Impacts of artisanal fisheries on food-web dynamics

We assessed the impacts of artisanal fisheries on food-web dynamics by simulating simultaneous fishing on all harvested species and assessing the subsequent effects on the biomass of all species in the food-web. We simulated three fishing scenarios, where we applied exploitation rates needed to decrease the biomass of all harvested species in 50%, 80%, and 100% (see F_{\max} in Supplementary Table S2). Note that basal species required much lower exploitation rate to decrease their biomass (see discussion) than filter-feeders, herbivores, and other consumers, which means that harvested basal species were the most sensitive species to fishing. Note also that a biomass decrease of 100% does not necessarily mean that the harvested species go extinct, because the biomass available to be removed by fishing is the biomass that was produced a time step earlier (i.e., fishing exploitation is simulated as part of the population dynamics of harvested species, see eqs. 1 and 2). These three fishing scenarios allowed us to simulate an approximately well managed fisheries (which removes between 40 and 60% of biomass stock²³), an overexploitation scenario (which removes 80%) and nearly extinction scenario, which allowed us to assess overall stability if all harvested species go extinct. For each fishing scenario, we first ran the model for 10 years

(3650 time-steps) to ensure that the system reached a dynamic equilibrium. Then, we applied the biomass removal ($F_{\max i} B_i$ in eqs. 1 and 2) at each time step in the model to all harvested species simultaneously and we ran the food-web dynamics for another 3650 time-steps to reach post perturbation equilibrium, when final biomasses were considered “after perturbation” state.

In each treatment and for each species i , we evaluated the effect of the simulated scenario as:

$$Biomass\ change_i = \left[\left(\frac{after\ perturbation_i}{before\ perturbation_i} \right) - 1 \right] * 100 \quad (eq. 11)$$

2.3. Impacts of plankton subsidy alteration on food-web dynamics

We assume that the food-web is subsidized by an external source, by including a subsidy in the plankton node, which is considered to be controlled by advective processes, unaffected by local benthic consumption. This represents well the situation of most marine benthic ecosystems⁵⁹. To compare the top-down effects of fisheries against bottom-up variation in productivity, we perturbed the plankton subsidy to simulate climate-induced changes in plankton productivity. We simulated both a decrease and an increase in plankton subsidy, as both long-term increased and decreased productivity has been documented to occur in the Humboldt Ecosystem⁵². We used three different perturbation intensities, decreasing or increasing basal subsidy in 50%, 80% and 100%. Note that, a 100% in the basal plankton subsidy decreasing does not translate into plankton extinction (Fig. 3C). A variation of 50% of the basal subsidy is in the order of natural seasonal variability of net primary productivity in central Chile⁴⁹. We assumed that a variation above 50% simulates the effects of extreme changes of plankton subsidy due to climate change, and also, such magnitudes allow

comparable perturbation intensities to those used to assess the impacts of fisheries on the food-web dynamics (see previous section). In each scenario, we first ran the model for 3650 time-steps to ensure that the system reached a dynamic equilibrium, and the final species biomasses obtained were considered “*before perturbation*” state. Then, we reduced/increased plankton subsidy at each time step and ran the model for another 3650 time-steps to reach post perturbation equilibrium. The final biomasses were considered “*after perturbation*” state. Changes in biomass were expressed as shown in Eq.11.

2.4. Interacting effects of fisheries and plankton-subsidy alteration on food-web dynamics

To evaluate combined effects of fisheries and climate-induced changes in plankton subsidy, we simulated both fishing on all harvested species and simultaneously altered plankton subsidy. We used the three fisheries scenarios (i.e., 50%, 80% and 100% biomass removed) and crossed these scenarios with each of the six productivity scenarios (i.e., increasing or decreasing plankton subsidy in 50%, 80% and 100%). In each treatment, we first ran the model for 3650 time-steps and the final species biomasses obtained were considered “*before perturbation*” state. Then, we applied a given plankton subsidy scenario, and at the same time, we started the fishing simulations. Changes in biomass were expressed as shown in Eq.11.

References:

1. Barnosky, A. D. *et al.* Has the Earth’s sixth mass extinction already arrived?. *Nature* **471**, 51–57 (2011).
2. McCauley, D. J. *et al.* Marine defaunation: Animal loss in the global ocean. *Science* **347**, 1255641–1255641 (2015).
3. Chapin III, F. S. *et al.* Consequences of changing biodiversity. *Nature* **405**, 234–242 (2000).
4. Díaz, S., Fargione, J., Chapin, F. S. & Tilman, D. Biodiversity Loss Threatens Human Well-Being. *PLoS Biol.* **4**, e277 (2006).
5. Yodzis, P. The Indeterminacy of Ecological Interactions as Perceived Through Perturbation Experiments. *Ecology* **69**, 508–515 (1988).

6. Dunne, J. A., Williams, R. J. & Martinez, N. D. Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecol. Lett.* **5**, 558–567 (2002).
7. Eklof, A. & Ebenman, B. Species loss and secondary extinctions in simple and complex model communities. *J. Anim. Ecol.* **75**, 239–246 (2006).
8. Brodie, J. F. *et al.* Secondary extinctions of biodiversity. *Trends Ecol. Evol.* **29**, 664–672 (2014).
9. Kuparinen, A., Boit, A., Valdovinos, F. S., Lassaux, H. & Martinez, N. D. Fishing-induced life-history changes degrade and destabilize harvested ecosystems. *Sci. Rep.* **6**, 22245 (2016).
10. Memmott, J. Food webs: a ladder for picking strawberries or a practical tool for practical problems?. *Philos. Trans. R. Soc. B Biol. Sci.* **364**, 1693–1699 (2009).
11. Valdovinos, F. S., Ramos-Jiliberto, R., Flores, J. D., Espinoza, C. & López, G. Structure and dynamics of pollination networks: the role of alien plants. *Oikos* **118**, 1190–1200 (2009).
12. Valdovinos, F. S. Mutualistic networks: moving closer to a predictive theory. *Ecol. Lett.* **22**, 1517–1534 (2019).
13. Pascual, M. & Dunne, J. A. *Ecological Networks: Linking Structure to Dynamics in Food Webs (Santa Fe Institute Studies on the Sciences of Complexity)*. (Oxford University Press, 2006).
14. Curtsdotter, A. *et al.* Robustness to secondary extinctions: Comparing trait-based sequential deletions in static and dynamic food webs. *Basic Appl. Ecol.* **12**, 571–580 (2011).
15. Ramos-Jiliberto, R., Valdovinos, F. S., Moisset de Espanés, P. & Flores, J. D. Topological plasticity increases robustness of mutualistic networks: Interaction rewiring in mutualistic networks. *J. Anim. Ecol.* **81**, 896–904 (2012).
16. Valdovinos, F. S., Moisset de Espanés, P., Flores, J. D. & Ramos-Jiliberto, R. Adaptive foraging allows the maintenance of biodiversity of pollination networks. *Oikos* **122**, 907–917 (2013).
17. Allesina, S. & Pascual, M. Googling Food Webs: Can an Eigenvector Measure Species' Importance for Coextinctions?. *PLoS Comput. Biol.* **5**, e1000494 (2009).
18. de Santana, C., Rozenfeld, A., Marquet, P. & Duarte, C. Topological properties of polar food webs. *Mar. Ecol. Prog. Ser.* **474**, 15–26 (2013).
19. Albert, R., Jeong, H. & Barabási, A. Error and attack tolerance of complex networks. *Nature* **406**, 378–382 (2000).
20. Ives, A. R. & Cardinale, B. J. Food-web interactions govern the resistance of communities after non-random extinctions. *Nature* **429**, 174–177 (2004).
21. Rebolledo, R., Navarrete, S. A., Kéfi, S., Rojas, S. & Marquet, P. A. An open-system approach to complex biological networks. *SIAM J. Appl. Math.* **79**, 619–640 (2019).
22. McCann, K. S. The diversity–stability debate. *Nature* **405**, 228–233 (2000).
23. Worm, B. *et al.* Rebuilding Global Fisheries. *Science* **325**, 578–585 (2009).
24. Defeo, O. & Castilla, J. C. More than One Bag for the World Fishery Crisis and Keys for Co-management Successes in Selected Artisanal Latin American Shellfisheries. *Rev. Fish Biol. Fish.* **15**, 265–283 (2005).
25. Pauly, D. & Zeller, D. Catch reconstructions reveal that global marine fisheries catches are higher than reported and declining. *Nat. Commun.* **7**, 10244 (2016).

26. Defeo, O. *et al.* Co-management in Latin American small-scale shellfisheries: assessment from long-term case studies. *Fish Fish.* **17**, 176–192 (2016).
27. Gelcich, S. *et al.* Fishers' perceptions on the Chilean coastal TURF system after two decades: problems, benefits, and emerging needs. *Bull. Mar. Sci.* **93**, 53–67 (2017).
28. Castilla, J. C., Gelcich, S. & Defeo, O. Successes, Lessons, and Projections from Experience in Marine Benthic Invertebrate Artisanal Fisheries in Chile. in *Fisheries Management* (eds. McClanahan, T. R. & Castilla, J. C.) 23–42 (Blackwell Publishing Ltd, 2007). doi:10.1002/9780470996072.ch2.
29. Gelcich, S. *et al.* Navigating transformations in governance of Chilean marine coastal resources. *Proc. Natl. Acad. Sci.* **107**, 16794–16799 (2010).
30. Kéfi, S. *et al.* Network structure beyond food webs: mapping non-trophic and trophic interactions on Chilean rocky shores. *Ecology* **96**, 291–303 (2015).
31. Pérez-Matus, A. *et al.* Temperate rocky subtidal reef community reveals human impacts across the entire food web. *Mar. Ecol. Prog. Ser.* **567**, 1–16 (2017).
32. Pérez-Matus, A., Carrasco, S. A., Gelcich, S., Fernandez, M. & Wieters, E. A. Exploring the effects of fishing pressure and upwelling intensity over subtidal kelp forest communities in Central Chile. *Ecosphere* **8**, e01808 (2017).
33. Gelcich, S. *et al.* Territorial User Rights for Fisheries as Ancillary Instruments for Marine Coastal Conservation in Chile: *Gelcich et al.* *Conserv. Biol.* **26**, 1005–1015 (2012).
34. Oyanedel, R., Keim, A., Castilla, J. C. & Gelcich, S. Illegal fishing and territorial user rights in Chile: Illegal Fishing. *Conserv. Biol.* **32**, 619–627 (2018).
35. Donlan, C. J., Wilcox, C., Luque, G. M. & Gelcich, S. Estimating illegal fishing from enforcement officers. *Sci. Rep.* **10**, 12478 (2020).
36. Andreu-Cazenave, M., Subida, M. D. & Fernandez, M. Exploitation rates of two benthic resources across management regimes in central Chile: Evidence of illegal fishing in artisanal fisheries operating in open access areas. *PLOS ONE* **12**, e0180012 (2017).
37. Castilla, J. C. Coastal marine communities: trends and perspectives from human-exclusion experiments. *Trends Ecol. Evol.* **14**, 280–283 (1999).
38. Somero, G. N. The physiology of climate change: how potentials for acclimatization and genetic adaptation will determine 'winners' and 'losers'. *J. Exp. Biol.* **213**, 912–920 (2010).
39. Hoegh-Guldberg, O. & Bruno, J. F. The Impact of Climate Change on the World's Marine Ecosystems. *Science* **328**, 1523–1528 (2010).
40. Brose, U. *et al.* Climate change in size-structured ecosystems. *Philos. Trans. R. Soc. B Biol. Sci.* **367**, 2903–2912 (2012).
41. Doney, S. C. *et al.* Climate Change Impacts on Marine Ecosystems. *Annu. Rev. Mar. Sci.* **4**, 11–37 (2012).
42. Kwiatkowski, L., Aumont, O. & Bopp, L. Consistent trophic amplification of marine biomass declines under climate change. *Glob. Change Biol.* **25**, 218–229 (2019).
43. Bakun, A. Coastal Ocean Upwelling. *Science* **247**, 198–201 (1990).
44. Bakun, A., Field, D. B., Redondo-Rodriguez, A. & Weeks, S. J. Greenhouse gas, upwelling-favorable winds, and the future of coastal ocean upwelling ecosystems. *Glob. Change Biol.* **16**, 1213–1228 (2010).

45. Thiel, M. *et al.* The Humboldt current system of northern and central Chile: oceanographic processes, ecological interactions and socioeconomic feedback. in *Oceanography and Marine Biology* (eds. Gibson, R., Atkinson, R. & Gordon, J.) vol. 20074975 195–344 (CRC Press, 2007).
46. Morales, C., Hormazabal, S., Andrade, I. & Correa-Ramirez, M. Time-Space Variability of Chlorophyll-a and Associated Physical Variables within the Region off Central-Southern Chile. *Remote Sens.* **5**, 5550–5571 (2013).
47. Aiken, C. M., Navarrete, S. A. & Pelegrí, J. L. Potential changes in larval dispersal and alongshore connectivity on the central Chilean coast due to an altered wind climate. *J. Geophys. Res.* **116**, G04026 (2011).
48. Blanchard, J. L. *et al.* Potential consequences of climate change for primary production and fish production in large marine ecosystems. *Philos. Trans. R. Soc. B Biol. Sci.* **367**, 2979–2989 (2012).
49. Testa, G., Masotti, I. & Farías, L. Temporal variability in net primary production in an upwelling area off central Chile (36°S). *Front. Mar. Sci.* **5**, 179 (2018).
50. Batten, S. D. *et al.* A Global Plankton Diversity Monitoring Program. *Front. Mar. Sci.* **6**, 321 (2019).
51. Chust, G. *et al.* Biomass changes and trophic amplification of plankton in a warmer ocean. *Glob. Change Biol.* **20**, 2124–2139 (2014).
52. Weidberg, N. *et al.* Spatial shifts in productivity of the coastal ocean over the past two decades induced by migration of the Pacific Anticyclone and Bakun’s effect in the Humboldt Upwelling Ecosystem. *Glob. Planet. Change* **193**, 103259 (2020).
53. Aguirre, C., García-Loyola, S., Testa, G., Silva, D. & Farias, L. Insight into anthropogenic forcing on coastal upwelling off south-central Chile. *Elem Sci Anth* **6**, 59 (2018).
54. Yodzis, P. & Innes, S. Body Size and Consumer-Resource Dynamics. *Am. Nat.* **139**, 1151–1175 (1992).
55. Brose, U., Williams, R. J. & Martinez, N. D. Allometric scaling enhances stability in complex food webs. *Ecol. Lett.* **9**, 1228–1236 (2006).
56. Dunne, J. A. *et al.* The roles and impacts of human hunter-gatherers in North Pacific marine food webs. *Sci. Rep.* **6**, 21179 (2016).
57. Binzer, A., Guill, C., Rall, B. C. & Brose, U. Interactive effects of warming, eutrophication and size structure: impacts on biodiversity and food-web structure. *Glob. Change Biol.* **22**, 220–227 (2016).
58. Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M. & West, G. B. Toward a metabolic theory of ecology. *Ecology* **85**, 1771–1789 (2004).
59. Menge, B. A. & Menge, D. N. L. Dynamics of coastal meta-ecosystems: the intermittent upwelling hypothesis and a test in rocky intertidal regions. *Ecol. Monogr.* **83**, 283–310 (2013).
60. Jackson, J. B. C. Historical Overfishing and the Recent Collapse of Coastal Ecosystems. *Science* **293**, 629–637 (2001).
61. Pauly, D. Fishing Down Marine Food Webs. *Science* **279**, 860–863 (1998).
62. Jordán, F., Okey, T. A., Bauer, B. & Libralato, S. Identifying important species: Linking structure and function in ecological networks. *Ecol. Model.* **216**, 75–80 (2008).

63. Camus, P. A., Arancibia, P. A. & Ávila-Thieme, M. I. A trophic characterization of intertidal consumers on Chilean rocky shores. *Rev. Biol. Mar. Oceanogr.* **48**, 431–450 (2013).
64. Lopez, D. N., Camus, P. A., Valdivia, N. & Estay, S. A. High temporal variability in the occurrence of consumer-resource interactions in ecological networks. *Oikos* **126**, 1699–1707 (2017).
65. Arim, M. & Marquet, P. A. Intraguild predation: a widespread interaction related to species biology: Intraguild predation. *Ecol. Lett.* **7**, 557–564 (2004).
66. Castilla, J. C. & Fernandez, M. Small-scale benthic fisheries in Chile: on co-management and sustainable use of benthic invertebrates. *Ecol. Appl.* **8**, S124–S132 (1998).
67. Teagle, H., Hawkins, S. J., Moore, P. J. & Smale, D. A. The role of kelp species as biogenic habitat formers in coastal marine ecosystems. *J. Exp. Mar. Biol. Ecol.* **492**, 81–98 (2017).
68. Vásquez, J. A. The Brown Seaweeds Fishery in Chile. in *Fisheries and Aquaculture in the Modern World* (ed. Mikkola, H.) (InTech, 2016). doi:10.5772/62876.
69. Belmadani, A., Echevin, V., Codron, F., Takahashi, K. & Junquas, C. What dynamics drive future wind scenarios for coastal upwelling off Peru and Chile?. *Clim. Dyn.* **43**, 1893–1914 (2014).
70. Wang, Y., Luo, Y., Lu, J. & Liu, F. Changes in ENSO amplitude under climate warming and cooling. *Clim. Dyn.* **52**, 1871–1882 (2019).
71. Cai, W. *et al.* Increased variability of eastern Pacific El Niño under greenhouse warming. *Nature* **564**, 201–206 (2018).
72. Cai, W. *et al.* Increased frequency of extreme La Niña events under greenhouse warming. *Nat. Clim. Change* **5**, 132–137 (2015).
73. Fussmann, K. E., Schwarzmüller, F., Brose, U., Jousset, A. & Rall, B. C. Ecological stability in response to warming. *Nat. Clim. Change* **4**, 206–210 (2014).
74. Hays, G., Richardson, A. & Robinson, C. Climate change and marine plankton. *Trends Ecol. Evol.* **20**, 337–344 (2005).
75. Jochum, M., Schneider, F. D., Crowe, T. P., Brose, U. & O’Gorman, E. J. Climate-induced changes in bottom-up and top-down processes independently alter a marine ecosystem. *Philos. Trans. R. Soc. B Biol. Sci.* **367**, 2962–2970 (2012).
76. Hallegraeff, G. M. A review of harmful algal blooms and their apparent global increase. *Phycologia* **32**, 79–99 (1993).
77. Morgan, S. G., Fisher, J. L., Miller, S. H., McAfee, S. T. & Largier, J. L. Nearshore larval retention in a region of strong upwelling and recruitment limitation. *Ecology* **90**, 3489–3502 (2009).
78. Ospina-Alvarez, A., Weidberg, N., Aiken, C. M. & Navarrete, S. A. Larval transport in the upwelling ecosystem of central Chile: The effects of vertical migration, developmental time and coastal topography on recruitment. *Prog. Oceanogr.* **168**, 82–99 (2018).
79. Sakai, A. K. *et al.* The population biology of invasive species. *Annu. Rev. Ecol. Syst.* **32**, 305–332 (2001).
80. Thierry, A. *et al.* Adaptive foraging and the rewiring of size-structured food webs following extinctions. *Basic Appl. Ecol.* **12**, 562–570 (2011).

81. Valdovinos, F. S., Ramos-Jiliberto, R., Garay-Narváez, L., Urbani, P. & Dunne, J. A. Consequences of adaptive behaviour for the structure and dynamics of food webs: adaptive behaviour in food webs. *Ecol. Lett.* **13**, 1546–1559 (2010).
82. Richard, J. W., Brose, U. & Martinez, N. D. Homage to Yodzis and Innes 1992: Scaling up feeding-based population dynamics to complex ecological networks. in *From Energetics to Ecosystems: The Dynamics and Structure of Ecological Systems* 37–51 (Springer Netherlands, 2006). doi:10.1007/978-1-4020-5337-5_2.
83. Williams, R. J. Effects of network and dynamical model structure on species persistence in large model food webs. *Theor. Ecol.* **1**, 141–151 (2008).
84. Ávila-Thieme, M. I., Corcoran, D., Valdovinos, F. S., Navarrete, S. A. & Marquet, P. A. *NetworkExtinction: Extinction Simulation in Food Webs*. (R package version 0.1.3., 2018).
85. Schneider, F. D., Brose, U., Rall, B. C. & Guill, C. Animal diversity and ecosystem functioning in dynamic food webs. *Nat. Commun.* **7**, 12718 (2016).
86. Williams, Rich J. Network 3D: visualizing and modelling food webs and other complex networks. *Microsoft Res. Camb. UK* (2010).

FIGURES

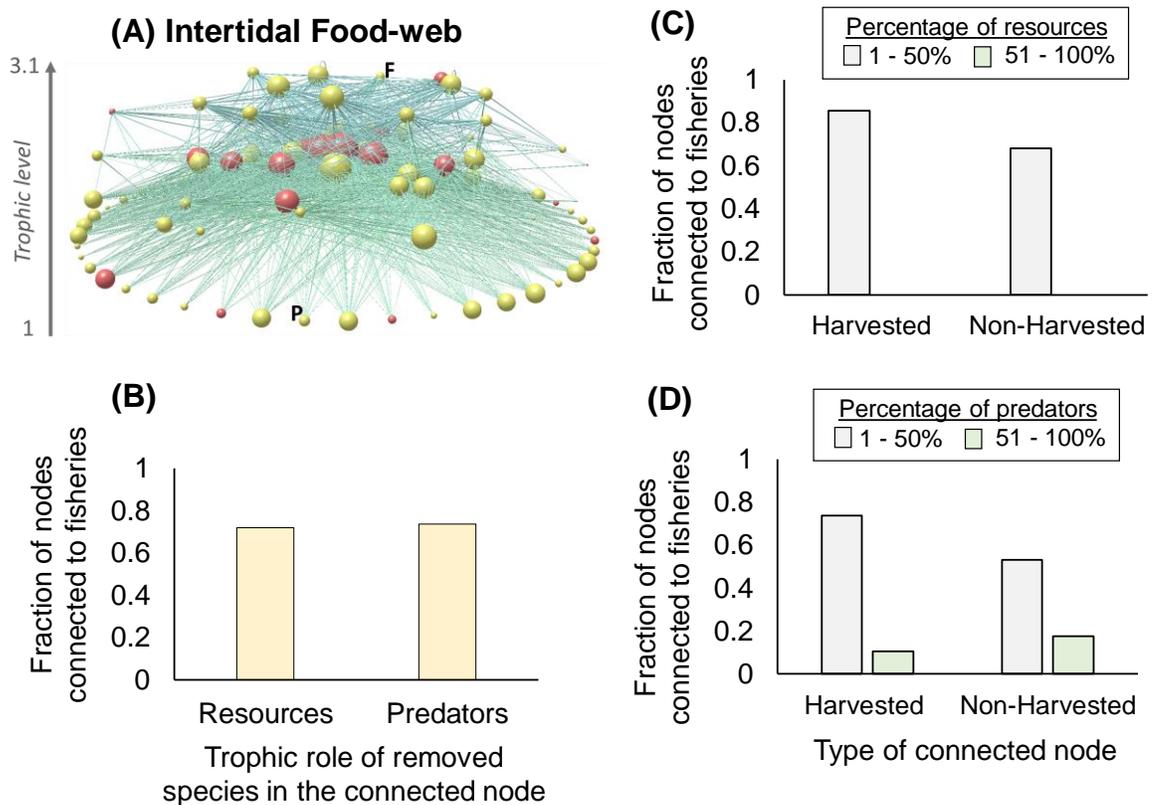


Figure 1. (A) Intertidal food-web. Node colors represent harvested (red) and non-harvested (yellow) species. Letter F and P represent the fisheries and plankton node, respectively. Node size represents the number of trophic interactions (degree) of each node. Nodes at the bottom represent basal species, while nodes at the top represent top predators. Y-axis represents trophic level (calculated as SWTL, see Methods). Drawn using Network3D software⁸⁶. (B) Fraction of species in the food web that are trophically connected (at least once) with exploited species that are either a resource and/or a predator (x-axis). Each bar presented in (B) is further divided in: (C) the percentage of resources shared with fisheries by the harvested and non-harvested consumers of the food-web, and (D) the percentage of predators of harvested and non-harvested species extracted by fisheries. Grey and green bars, respectively, represent the categories of 1-50% and 51-100% of the resource species consumed by harvested and non-harvested species (C) and of the consumer species preying upon harvested and non-harvested species (D).

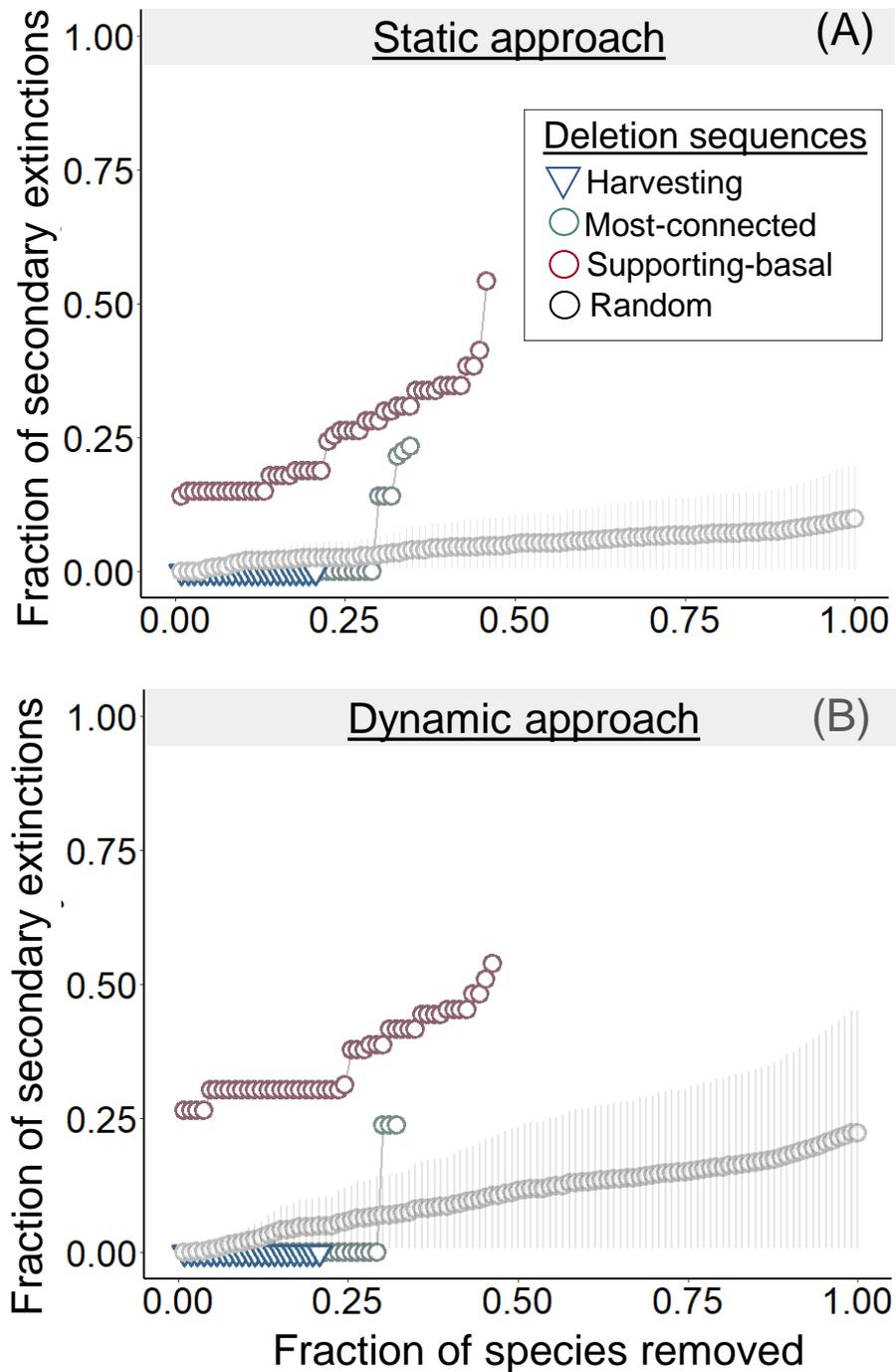


Figure 2. Fraction of secondary extinctions (y-axis) produced by the sequential removal of species (x-axis) with static (A) and dynamic (B) approaches. Gray and red circles represent most-connected and supporting-basal deletion sequences, while blue triangle represents harvesting deletion sequence. In the random deletion sequence, circles represent the average and the error bars represent the 95% confidence interval over 1000 simulations.

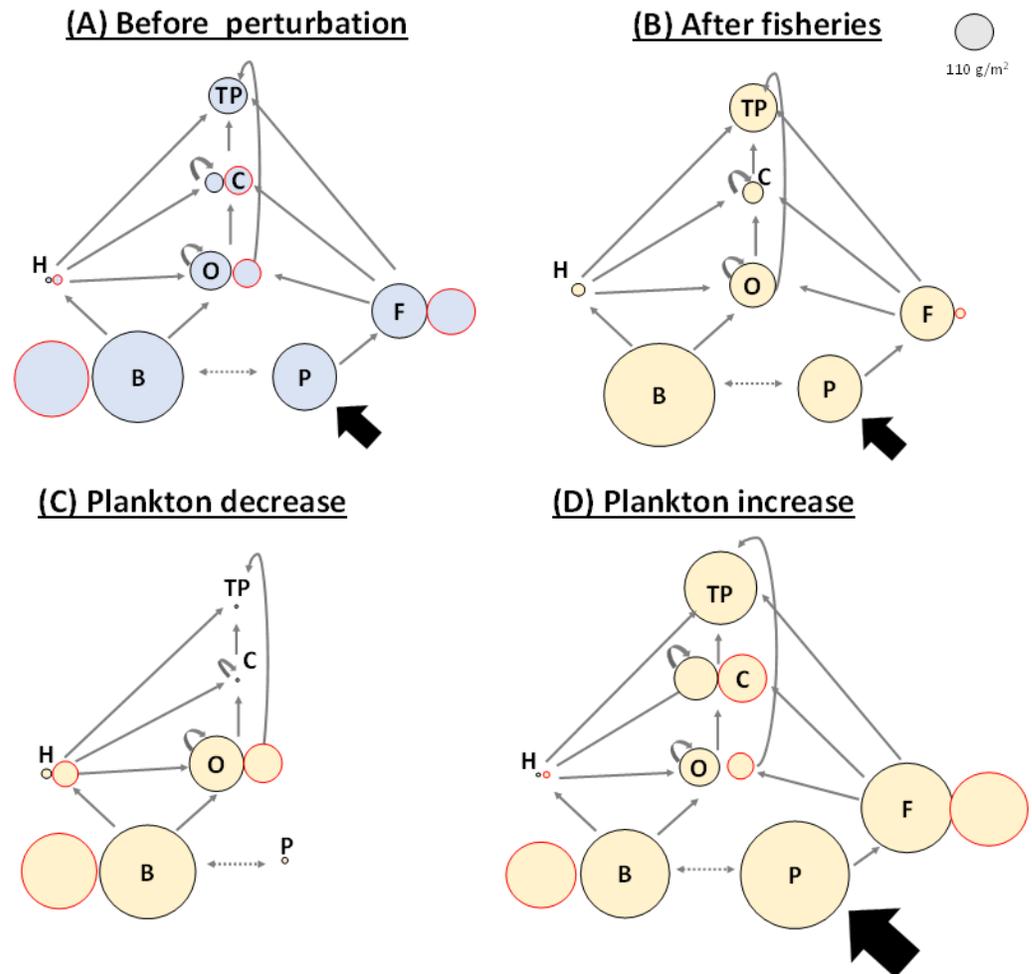


Figure 3. Diagram illustrating the effect of fisheries (B) and the effect of perturbing plankton subsidy (C and D) on food-web dynamics. Nodes represent the total biomass of each trophic level before (A) and after reducing in 100% the biomass of all harvested species (B) and after decreasing (C) or increasing (D) plankton subsidy in 100%. Each trophic level is indicated by TP: top predators, C: carnivores, O: omnivores, H: herbivores, F: filters-feeders, B: basal species, and P: plankton. Red and black outlined nodes represent the biomass of harvested and non-harvested species, respectively. Solid black, solid grey, and dashed grey arrows represent the plankton subsidy (7355 g/m²), the trophic interactions, and competitive interactions, respectively. Note that the ATN model explicitly models competition only between basal species, while competition between consumers emerges from the depletion of shared resources.

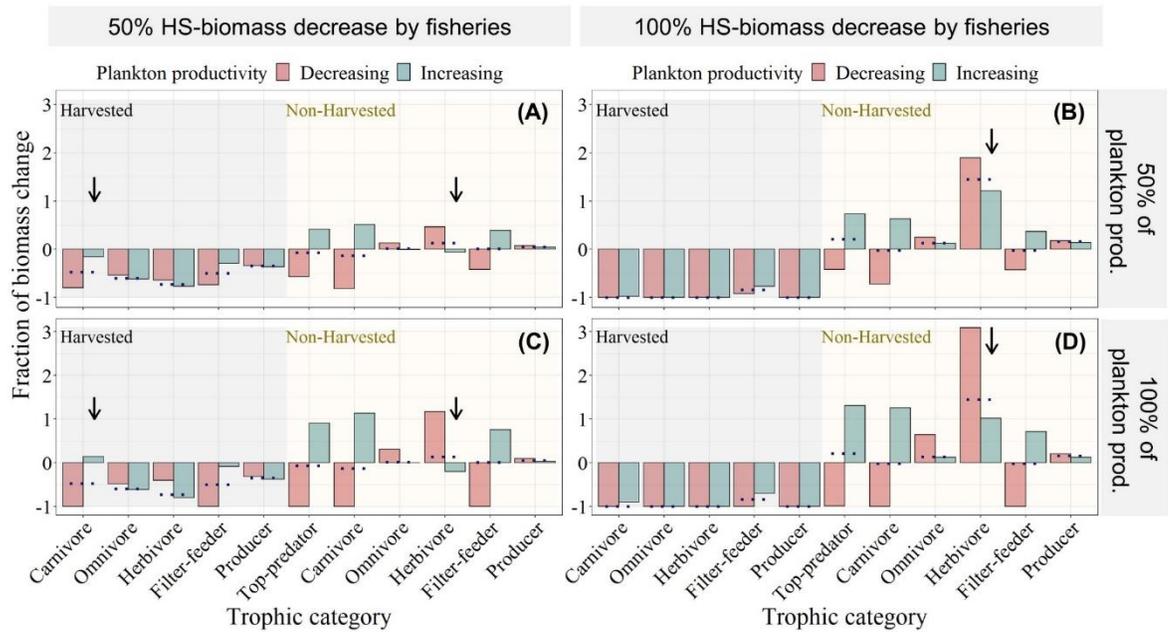


Figure 4. Combined effects of artisanal fisheries and plankton-productivity alterations on food-web dynamics. Fraction of total biomass change (y-axis) of each trophic category (x-axis) after decreasing (red bars) and increasing (blue bars) the plankton productivity (PP) in 50% (A and B) and 100% (C and D), and after decreasing the biomass of all harvested species (HS) in a 50% (A and C) and in a 100% (B and D). The grey and yellow shading represent the biomass change of harvested and non-harvested species, respectively. The arrows highlight the most remarkable changes between the two levels of plankton subsidy perturbation and the two levels of fishing. The dotted lines represent the independent effect fishing (i.e., without plankton subsidy perturbation) on the biomass of each trophic category as a reference point.

INFORMACIÓN SUPPLEMENTARIA (CAPÍTULO 2)

COASTAL PRODUCTIVITY CHANGES DRIVEN BY ENVIRONMENTAL FLUCTUATION WOULD NEGATIVELY AFFECT COASTAL SOUTH PACIFIC FOOD-WEBS MORE STRONGLY THAN ARTISANAL FISHERIES

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Food-web description

We studied the food-web of the intertidal rocky-shore ecosystem of central Chile. This food-web is influenced by the highly productive Humboldt Current System¹ (HCS) and harvested exclusively by small scale artisanal fisheries². The web represents all species that are found to co-occur on wave exposed rocky platforms of central Chile, from the very low to the highest intertidal and is composed of 107 species (including fisheries node), with 44% of its species corresponding to primary producers, 53% to invertebrates, and 3% to endotherm vertebrates³. A total of 1381 consumption type interactions have been documented in the web, with approximately linear increase in species degree (number of interactions per node) and species rank³, and connectance of 0.12. In the food-web, we consider as basal level all species of benthic primary producers (e.g. algae) plus plankton (phytoplankton + zooplankton, single node). Therefore, we represented filter-feeders (sessile filter-feeders + porcenallidae crabs) as specialist consumers of plankton and not as a basal species, which could be alternative approach if they were not connected with the plankton. Benthic diatoms were considered as an independent node, separate from plankton. Detailed methods and general description of food web attributes, as well as patterns of spatial variability can be found in [3–5].

Relative importance of harvested species for the food-web structure

Using the static approach (without population dynamics), we compared the structure of the food-web with and without the harvested species to the distribution of 1000 food-web structures produced by randomly removing the same amount of harvested species. This comparison used: number of species (S), number of trophic links (L), connectance (L/S^2), number of omnivores, and averaged trophic level (MeanSWTL). We calculated all these structural metrics using `cheddar` package in R. After removing all harvested species using our static approach, the food-web resulted in lower link density (L/S , where L and S are numbers of trophic interactions and species, respectively) and connectance ($C = L/S^2$) than removing the same number of species at random (Table S3). This decrease in connectance is counter-intuitive because the pure removal of species should increase connectance based on its mathematical definition. Therefore, this result shows that disproportionately more interactions than species are lost with the removal of harvested species. In addition, the removal of harvested species decreased the fraction of omnivore species and the mean trophic level but this decrease is not different to that produced by the random removal of the same number of species (Table S3), suggesting that the impact of artisanal fisheries may not be strong enough to destabilize⁶ and shorten⁷ the intertidal food-web. Finally, the number of secondary extinctions produced by the removal of harvested species was less than the average number of secondary extinctions obtained when removing the same number of species but selected at random (Table S3). These results reinforce the observation that artisanal fisheries share prey with other consumers that also forage on other non-harvested species in the food-web, so alternative resources remain when all harvested species go extinct.

Model Parametrization

Supplementary Table S4 shows all the model parameters with their initial values and descriptions. We used empirical measures of species body size, which was extracted from [3], to allometrically parameterize intrinsic growth rate of autotroph, as well as metabolic rate, and maximum consumption rate of each species (see Methods in main text).

The initial biomass was estimated from density (mobile species + cnidaria) and the surface cover (sessile species) recorded during six years of sampling in the Chilean marine reserve “Estacion Costera de Investigaciones Marinas” (ECIM) at the central-south of Chile. The density of mobile species was multiplied by the species average body size. For sessile species, the surface cover was multiplied by the weight of each species per unit of cover (e.g. [8]).

We calculated the community-level carrying capacity, K , by dividing all the primary producers into six functional groups (microalgae, ephemerals, corticates, crust, corallines, and kelps)⁴. In each functional group, we multiplied the biomass of the species exhibiting the highest growth rate with the number of species that compose its functional group. Finally, we summed the resulting biomass over all functional groups.

Based on empirical experiments in aquatic⁹ and terrestrial ecosystems¹⁰, we assumed that the half-saturation density parameter (B_0) decreases while the trophic levels increase in 10^3 order of magnitude. We use the values of Boit et al.¹¹ as a reference value. To herbivores, we fit the B_0 to ensure their persistence. For the other parameters, we used values from Calbet, A. & Saiz⁹ (see Supplementary Table S4).

References:

1. Thiel, M. *et al.* The Humboldt current system of northern and central Chile: oceanographic processes, ecological interactions and socioeconomic feedback. in *Oceanography and Marine Biology* (eds. Gibson, R., Atkinson, R. & Gordon, J.) vol. 20074975 195–344 (CRC Press, 2007).
2. Gelcich, S. *et al.* Navigating transformations in governance of Chilean marine coastal resources. *Proceedings of the National Academy of Sciences* **107**, 16794–16799 (2010).
3. Kéfi, S. *et al.* Network structure beyond food webs: mapping non-trophic and trophic interactions on Chilean rocky shores. *Ecology* **96**, 291–303 (2015).
4. Kéfi, S., Miele, V., Wieters, E. A., Navarrete, S. A. & Berlow, E. L. How Structured Is the Entangled Bank? The Surprisingly Simple Organization of Multiplex Ecological Networks Leads to Increased Persistence and Resilience. *PLoS Biol* **14**, e1002527 (2016).
5. Lurgi, M. *et al.* Geographical variation of multiplex ecological networks in marine intertidal communities. *Ecology* (2020) doi:10.1002/ecy.3165.
6. Kuparinen, A., Boit, A., Valdovinos, F. S., Lassaux, H. & Martinez, N. D. Fishing-induced life-history changes degrade and destabilize harvested ecosystems. *Sci Rep* **6**, 22245 (2016).
7. Pauly, D. Fishing Down Marine Food Webs. *Science* **279**, 860–863 (1998).
8. Wieters, E. A., Broitman, B. R. & Brancha, G. M. Benthic community structure and spatiotemporal thermal regimes in two upwelling ecosystems: Comparisons between South Africa and Chile. *Limnol. Oceanogr.* **54**, 1060–1072 (2009).
9. Calbet, A. & Saiz, E. Effects of trophic cascades in dilution grazing experiments: from artificial saturated feeding responses to positive slopes. *Journal of Plankton Research* **35**, 1183–1191 (2013).
10. Mulder, C. & Hendriks, A. J. Half-saturation constants in functional responses. *Global Ecology and Conservation* **2**, 161–169 (2014).
11. Boit, A., Martinez, N. D., Williams, R. J. & Gaedke, U. Mechanistic theory and modelling of complex food-web dynamics in Lake Constance: Mechanistic modelling of complex food web dynamics. *Ecology Letters* **15**, 594–602 (2012).
12. Gómez-Canchong, P., Quiñones, R. A. & Brose, U. Robustness of size–structure across ecological networks in pelagic systems. *Theor Ecol* **6**, 45–56 (2013).
13. Brose, U., Williams, R. J. & Martinez, N. D. Allometric scaling enhances stability in complex food webs. *Ecol Letters* **9**, 1228–1236 (2006).
14. Testa, G., Masotti, I. & Farías, L. Temporal variability in net primary production in an upwelling area off central Chile (36°S). *Front. Mar. Sci.* **5**, 179 (2018).
15. Williams, Rich J. Network 3D: visualizing and modelling food webs and other complex networks. *Microsoft Research, Cambridge, UK* (2010).

Tables

Table S1. Rank of the 30 most connected species of the intertidal food-web

Rank	Species name	Harvested	Total degree
1	<i>Fissurella limbata</i>	yes	67
2	<i>Fissurella crassa</i>	yes	63
3	<i>Acanthopleura echinata</i>	yes	60
4	<i>Fissurella costata</i>	yes	60
5	<i>Chiton granosus</i>	yes	59
6	<i>Chiton latus</i>	no	57
7	<i>Chiton cummingii</i>	no	56
8	<i>Enoplochiton niger</i>	no	56
9	<i>Chaetopleura peruviana</i>	no	52
10	<i>Fissurella cummingii</i>	yes	47
11	<i>Heliaster helianthus</i>	no	43
12	<i>Scurria araucana</i>	no	41
13	<i>Siphonaria lesoni</i>	no	41
14	Gulls	no	41
15	<i>Acanthocyclus gayi</i>	no	40
16	<i>Fissurella maxima</i>	yes	39
17	<i>Tegula atra</i>	yes	39
18	<i>Tonicia benaventii</i>	no	39
19	<i>Tonicia chilensis</i>	no	39
20	<i>Tonicia elegans</i>	no	39
21	<i>Scurria ceciliana</i>	no	38
22	<i>Scurria variabilis</i>	no	38
23	<i>Fissurella picta</i>	yes	37
24	<i>Fissurella puhlcræ</i>	yes	37
25	<i>Scurria plana</i>	no	37
26	<i>Scurria viridula</i>	no	37
27	<i>Acanthocyclus hassleri</i>	no	36
28	<i>Balanus laevis</i>	no	36
29	<i>Nothobalanus flosculus</i>	no	36
30	<i>Lottia orbigny</i>	no	35

Table S2. F_{\max} values used to produce the total biomass decrease of the harvested basal species, harvested filter-feeders, and the other harvested species in a 50%, 80% and 100%. $F_{\max} = 0.001$ means that fisheries remove 0.1% of the available biomass of the harvested species; while $F_{\max} = 1$ means that fisheries remove 100% of the available biomass of the harvested species.

Type of harvested species	Biomass decrease of interest in harvested species	F_{\max} value that produce the biomass decrease of interest
Basal species	50%	0.00125
	80%	0.0022
	100%	0.01
Filter-feeders and herbivores	50%	0.23
	80%	0.8
	100%	1
Others consumers	50%	0.23
	80%	0.8
	100%	1

Table S3. Structural properties of the intertidal food-web before and after removing all 22 harvested species (i.e., “After non-random removal”), and after removing the same number of species randomly (i.e., “After random removal”). The “After random removal” column shows the mean and 95% confidence interval of structural property values of 1000 iterations of randomly removing 22 species out of the 107 species in the food-web. The fourth column represents the percentage of change of each structural property, calculated as [(“after non-random removal” – “before any species removal”)/ “before any species removal”]. The sixth column indicate whether the change of the structural properties produced by the loss of harvested species (non-random deletion) is different to the changes produced by random deletions. SWTLMean is the short-weighted trophic level of a food-web.

Structural property	Before any species removal	After non-random removal	Percentage of change (%)	After random removal	Non-random vs random removal
Richness	107	85	-21	82 ± 0.4	≠
Number of links	1381	718	-48	819 ± 6	≠
Connectance	0.12	0.10	-18	0.13 ± 0	≠
%-Omnivore	37	32	-12	32 ± 0	=
MeanSWTL	1.64	1.62	-1	1.62 ± 0.01	=

Table S4. Initial parameter values used in our version of the Allometric Trophic Network (ATN) model. In references column ECIM refers to the coastal marine research station of the Pontificia Universidad Catolica de Chile.

Parameter	Unit of measurement	Definition	Initial values min., max	References
B	g / m ²	Population abundance	1.26 x 10 ⁻⁴ , 112107	Empirical values from ECIM, Diatoms, and Plankton values from [12]
M	g	Body mass	1 x 10 ⁻⁵ , 500	[3]
r	1 / day	Mass-specific growth rate of basal species	0.1075, 3.76	Calculated using [13]
x	1 / day	Mass-specific metabolic rate of consumers	0.7284, 70.96	Calculated using [13]
y	-	Maximum consumption rate	1, 5.8	Calculated using [13]
K	g / m ²	Carrying capacity of basal species	176299	K adapted from [11]
c	-	Competition coefficient of basal species	1	[11]
fa	-	The fraction of biomass that is assimilated from consumer	0.4	[11]
fm	-	The fraction of biomass that is respired to metabolic maintenance	0.1	[11]

e	-	Assimilation efficiency	0.45, 0.85	[13]
d	m^2 / g	Intra-specific interference	0.5	[11]
q	-	Functional response	1.2	[11]
w	-	Resources preference	$1/n_{\text{resources}}$	[11]
p	-	Fractions of shared resources	0, 1	[11]
B0	g / m^2	Half-saturation density	150, 15000	Adapted from [11]
s	g / m^2	The subsidy that is considered in plankton dynamic.	12% of the initial biomass	[14]

Table S5. Species name corresponding to the species number shown in the x-axis of Supplementary Figs. S2 and S4.

Code	Specie Name	Code	Specie Name	Code	Specie Name
1	<i>Acanthina monodon</i>	47	<i>Scurria viridula</i>	93	<i>Peysoneilla</i> spp.
	<i>Concholepas</i>				<i>Plocamium</i>
2	<i>concholepas</i>	48	<i>Scurria zebrina</i>	94	<i>cartilagineum</i>
	<i>Acanthopleura</i>				
3	<i>echinata</i>	49	<i>Siphonaria lessoni</i>	95	<i>Prionitis</i> spp.
			<i>Echinolittorina</i>		<i>Gastroclonium</i>
4	<i>Chiton granosus</i>	50	<i>peruviana</i>	96	<i>cylindricum</i>
			<i>Austrolittorina</i>		
5	<i>Fissurella costata</i>	51	<i>araucana</i>	97	<i>Rhodymenia</i> sp.
6	<i>Fissurella crassa</i>	52	<i>Onchidella</i> sp.	98	<i>Schottera nicaensis</i>
7	<i>Fissurella cummingi</i>	53	<i>Balanus laevis</i>	99	<i>Schyzimonia doryophora</i>
8	<i>Fissurella limbata</i>	54	<i>Jhelius cirratus</i>	100	<i>Trematocarpus</i> spp.
					<i>Corallina officinalis</i> var.
9	<i>Fissurella maxima</i>	55	<i>Nothobalanus flosculus</i>	101	Chilensis
			<i>Nothochthamalus</i>		<i>Hildenbrandia</i>
10	<i>Fissurella picta</i>	56	<i>scabrosus</i>	102	<i>lecanelierii</i>
			<i>Brachidontes</i>		
11	<i>Fissurella puhlcræ</i>	57	<i>granulata</i>	103	<i>Lithothamnion</i> spp.
			<i>Perumytilus</i>		
12	<i>Scurria scurra</i>	58	<i>purpuratus</i>	104	<i>Ralfsia californica</i>
13	<i>Tegula atra</i>	59	<i>Semimytilus algosus</i>	105	Benthic diatoms
	<i>Austromegabalanus</i>		<i>Allelopetrolisthes</i>		
14	<i>psittacus</i>	60	<i>punctatus</i>	106	Plankton
15	<i>Pyura chilensis</i>	61	<i>Petrolisthes spinifrons</i>		
16	<i>Durvillaea antarctica</i>	62	<i>Petrolisthes angulosus</i>		
			<i>Petrolisthes</i>		
17	<i>Lessonia nigrescens</i>	63	<i>tuberculatus</i>		
			<i>Petrolisthes</i>		
18	<i>Gelidium rex</i>	64	<i>tuberculosis</i>		
19	<i>Sarcothalia</i> spp.	65	<i>Phragmatopoma</i> spp.		
	<i>Mazzaella</i>				
20	<i>laminarioides</i>	66	<i>Bryopsis</i> spp.		
21	<i>Pyropia</i> spp.	67	<i>Centroceras</i> spp.		
22	<i>Ulva rigida</i>	68	<i>Ceramium</i> spp.		
23	Gulls	69	<i>Chaetomorpha</i> spp.		
	<i>Cinclodes</i>				
24	<i>nigrofumosus</i>	70	<i>Cladophora</i> spp.		

25	<i>Anthotoe</i> spp.	71	<i>Ectocarpus silicosus</i>
			<i>Enteromorpha</i>
26	<i>Bunodactis</i> spp.	72	<i>compressa</i>
27	<i>Oulactis concinnata</i>	73	<i>Halopteris funicularis</i>
28	<i>Parantheopsis</i> spp.	74	<i>Polysiphonia</i> spp.
			<i>Rhizoclonium</i>
29	<i>Phymactis</i> spp.	75	<i>ambiguum</i>
	<i>Trimusculus</i>		<i>Scythosiphon</i>
30	<i>peruvianus</i>	76	<i>lomentaria</i>
31	<i>Heliaster helianthus</i>	77	<i>Ulvella</i> spp.
32	<i>Stichaster striatus</i>	78	<i>Adenocystis utricularis</i>
33	<i>Acanthocyclus gayi</i>	79	<i>Ahnfeltiopsis</i> spp.
			<i>Chondrus</i>
34	<i>Acanthocyclus hassleri</i>	80	<i>canaliculatus</i>
	<i>Chaetopleura</i>		
35	<i>peruviana</i>	81	<i>Codium dimorpha</i>
			<i>Colpomenia</i>
36	<i>Chiton cummingsi</i>	82	<i>phaeodactyla</i>
37	<i>Chiton latus</i>	83	<i>Colpomenia sinuosa</i>
38	<i>Enoplochiton niger</i>	84	<i>Gelidium</i> spp.
39	<i>Tonicia lineolata</i>	85	<i>Glossophora kunthii</i>
40	<i>Tonicia chilensis</i>	86	<i>Grateloupia</i> spp.
			<i>Gymnogongrus</i>
41	<i>Tonicia elegans</i>	87	<i>furcellatus</i>
42	<i>Lottia orbignyi</i>	88	<i>Laurencia chilensis</i>
43	<i>Scurria araucana</i>	89	<i>Montemaria horridula</i>
44	<i>Scurria ceciliana</i>	90	<i>Nothogenia</i> spp.
45	<i>Scurria plana</i>	91	<i>Petalonia Fascia</i>
46	<i>Scurria variabilis</i>	92	<i>Petroglossum</i> spp.

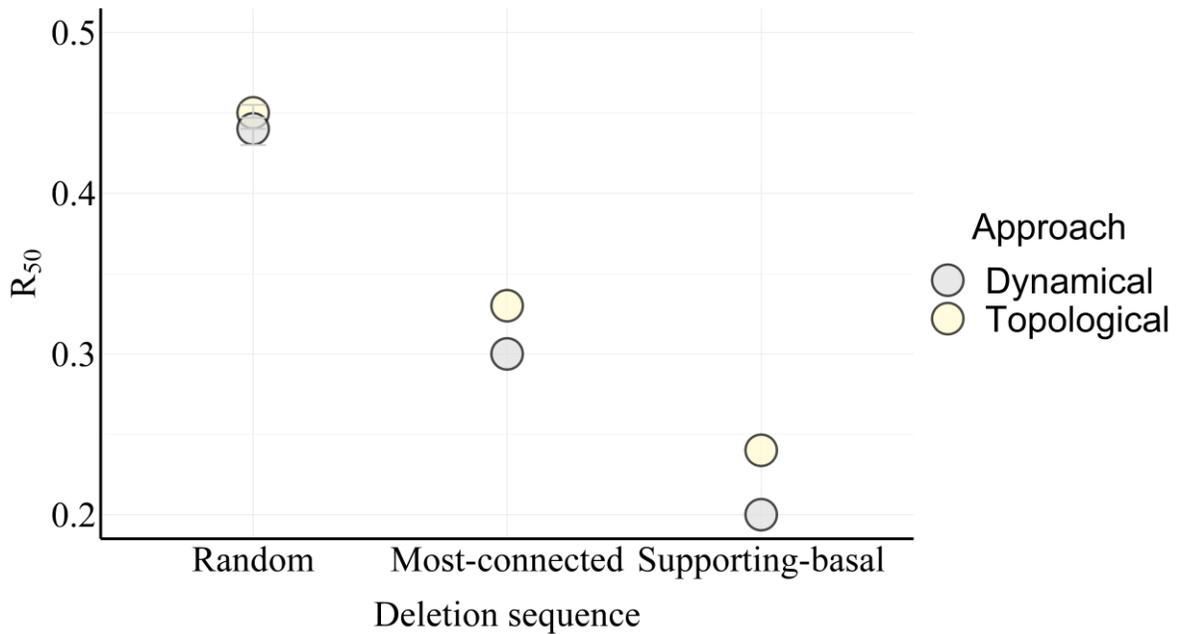
Fig. S1.

Figure S1. Food-web robustness (R_{50}) to three deletion sequences and using a static (yellow circle) vs. dynamical (grey circle) approach. The performed deletion sequences removed species: (1) randomly (hereafter “random”), (2) from the most to the least connected species (hereafter “most-connected”), and (3) from the most connected species that trophically support highly connected species to the least connected species supporting low connected species (hereafter “Supporting-basal”). In the case of the random deletion sequence, the circles represent the average and the error bars the ± 95 . C.I. of 1000 random deletion sequences.

Fig. S2

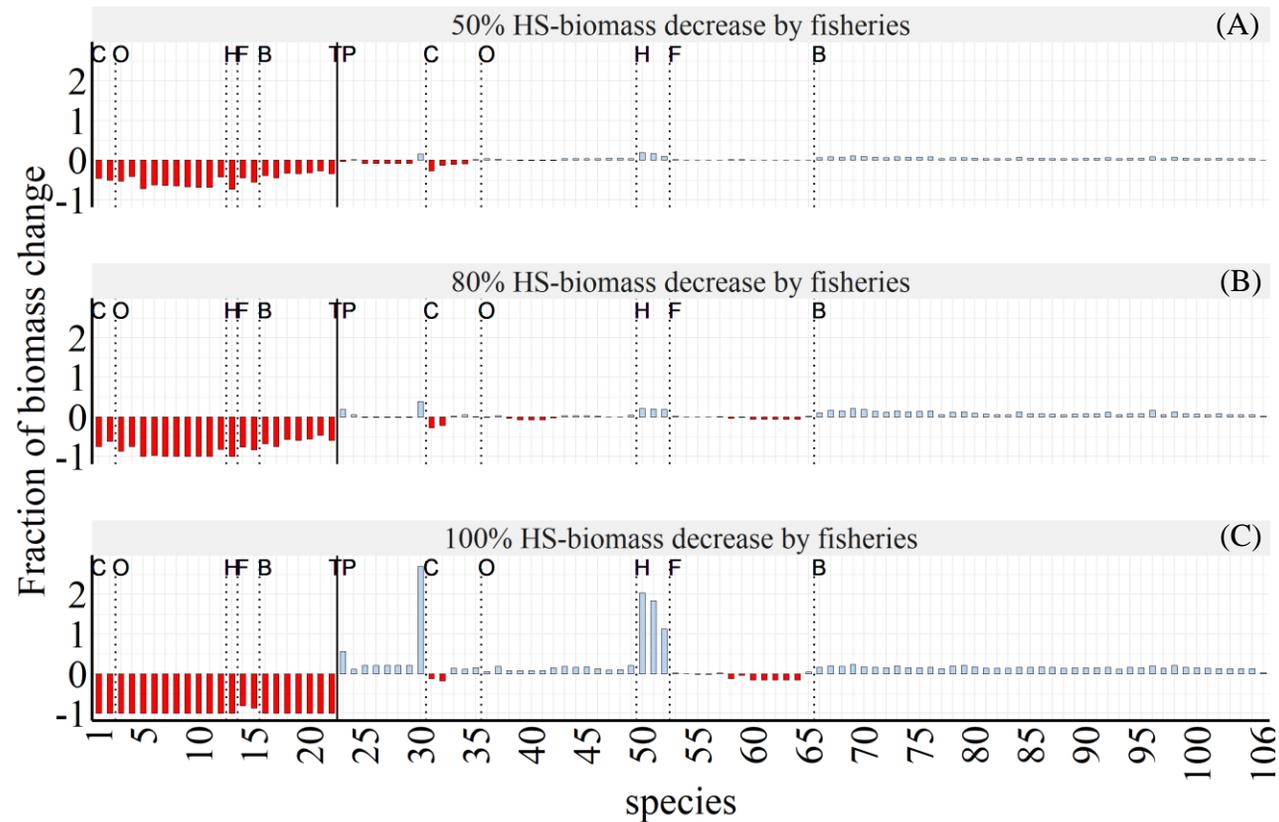


Figure S2. Fraction of biomass change (y-axis) of each species (x-axis) of the intertidal food-web after simultaneously reducing the biomass of all harvested species in a 50% (A), 80% (B) and 100% (C). Red bars represent negative effects on species biomass, while blue bars represent positive effects. From the bold vertical line to the left, the figure shows all the harvested species (HS). From the bold line to the right, the figure shows all the non-harvested species. Species are organized by trophic level (TP: top-predators, C: carnivores, O: omnivores, H: herbivores, F: filter-feeders, B: basal species) and their identity can be found by matching their number id with the numbers in Supplementary Table S5.

Fig. S3

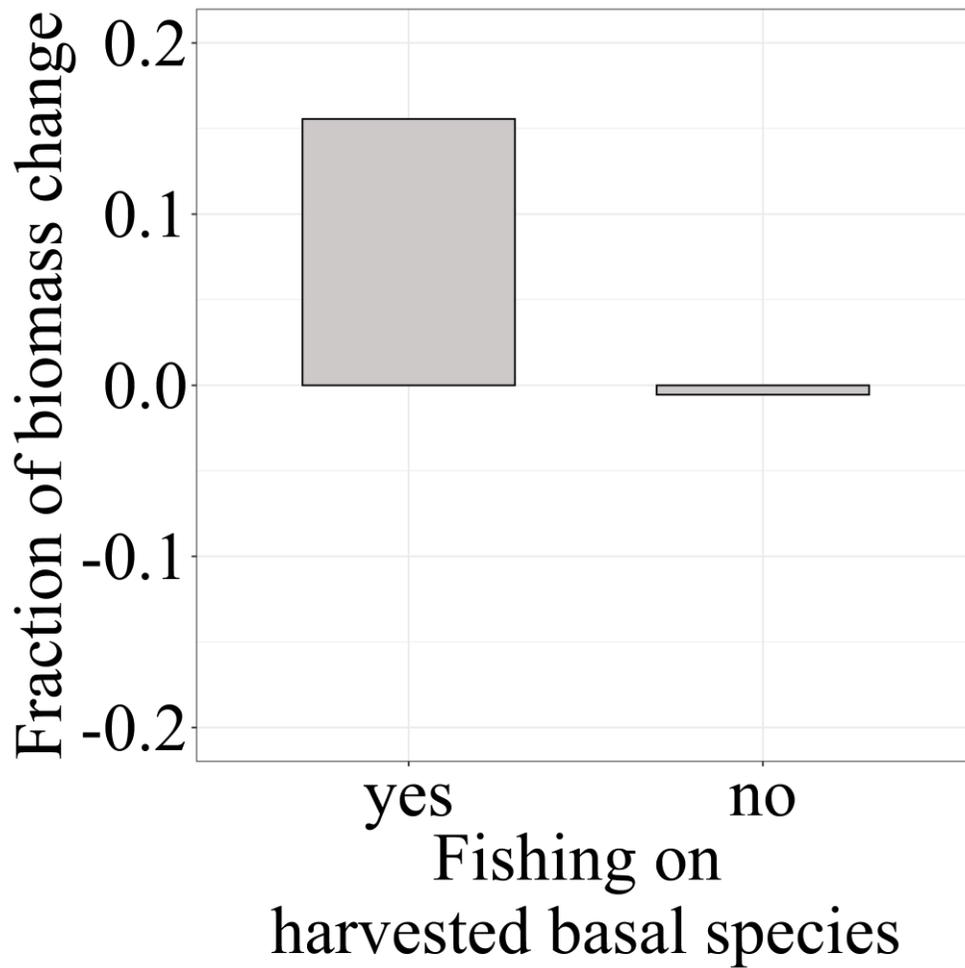


Figure S3. Contribution of harvested basal species over the biomass of non-harvested basal species. The figure represents the fraction of the total biomass change of non-harvested basal species (y-axis) after fishing with the maximum exploitation rate ($F_{\max} = 1$) for all harvested species, including (yes) and without including (no) harvested macroalgae in the list of harvested species.

Fig. S4

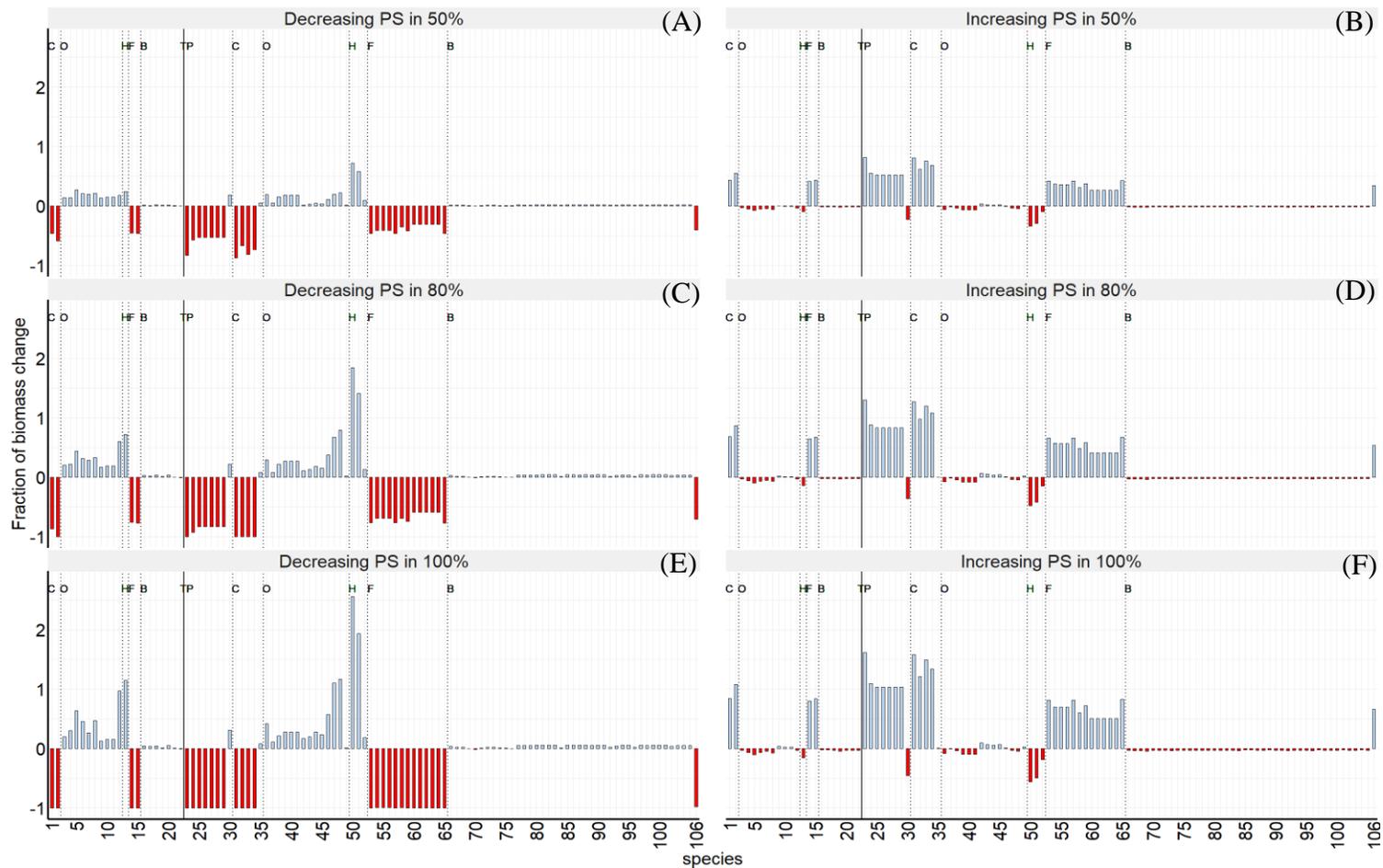


Figure S4. Fraction of biomass change (y-axis) of each species (x-axis) of the intertidal food-web after decreasing (A,C,E) and increasing (B,D,F) plankton subsidy (species 106) in 50% (A,B), 80% (C,D), 100% (E,F) of their basal productivity. The red bar represents negative effects on species biomass, while blue bars represent positive effects. From the bold vertical line to the left, the figure shows all the

harvested species. From the bold line to the right, the figure shows all the non-harvested species. Species are organized by trophic level and their identity can be found by matching their number id with the numbers in Supplementary Table S5.

Fig. S5

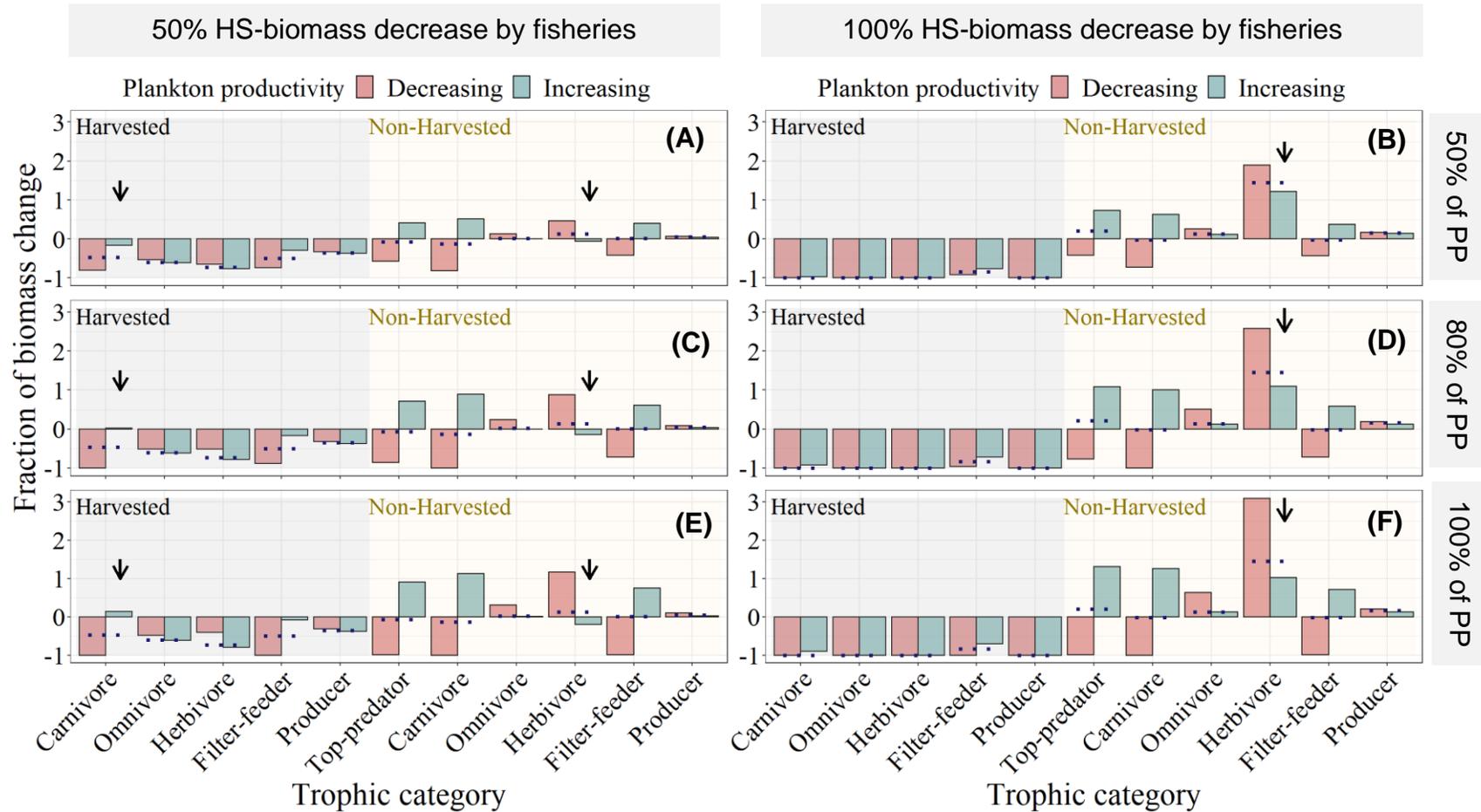


Figure S5. Combined effects of artisanal fisheries and plankton-productivity alterations on food-web dynamics. Fraction of total biomass change (y-axis) of each trophic category (x-axis) after decreasing (red bars) and increasing (blue bars) the plankton productivity (PP) in 50% (A and B), 80% (C and D), and 100% (E and F), and after decreasing the biomass of all harvested species (HS) in a 50% (A and C) and in a 100% (B and D). The grey and yellow shading represent the biomass change of harvested and non-

harvested species, respectively. The arrows highlight the most remarkable changes between the two levels of plankton subsidy perturbation and the two levels of fishing. The dotted lines represent the independent effect fishing (i.e., without plankton subsidy perturbation) on the biomass of each trophic category as a reference point.

Fig. S6

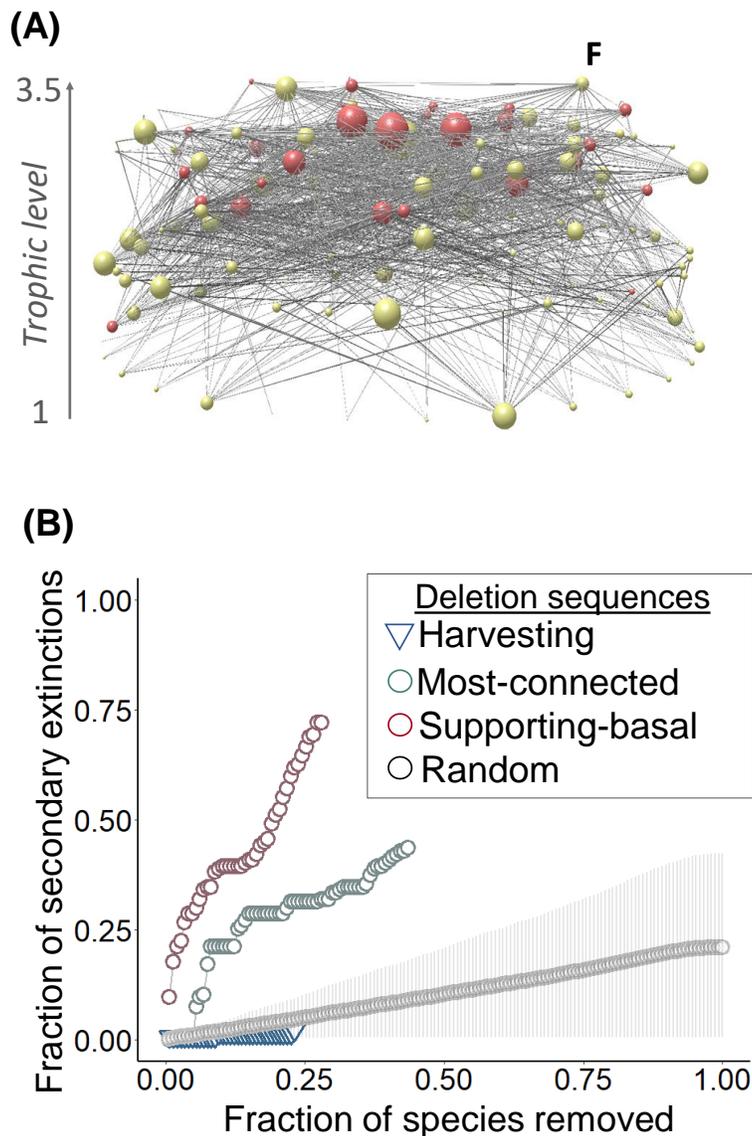


Figure S6. Shallow-subtidal marine Chilean food-web. (A) Color node represents the harvested (red) and non-harvested (yellow) species. Letter F represents the fisheries node. Node size represents the number of trophic interactions (degree) of each node. Bottom nodes represent basal species, and the nodes of the top represent top predators. The left axes represent the trophic level (SWTL) from the minimum to the maximum trophic level. Drawn using Network3D software¹⁵. Harvested species was recognized from the official governmental webpage of the Chilean fishing service (www.sernapesca.cl). (B) Fraction of secondary extinctions (y-axis) produced in this food-web after the sequential removal of species (x-axis) with a static approach. Gray and red circle represent most-connected and supporting-basal deletion sequence, while blue triangle represents harvesting deletion sequence. In the random deletion sequence, circles represent the average and the error bars represent the 95% confidence interval of 1000 simulations.

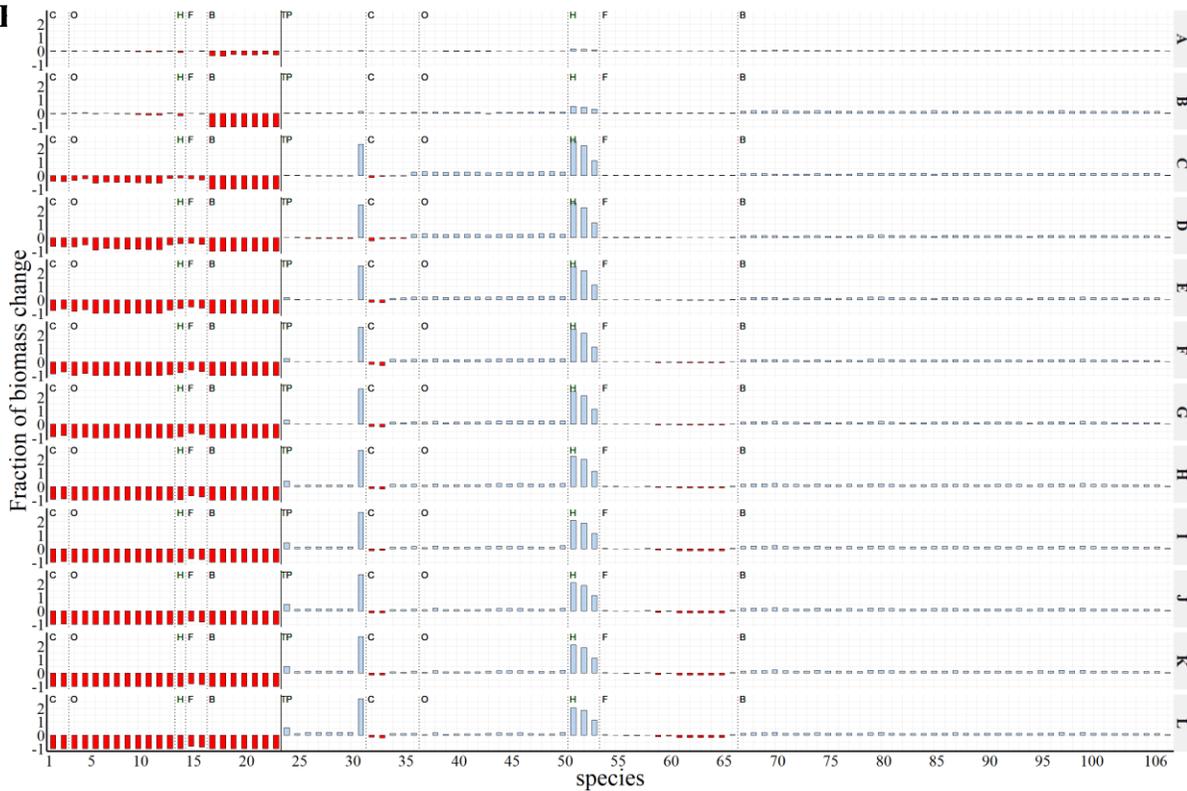


Figure S7. Biomass change (y-axis) of each species (x-axis) after simultaneously fishing on all harvested species through an increase in the exploitation rate (F_{\max}). F_{\max} in panels A and B are 0.001 and 0.01, respectively, and then F_{\max} increases in 0.01 from panels C to L, that is, 0.02, 0.03, [...], 1. Red and blue bars represent negative and positive effects, respectively. From the bold vertical line to the left, the figure shows all the harvested species. From the bold line to the right, the figure shows all the non-harvested species. Species are organized by trophic level (TP: top-predators, C: carnivores, O: omnivores, H: herbivores, F: filter-feeders, B: basal species) and their identity can be found by matching their number id with the numbers in Supplementary Table S5

CAPÍTULO 3.

KELPS ARE THE MOST SENSITIVE HARVESTED SPECIES TO SMALL-SCALE ARTISANAL FISHERIES

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Abstract

One of the critical problems for sustainable fisheries management stems from the inevitable propagation of the effects on the target species to the entire ecosystem via interactions with many other species, which may or may not be themselves fished by humans. Thus, even when a single species is ‘well-managed’, there is large uncertainty on the impacts such exploitation is having on the rest of the ecosystem. Dynamical, multi-species networks can help elucidate the main pathways of propagation and the potentially nodes (species) and interactions (links) that can be critical for persistence and stability of the ecosystem. We use a multiple species model to examine some of the community-wide consequences of harvesting on two heavily exploited coastal marine food-webs, the intertidal rocky-shore and shallow-subtidal food-webs of central Chile. The diverse and

complex network of consumption-type of interactions have been well resolved in these coastal ecosystems and we parameterize the model using empirical information and the Allometric Trophic Network (ATN) approach. In each system, we simulated fishing pressure on all species that are currently harvested by the artisanal fisheries, under ten different exploitation rates. After each exploitation scenario, we evaluated the effect of fishing over the long-term biomass change of each species in the food-web, harvested and non-harvested, with respect to a no-fisheries basal level. Under all exploitation scenarios and in both food-webs, fishing affected the biomass of all the species of the food-web, with generally positive effects on the biomass of most non-harvested species, but with widely different responses among them. Generally, filter-feeders species plus carnivores plus top-predators and herbivores were the most positively affected species in the subtidal and intertidal food-web, respectively. Among harvested species, kelps were the most sensitive to harvesting pressure in both food-webs. Despite these similar patterns, the harvested species of the subtidal food-web - where most of the artisanal fisheries concentrates- were on average 1.8 times more sensitive to exploitation pressure than intertidal harvested species. We highlight the sensitivity of kelps to even moderate fishing pressure in our models, which highlights the need for management plans for these highly exploited primary producers.

INTRODUCTION

Marine fish stocks have tremendous importance in the world food system and are particularly important in world developing countries. Fishing pressure has increased in recent years resulting in the widespread collapse of stocks threatening the health of marine ecosystems as well as food and economic security (FAO, 2018; Worm, 2016; Worm et al., 2006). In 2010 the collapse of fisheries stocks reached 60%, and projections of the state of the fisheries suggest

that in 2050 these collapses will increase to 90% (Costello et al., 2016). Recent studies suggest that in regions with less-developed fisheries management is where intensive overfishing takes place, an increase of 3-fold more harvesting rates occur as opposed to areas with intense management (Hilborn et al., 2020). Efforts generated to produce sustainable fisheries are challenging and deficient in many places of the world since fisheries management is mainly focused on single-species models, despite the acknowledged need to move towards more holistic multi-species and ecosystem-based models and approaches (Collie et al., 2016; Garcia, 2003; Pikitch, 2004; Zabel et al., 2003).

The focus of multispecies approaches emphasizes the ecological web of interactions in which harvested species are embedded. Species coexist and interact with several other species by a number of trophic and non-trophic interactions (Kéfi et al., 2015). When fisheries remove a fraction of the biomass of a species, several impacts may emerge. Fisheries commonly harvest multiple species, including highly connected as well as strongly and weakly interacting ones (Dunne et al., 2002; Pérez-Matus et al., 2017) at all trophic levels (Pauly, 1998), which could induce both top down and bottom up changes on communities with cascading effects on both harvested and non-harvested species (Kuparinen et al., 2016; Pérez-Matus et al., 2017) and with a myriad of lagged, non-linear, and unexpected dynamics, which are very difficult to foresee let alone understand from single-species models (e.g., Freilich et al., 2020; Yodzis, 2001, 1988). Multispecies approaches to fisheries unveil the complexity brought about by the propagation of impacts on target and non-target species and their importance to achieve a sound management. Here, we use a multiple species model to examine some of the community-wide consequences of harvesting on two heavily exploited coastal marine food-webs, the intertidal rocky-shore and shallow-subtidal food-webs of central Chile.

Small-scale fisheries contribute with the 57% of the total national catch and among artisanal fisheries (Fernández et al., 2020), from which the benthic fishery plays an important social and economic role in fishers well-being (Defeo et al., 2016). Artisanal fisheries are composed by divers and coastal gatherers (Gelcich et al., 2010). They mainly extract their resources from shallow-subtidal ecosystems using diving gear (hookah or free diving), spearing and pot trapping, but through hand-picking also harvest a small proportion from the intertidal zone (Castilla and Defeo, 2001; Gelcich et al., 2010). In central Chile, the small-scale fisheries target 23% and 21% of the 147 and 107 species described in the shallow-subtidal (Pérez-Matus et al., 2017a) and rocky-shore intertidal (Ávila-Thieme et al., unpublished data) trophic coastal community, respectively. Also, fisheries target highly connected species and remove at least one predator or prey of more than 70% of the species (Ávila-Thieme et al., unpublished data; Pérez-Matus et al., 2017a). A recent study (Ávila-Thieme et al., ms) using the allometric trophic network model (ATN model, Boit et al., 2012; Brose et al., 2006) to assess the impact of small-scale fisheries on the intertidal food-web of central Chile revealed that the simultaneous fishing of all harvested species propagate through, impacting the abundance of all species that compose the food-web (Ávila-Thieme et al., unpublished data). A multispecies approach to the shallow-subtidal ecosystem is still lacking. The same as in the intertidal, the shallow-subtidal artisanal fisheries harvest on highly connected species (Pérez-Matus et al., 2017), thus we predict that artisanal fisheries also affect the abundance of all the species in this food-web, but probably the impact is stronger considering that the largest proportion of harvested biomass comes from subtidal species.

Chilean artisanal fisheries management is based in spatial property rights through territorial use rights for fisheries (TURFs), which grant to a group of fishers' exclusive access to

harvest and co-manage resources within a designated area (Gelcich et al., 2010). TURFs improved the sustainability of socio-ecological systems, overcome overexploitation, rebuilt benthonic fisheries stocks (Beckensteiner et al., 2020; Defeo et al., 2016; Gelcich et al., 2010), and improved kelp forest ecosystems (Pérez-Matus et al., 2017b). However, 40% of Chilean TURFs are inactive or currently abandoned (Gelcich et al., 2017) and fishers recognize low levels of cooperation, high levels of illegal fishing (Oyanedel et al., 2018), and usually exceed the designed area to fishing on open-access areas (de Juan et al., 2018). In consequence, depending on the strength of exploitation, artisanal fishers may overharvest their resources. Therefore, gathering information about how sensitive harvested species are is key to suggest in which species management should be prioritized. For example, in the rocky-shore intertidal of central Chile has been recognized that macroalgae (including kelps) are the most sensible harvested species to fishing (Ávila-Thieme et al., unpublished data), so kelps management should be prioritized. This is very important since kelps play an essential ecological, economic, and sociological role in Chile (Miller and Rudolf, 2011). However, kelps harvesting is increasing due to artisanal fisheries used to focus on benthic invertebrates but currently is shifting towards kelp harvesting (de Juan et al., 2018). Moreover, the high international price and demand of kelps (Vásquez, 2016) in combination with their low enforcement (due to the topography of coastal territory, extension, and accessibility where these natural populations of kelp occur), has encouraged the illegal fishing of kelps (Frangouides, 2011) and sharply reduced its abundance (Krumhansl et al., 2016). A comparison of the sensitivity of harvested species to fishing in the shallow-subtidal of central Chile, where artisanal fisheries focus their fishing efforts, is important from a management as well as an ecological perspective. Thus, in this work we aim at assessing

the sensitivity of harvested shallow-subtidal species to different intensities of fishing pressure with a particular focus on kelp species.

In this study (1) we compare the vulnerability to fishing of all harvested species (including both, animals and macroalgae), and (2) the indirect effects of that fishing in the biomass of all non-harvested species from the shallow-subtidal food-web against the species from the intertidal rocky-shore food-web. For each food-web, we simulate fishing of all harvested species simultaneously, and evaluate its effect on the biomass of all the species of each food-web. We repeat this analysis along a gradient in fishing pressure of ten different exploitation rates.

METHODS

Food-webs description

We evaluated the effect of artisanal fisheries on two comprehensively studied coastal marine food-webs of central Chile (Kéfi et al., 2015; Pérez-Matus et al., 2017), (i) the rocky shallow subtidal reefs (hereafter subtidal food-web, Fig. 3a) and (ii) the rocky intertidal shore (hereafter intertidal food-web, Fig. 3b). Both food-webs are influenced by the highly productive Humboldt Current System (Thiel et al., 2007) (HCS) and harvested exclusively by small scale artisanal fisheries (Gelcich et al., 2010). The subtidal food-web have, 147 species, 1204 trophic interactions, and connectance of 0.05 (Pérez-Matus et al., 2017a); while the intertidal food-web has 107 species, 1381 trophic interactions, and connectance of 0.12 (Ávila-Thieme et al., unpublished data; Kéfi et al., 2015). The subtidal and intertidal food-webs differ in the proportion of primary producers, with 21% vs 44% of the species, invertebrates, with 59% vs 53%, fishes, with 19% vs 0%, and vertebrate endotherms, with 0.7% and 3%, respectively. In each food-web,

artisanal fisheries harvest on 34 (23%) and 22 (21%) of the species in the subtidal (Pérez-Matus et al., 2017a) and intertidal (Ávila-Thieme et al., unpublished data) food-web, respectively (F node in Fig. 1), including numerous species of macroalgae (including kelps) and invertebrates, as well as several fishes in the subtidal food-web. Moreover, in both food-webs, fisheries harvest on highly connected species and harvest at least one predator and one prey of several species in the food-web (Ávila-Thieme et al., unpublished data; A Pérez-Matus et al., 2017a).

Effects of fisheries on food-webs dynamics

We assessed the impacts of small-scale artisanal fisheries on the subtidal and intertidal food-web dynamics, fishing simultaneously over all harvested species, and evaluate its subsequent effect on the biomass of all the species in each food-web. We coupled the allometric trophic network model (ATN) to both food-webs (see model description below and parametrization in appendix section), simulated the simultaneous fishing of all the species that are naturally harvested by artisanal fishing (34 and 22 species in the subtidal and intertidal food-web, respectively), and assessed its subsequent impact on the biomass of all the species in each food-web. In each food-web, we simulate ten fishing scenarios, each one with a different exploitation rate (F_{\max} parameter in the ATN model). The exploitation rate varied between the values 0.1 to 1. A value of $F_{\max} = 0.1$ means that the fisheries harvest 10% of the fishing stock of each harvested species, while a value of $F_{\max} = 1$ means that fisheries harvest 100% of the fishing stock of each harvested species. Within each fishing scenario, we simulated the simultaneously fishing of all harvested species with the same exploitation rate. We use these exploitation rates due to the high uncertainty that exists around official landings figures (Oyanedel et al., 2018).

In each fishing scenario, we first run the model for 15000 time-steps (equivalent to 41.1 years) and 3650 time-steps (equivalent to 10 years) in the subtidal and intertidal food-web,

respectively, to ensure that the system reached a dynamic equilibrium, and the final species biomasses obtained were considered “before fishing” state ($F_{\max} = 0$). Then, we run the food-web dynamics for another 15000 and 3650 time-steps in the subtidal and intertidal food-web, respectively to reach a post perturbation equilibrium, and final biomasses were considered “after fishing” state ($F_{\max} > 0$). Species were considered extinct if their biomasses diminished below 10^{-6} (Schneider et al., 2016)

In each fishing scenario and for each species i of each food-web, we evaluated the effects of artisanal fisheries as:

$$Biomass\ change_i = \left[\left(\frac{after\ fishing_i}{before\ fishing_i} \right) - 1 \right] * 100 \quad (eq. 1)$$

The harvested species that after fishing had the highest biomass declines, were considered the most sensitive species in the food-web.

The dynamic model

The ATN model consists of two sets of equations, one describing the biomass changes of primary producers (eq. 2) and the other describing that of consumers (eq. 3), where \mathbf{B} is the biomass vector with the biomasses of every population in the food-web and B_i is the biomass of the population i , as follows:

$$\frac{dB_i}{dt'} = \overbrace{r_i B_i G_i(\mathbf{B})}^{\text{Autotrophic growth gain}} - \overbrace{\sum_j \frac{x_j y_{ji} B_j F_{ji}(\mathbf{B})}{e_{ji}}}_{\text{Herbivory loss}} - \overbrace{F_{\max i} B_i}_{\text{Fisheries loss}} \quad (eq. 2)$$

$$\frac{dB_i}{dt'} = \overbrace{f_a x_i B_i \sum_j y_{ij} F_{ij}(B)}^{\text{Resources consumption gain}} - \overbrace{f_m x_i B_i}_{\text{Maintenance loss}} - \overbrace{\sum_j \frac{x_j y_{ji} B_j F_{ji}(\mathbf{B})}{e_{ji}}}_{\text{Predation loss}} - \overbrace{F_{\max i} B_i}_{\text{Fisheries loss}} \quad (eq. 3)$$

These equations describe the biomass changes of primary producers (eq. 2) and consumers (eq. 3), where \mathbf{B} is the biomass vector with the biomasses of every population in the food-web and B_i is the biomass of the population i . The biomass of producer i changes according to the balance of autotrophic growth gain and predation loss (eq. 2). The net autotrophic growth is determined by the logistic growth function $G_i(B) = 1 - (\sum_{j=productores} c_{ij}B_j)/K$, where r_i is intrinsic growth rate of producer i , c_{ij} is inter-specific competition coefficient between producer i and j , and K is total carrying capacity of primary producers in the system, respectively. The biomass loss of producer i by herbivory (caused by herbivores or omnivores) increases with the mass-specific metabolic (x_j) and attack (y_j) rates of consumer i , and decreases with the assimilation efficiency of consumer i for resource j (e_{ij}). The consumers' population dynamics (Eq. 3) depend on its mass-specific metabolic rate (x_j) and on the balance between biomass gain by resource consumption, biomass loss by metabolic maintenance, and biomass loss by predation. From the total amount of resources ingested by the consumer population i , $\sum_j y_{ij}F_{ij}(\mathbf{B})$, only a fraction f_a is assimilated into consumer biomass. The functional response $F_{ij}(\mathbf{B})$ determines the consumption rate of each consumer i for each resource j , defined by:

$$F_{ij}(\mathbf{B}) = \frac{\omega_{ij}B_j^q}{B_0_{ij}^q + d_i B_i B_0_{ij} + \sum_{l=resources} \omega_{il}B_l^q} \quad (\text{eq. 4})$$

where ω_{ij} is the relative preference of consumer i for resource j , q controls the shape of eq. 4 which becomes an intermediate functional response between type II and type III when $q=1.2$ (Williams, 2008). B_0_{ij} is the biomass of resource j at which the consumer i achieves half of its maximum consumption rate on resource j , and d_i is the intra-specific interference of consumer i when it forages resource j . In Eq. 3, f_m defines the fraction of the consumer biomass that is respired

as maintenance. F_{max} define the fraction of biomass i that is removed by small-scale artisanal fisheries.

The biological rates of production, R , metabolism, X , and maximum consumption, Y , follow a negative power law with the species body size, with an exponent -1.4:

$$R_P = a_r M_P^{-0.25} \quad (\text{eq. 5})$$

$$X_C = a_x M_C^{-0.25} \quad (\text{eq. 6})$$

$$Y_c = a_y M_C^{-0.25} \quad (\text{eq. 7})$$

Where a_r , a_x , and a_y are allometric constant and the subscripts P and C are the producers and consumer parameters, respectively. The time scale of the system was defined based on the primary producer with higher mass-specific growth rate (reference species). The mass-specific growth rate and the metabolic rate of all the species were normalized by the scale time of the reference species, and the maximum consumption rate was normalized by the metabolic rate (Brose et al., 2006). These assumptions translate to the following expressions of intrinsic growth rate (r_i), metabolic rate (x_i), and maximum consumption rate (y_i) of each species i :

$$r_i = \frac{R_P}{R_{P_{ref}}} = 1 \left(\frac{M_P}{M_{P_{ref}}} \right)^{-0.25} \quad (\text{eq. 8})$$

$$x_i = \frac{X_C}{R_{P_{ref}}} = \frac{a_x}{a_r} \left(\frac{M_C}{M_{P_{ref}}} \right)^{-0.25} \quad (\text{eq. 9})$$

$$y_i = \frac{Y_C}{X_C} = \frac{a_y}{a_x} \quad (\text{eq. 10})$$

Implementation of the dynamic model

The marine ecosystems of Chile are one of the most productive ecosystems on the planet, mainly because of the nutrient enrichment caused by the Humboldt Current and upwelling systems (Thiel et al., 2007). This enrichment subsidizes most of the basal species (Testa et al., 2018), especially in plankton and detritus. That is, plankton and detritus experience an open-system population dynamic with population gains continually coming from advective flows associated to currents. To account for this phenomenon, our implementation of the ATN model assumes that the coastal currents and waves are permanently subsidizing the biomass of plankton and detritus. Therefore, we incorporated a constant of biomass subsidy into the biomass dynamics of plankton (in both food-webs) and detritus (in subtidal food-web) as:

$$\frac{dB_i}{dt} = d_{local} + s, \quad (\text{eq. 11})$$

where d_{local} represents their local dynamics (right hand of eq. 2) and s the biomass subsidy (Pascual and Caswell, 1991; Schreiber and Moore, 2018).

RESULTS

Vulnerability to fishing of the harvested species

We found that in the subtidal food-web kelps were the most vulnerable species to fishing, the same as previously observed in the intertidal food-web. In the subtidal food-web, harvested kelps *Lessonia trabeculata* and *Macrocystis pyrifera* became extinct even when they were harvested with the lowest exploitation rate that was simulated in this work (see harvested producers bar in Fig. 2). Unlike the intertidal food-web, we found that in the subtidal food-web, the harvested rocky reef fish *Paralichthys microps* were also vulnerable to the lower exploitation rate, becoming

extinct under this scenario. Therefore, the high vulnerability of macroalgae to fishing, especially kelps, is independent of the ecosystem in which these species are.

The harvested species of the subtidal food-web were on average 1.8 times more sensitive to exploitation pressure than intertidal harvested species. For the harvested macroalgae, we looked for the fishing exploitation threshold that they may tolerate without becoming extinct. Interestingly, we find that the harvested macroalgae from the subtidal food-web (harvested producers in Fig. 2) are more vulnerable to fishing than those from the intertidal (harvested producers in Fig. 3). In the subtidal food-web, the harvested kelps become extinct when we used an exploitation rate (F_{\max}) of 5×10^{-4} , which is when fisheries removed 0.05 % of their biomass. In the intertidal food-web, the harvested algae become extinct when we used an exploitation rate (F_{\max}) of 0.01, which is when fisheries removed 1 % of their biomass. At the same time, we compare the intensity at which the biomass of the subtidal harvested consumers decreased against the intertidal harvested consumers. Like harvested macroalgae, the harvested consumers from the subtidal food-web (Fig. 2) are more sensitive to fishing than those from the intertidal (Fig. 3). When we simultaneously removed 10% of the available biomass ($F_{\max} = 0.1$, lowest exploitation rate simulated in this work) of each of the harvested consumer species, we found that the total biomass of the harvested consumers from the subtidal decreased by 94% (Fig. 2A); while the total biomass of the harvested consumers from the intertidal decreased by 43% (Fig. 3A). Consequently, the coastal areas where the greatest effort of artisanal fisheries predominates are also the most sensitive to fishing. These results highlight the importance and urgency of promoting efficient management and control strategies, especially in those species that have been neglected

Indirect effects of fisheries in the biomass of all non-harvested species

In both food-webs and throughout the exploitation rate gradient, fishing mainly produced a positive impact on the biomass of non-harvested species, especially in the herbivores, carnivores and top-predators of the subtidal food-web (non-harvested species from Fig. 2) and in herbivores of the intertidal food-web (non-harvested species from Fig. 3). With the maximum exploitation rate ($F_{\max} = 1$), 86% (96 species) and 89% (84 species) of non-harvested species increased by 15% and 0.06% after fishing in the subtidal (Fig. S1J) and intertidal food-web (Fig. S2J), respectively. The combination of two mechanisms explains the positive effects of fisheries on the biomass of non-harvested species. On the one hand, biomass decrease of harvested consumers reduces the predation intensity on the harvested species preys. On the other hand, a biomass decrease of harvested basal species relaxes the competition between basal species. Therefore, although artisanal fisheries directly decrease the biomass of harvested species, indirectly may enhance the persistence of the rest of the species in the intertidal ecosystem.

In both food-webs, we just found negative effects in the biomass of 10% of the non-harvested species. However, it seems that the trophic levels at which the non-harvested species that were negatively affected by fisheries depend on the ecosystem at which fisheries are acting. In the subtidal food-web and regardless of exploitation rate scenario, fishing mainly produces negative effects on the biomass of species from lower trophic levels (basal species on Fig. S1). Also, fisheries produce the secondary extinction of two specialist consumers, which represent the 0.08% of non-harvested carnivores and 25% of non-harvested herbivores species (Fig. S1). In the intertidal food-web, the species that were negatively affected by fishing depended on the intensity of the simulated exploitation rate. When the exploitation rates are below 0.4, fishing produces weak negative effects on the biomass of species from higher trophic levels (top predators and carnivores on Fig. S2 from A to D). While, when the exploitation rates are above 0.6, fishing

negatively affects the biomass of species from lower trophic levels (filter-feeders on Fig. S2 from F to J).

DISCUSSION

We compare the sensitivity to fishing of the harvested species by small-scale artisanal fisheries and the indirect effects of fishing in the biomass of all non-harvested species of two coastal ecosystems, the shallow-subtidal and the intertidal rocky-shore food-webs of central Chile. We found that in both food-webs, the fishing of all harvested species alters the biomass of all species in the food-web. Among harvested species, macroalgae (including kelps) were the most sensitive harvested species to fishing, as they became extinct at very low exploitation rates. On the other hand, the subtidal food-web was more susceptible to fishing than the intertidal food-web. Compared to the same exploitation rate, the biomass decreasing of the subtidal harvested species was almost twice as the biomass decrease of the intertidal harvested species. Finally, we found that in both food-webs, fisheries indirectly produce positive effects on the biomass of the most non-harvested species.

Sensitivity to fishing of the harvested species

We found that in the subtidal food-web kelps were the most vulnerable species to fishing, the same as previously observed in the intertidal food-web (Ávila-Thieme et al., unpublished data). This could be explained by biological aspects of the harvested macroalgae themselves, since they are the macroalgae species with the lowest growth rates due to in average they have the largest body sizes. But also, the vulnerability of the algae can be explained by the structure of the food-webs. Since the harvested macroalgae are basal species, they have 2.7 to 3.4 times more predators

than animals. Furthermore, in the subtidal food-web, harvested macroalgae have a lower proportion of harvested predators than harvested consumers. In the intertidal food-web, the biomass of non-harvested predators of harvested algae increases by 32% more than the biomass of non-harvested predators of harvested consumers increases. This means that fishing indirectly could intensify predation on harvested macroalgae, an effect that is impossible to observe with single-species approaches.

The high sensitivity of harvested macroalgae concerns since, among them, are the brown algae of the genus *Durvillaea*, *Lessonia*, and *Macrocystis* that represent the intertidal and subtidal kelps of Central Chile (Beckensteiner et al., 2020). Kelps play a key ecological role in intertidal and subtidal ecosystems, as they promote biodiversity through the provision of habitats for the reproduction, settlement, development, protection, and feeding of diverse species (Vásquez, 2016; Villegas et al., 2019). At the same time, kelps are intensively exploited and exported for the alginate, food, and cosmetics industry (Villegas et al., 2019; Westermeier et al., 2019), in which Chile is responsible for the largest landings of natural kelp populations in the world (Vásquez, 2016). The high value and demand for kelps are causing fishers to focus their efforts on collecting these algae and encouraged high levels of illegal fishing (Frangoudes, 2011; Westermeier et al., 2019). The massive mortalities of kelps threaten the recovery of these natural populations, which can take between two to six years (Parada et al., 2016; Teagle et al., 2017). Therefore, our results highlight the urgency to encourage and improve the management and supervision of kelp.

Interestingly, we found that species that are harvested from the subtidal food-web were more sensitive to fishing than those that are harvested from the intertidal food-web. The subtidal ecosystems have the greatest diversity of fishing gear (diving, the use of tools such as bars, harpoons, and traps) and landings (Castilla and Defeo, 2001; Pérez-Matus et al., 2017); while the

resources of the intertidal ecosystem, are manually collected during periods of low tide (Castilla and Defeo, 2001). This means that the most vulnerable ecosystem to fishing is, in turn, the ecosystem that receives the greatest fishing efforts. Chilean non-algal resources are also exposed to illegal fishing, where fishermen harvest more than agreed, harvest directly from freely accessible areas, and / or lie in the intensity of their landings (Gelcich et al., 2017), specially , in which their landings can be up to six times what is officially reported by fishermen (Oyanedel et al., 2018). Therefore, if higher extraction of resources occurs in the subtidal zone, there should also be a higher intensity of illegal fishing, which could push resources to states of local collapse. The above does not mean that fisheries should stop fishing. When management is efficient, the abundance of the species is greater than in areas of free access (Pérez-Matus et al., 2017), being able even to reach values similar to those found in marine reserves (Gelcich et al., 2012). The heterogeneity in the response between the intertidal and subtidal ecosystem highlights the importance of improving management and enforcement strategies in those species that are sensitive to fishing, especially in those with precarious enforcement.

Indirect effects of fisheries in the biomass of all non-harvested species

We found that the indirect effects of artisanal fishing produced a positive impact on the biomass of species that are not harvested. Two contrasting interpretations could emerge from these results. On the one hand, the loss in biomass produced by the fishing of harvested species means that fisheries produce niche releases in the ecosystem. Consequently, the release of niche could produce compensatory dynamics (MacArthur et al., 1972; Mittelbach, 2012) and produce the growth of the species that are members of the community, as observed in this work, or be compensated with the biomass of a new species to the ecosystem. In the first case, the positive effects on the biomass of non-harvested species suggest that artisanal fisheries, although removes

biomass from the species that are harvested, it could play a key role in promoting the persistence of the ecosystems (Dunne et al., 2016). In the second case, the arrival of new species could affect the interspecific competition, the processes of habitat formation or food provision, and thus generate unpredictable trajectories in the biomass of species that are members of the local community (Bradley et al., 2019; Ponisio et al., 2019; Thomsen et al., 2014). However, in the modeling carried out in this work, we do not allow the potential arrival of new species as a mechanism, and it is undoubtedly an interesting next evaluation step.

Ecological interactions between coexisting species involve more than just food, being habitat modification, interference competition, a refuge from predation, mutualism, behavior modifications, among others, important interactions that affect the persistence of the species (Bascompte, 2007; Castilla, 1999; Kéfi et al., 2015; Ramos-Jiliberto et al., 2012; Thebault and Fontaine, 2010). Therefore, the positive trophic effects of fisheries in the biomass of non-harvested species could change if we incorporated the non-trophic interactions, especially if we included the key bioengineering role of kelps in the food-web dynamic (Vásquez, 2016; Villegas et al., 2019). Therefore, understanding the studied ecosystems is critical to complement the numerical results of simulations.

Finally, using a multispecies approach, this work contributes with important results that can be considered in the future management of natural resources of the coast of central Chile, such as the need to encourage and improve the management and control of macroalgae, especially in subtidal ecosystems. the multi-species approach contributes to general trends in how species respond to fishing, which is impossible to observe from single-species approaches

REFERENCES

- Ávila-Thieme, M.I., Corcoran, D., Pérez-Matus, A., Navarrete, S.A., Marquet, P.A., Valdovinos, F.S., unpublished data. Plankton biomass changes would negatively affect coastal South Pacific food-webs more strongly than artisanal fisheries.
- Bascompte, J., 2007. Networks in ecology. *Basic and Applied Ecology* 8, 485–490. <https://doi.org/10.1016/j.baae.2007.06.003>
- Beckensteiner, J., Scheld, A.M., Fernández, M., Kaplan, D.M., 2020. Drivers and trends in catch of benthic resources in Chilean TURFs and surrounding open access areas. *Ocean & Coastal Management* 183, 104961. <https://doi.org/10.1016/j.ocecoaman.2019.104961>
- Boit, A., Martinez, N.D., Williams, R.J., Gaedke, U., 2012. Mechanistic theory and modelling of complex food-web dynamics in Lake Constance: Mechanistic modelling of complex food web dynamics. *Ecology Letters* 15, 594–602. <https://doi.org/10.1111/j.1461-0248.2012.01777.x>
- Bradley, B.A., Laginhas, B.B., Whitlock, R., Allen, J.M., Bates, A.E., Bernatchez, G., Diez, J.M., Early, R., Lenoir, J., Vilà, M., Sorte, C.J.B., 2019. Disentangling the abundance–impact relationship for invasive species. *Proc Natl Acad Sci USA* 116, 9919–9924. <https://doi.org/10.1073/pnas.1818081116>
- Brose, U., Williams, R.J., Martinez, N.D., 2006. Allometric scaling enhances stability in complex food webs. *Ecol Letters* 9, 1228–1236. <https://doi.org/10.1111/j.1461-0248.2006.00978.x>
- Castilla, J.C., 1999. Coastal marine communities: trends and perspectives from human-exclusion experiments. *Trends in Ecology & Evolution* 14, 280–283. [https://doi.org/10.1016/S0169-5347\(99\)01602-X](https://doi.org/10.1016/S0169-5347(99)01602-X)
- Castilla, J.C., Defeo, O., 2001. Latin American benthic shellfisheries: Emphasis on co-management and experimental practices. *Reviews in Fish Biology and Fisheries* 11, 1–30. <https://doi.org/10.1023/A:1014235924952>
- Collie, J.S., Botsford, L.W., Hastings, A., Kaplan, I.C., Largier, J.L., Livingston, P.A., Plagányi, É., Rose, K.A., Wells, B.K., Werner, F.E., 2016. Ecosystem models for fisheries management: finding the sweet spot. *Fish Fish* 17, 101–125. <https://doi.org/10.1111/faf.12093>
- Costello, C., Ovando, D., Clavelle, T., Strauss, C.K., Hilborn, R., Melnychuk, M.C., Branch, T.A., Gaines, S.D., Szuwalski, C.S., Cabral, R.B., Rader, D.N., Leland, A., 2016. Global fishery prospects under contrasting management regimes. *Proc Natl Acad Sci USA* 113, 5125–5129. <https://doi.org/10.1073/pnas.1520420113>
- de Juan, S., Subida, M.D., Gelcich, S., Fernandez, M., 2018. Ecosystem health in coastal areas targeted by small-scale artisanal fisheries: Insights on monitoring and assessment. *Ecological Indicators* 88, 361–371. <https://doi.org/10.1016/j.ecolind.2018.01.054>
- Defeo, O., Castrejón, M., Pérez-Castañeda, R., Castilla, J.C., Gutiérrez, N.L., Essington, T.E., Folke, C., 2016. Co-management in Latin American small-scale shellfisheries: assessment from long-term case studies. *Fish Fish* 17, 176–192. <https://doi.org/10.1111/faf.12101>
- Dunne, J.A., Maschner, H., Betts, M.W., Huntly, N., Russell, R., Williams, R.J., Wood, S.A., 2016. The roles and impacts of human hunter-gatherers in North Pacific marine food webs. *Sci Rep* 6, 21179. <https://doi.org/10.1038/srep21179>
- Dunne, J.A., Williams, R.J., Martinez, N.D., 2002. Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecol Letters* 5, 558–567. <https://doi.org/10.1046/j.1461-0248.2002.00354.x>
- FAO (Ed.), 2018. Meeting the sustainable development goals, The state of world fisheries and aquaculture. Rome.

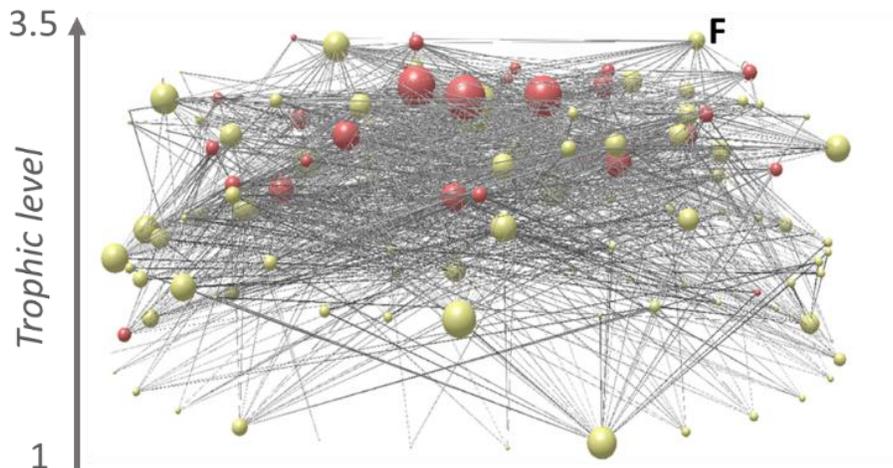
- Fernández, M., Kriegl, M., Garmendia, V., Aguilar, A., Subida, M.D., 2020. Evidence of illegal catch in the benthic artisanal fisheries of central Chile: patterns across species and management regimes. *Lat. Am. J. Aquat. Res.* 48, 287–303. <https://doi.org/10.3856/vol48-issue2-fulltext-2475>
- Frangoudes, K., 2011. Seaweeds Fisheries Management in France, Japan, Chile and Norway 9.
- Freilich, M.A., Rebolledo, R., Corcoran, D., Marquet, P.A., 2020. Reconstructing ecological networks with noisy dynamics. *Proc. R. Soc. A.* 476, 20190739. <https://doi.org/10.1098/rspa.2019.0739>
- Garcia, S.M., 2003. The ecosystem approach to fisheries: issues, terminology, principles, institutional foundations, implementation and outlook. Food & Agriculture Org.
- Gelcich, S., Cinner, J., Donlan, C., Tapia-Lewin, S., Godoy, N., Castilla, J., 2017. Fishers' perceptions on the Chilean coastal TURF system after two decades: problems, benefits, and emerging needs. *bms* 93, 53–67. <https://doi.org/10.5343/bms.2015.1082>
- Gelcich, S., Fernández, M., Godoy, N., Canepa, A., Prado, L., Castilla, J.C., 2012. Territorial User Rights for Fisheries as Ancillary Instruments for Marine Coastal Conservation in Chile: *Gelcich et al* . *Conservation Biology* 26, 1005–1015. <https://doi.org/10.1111/j.1523-1739.2012.01928.x>
- Gelcich, S., Hughes, T.P., Olsson, P., Folke, C., Defeo, O., Fernandez, M., Foale, S., Gunderson, L.H., Rodriguez-Sickert, C., Scheffer, M., Steneck, R.S., Castilla, J.C., 2010. Navigating transformations in governance of Chilean marine coastal resources. *Proceedings of the National Academy of Sciences* 107, 16794–16799. <https://doi.org/10.1073/pnas.1012021107>
- Hilborn, R., Amoroso, R.O., Anderson, C.M., Baum, J.K., Branch, T.A., Costello, C., de Moor, C.L., Faraj, A., Hively, D., Jensen, O.P., Kurota, H., Little, L.R., Mace, P., McClanahan, T., Melnychuk, M.C., Minto, C., Osio, G.C., Parma, A.M., Pons, M., Segurado, S., Szuwalski, C.S., Wilson, J.R., Ye, Y., 2020. Effective fisheries management instrumental in improving fish stock status. *Proc Natl Acad Sci USA* 117, 2218–2224. <https://doi.org/10.1073/pnas.1909726116>
- Kéfi, S., Berlow, E.L., Wieters, E.A., Joppa, L.N., Wood, S.A., Brose, U., Navarrete, S.A., 2015. Network structure beyond food webs: mapping non-trophic and trophic interactions on Chilean rocky shores. *Ecology* 96, 291–303. <https://doi.org/10.1890/13-1424.1>
- Krumhansl, K.A., Okamoto, D.K., Rassweiler, A., Novak, M., Bolton, J.J., Cavanaugh, K.C., Connell, S.D., Johnson, C.R., Konar, B., Ling, S.D., Micheli, F., Norderhaug, K.M., Pérez-Matus, A., Sousa-Pinto, I., Reed, D.C., Salomon, A.K., Shears, N.T., Wernberg, T., Anderson, R.J., Barrett, N.S., Buschmann, A.H., Carr, M.H., Caselle, J.E., Derrien-Courtel, S., Edgar, G.J., Edwards, M., Estes, J.A., Goodwin, C., Kenner, M.C., Kushner, D.J., Moy, F.E., Nunn, J., Steneck, R.S., Vásquez, J., Watson, J., Witman, J.D., Byrnes, J.E.K., 2016. Global patterns of kelp forest change over the past half-century. *Proc Natl Acad Sci USA* 113, 13785–13790. <https://doi.org/10.1073/pnas.1606102113>
- Kuparinen, A., Boit, A., Valdovinos, F.S., Lassaux, H., Martinez, N.D., 2016. Fishing-induced life-history changes degrade and destabilize harvested ecosystems. *Sci Rep* 6, 22245. <https://doi.org/10.1038/srep22245>
- MacArthur, R.H., Diamond, J.M., Karr, J.R., 1972. Density Compensation in Island Faunas. *Ecology* 53, 330–342. <https://doi.org/10.2307/1934090>

- Miller, T.E.X., Rudolf, V.H.W., 2011. Thinking inside the box: community-level consequences of stage-structured populations. *Trends in Ecology & Evolution* 26, 457–466. <https://doi.org/10.1016/j.tree.2011.05.005>
- Mittelbach, G.G., 2012. *Community Ecology*. Sinauer associates, Sunderland, Massachusetts U.S.A.
- Oyanedel, R., Keim, A., Castilla, J.C., Gelcich, S., 2018. Illegal fishing and territorial user rights in Chile: Illegal Fishing. *Conservation Biology* 32, 619–627. <https://doi.org/10.1111/cobi.13048>
- Parada, G.M., Tellier, F., Martínez, E.A., 2016. Spore dispersal in the intertidal kelp *Lessonia spicata*: macrochallenges for the harvested *Lessonia* species complex at microscales of space and time 7.
- Pascual, M., Caswell, H., 1991. The dynamics of a size-classified benthic population with reproductive subsidy. *Theoretical Population Biology* 39, 129–147. [https://doi.org/10.1016/0040-5809\(91\)90032-B](https://doi.org/10.1016/0040-5809(91)90032-B)
- Pauly, D., 1998. Fishing Down Marine Food Webs. *Science* 279, 860–863. <https://doi.org/10.1126/science.279.5352.860>
- Pérez-Matus, Alejandro, Carrasco, S.A., Gelcich, S., Fernandez, M., Wieters, E.A., 2017. Exploring the effects of fishing pressure and upwelling intensity over subtidal kelp forest communities in Central Chile. *Ecosphere* 8, e01808. <https://doi.org/10.1002/ecs2.1808>
- Pérez-Matus, A., Ospina-Alvarez, A., Camus, P., Carrasco, S., Fernandez, M., Gelcich, S., Godoy, N., Ojeda, F., Pardo, L., Rozbaczylo, N., Subida, M., Thiel, M., Wieters, E., Navarrete, S., 2017. Temperate rocky subtidal reef community reveals human impacts across the entire food web. *Mar. Ecol. Prog. Ser.* 567, 1–16. <https://doi.org/10.3354/meps12057>
- Pikitch, E.K., 2004. ECOLOGY: Ecosystem-Based Fishery Management. *Science* 305, 346–347. <https://doi.org/10.1126/science.1098222>
- Ponisio, L.C., Valdovinos, F.S., Allhoff, K.T., Gaiarsa, M.P., Barner, A., Guimarães, P.R., Hembry, D.H., Morrison, B., Gillespie, R., 2019. A Network Perspective for Community Assembly. *Front. Ecol. Evol.* 7, 103. <https://doi.org/10.3389/fevo.2019.00103>
- Ramos-Jiliberto, R., Valdovinos, F.S., Moisset de Espanés, P., Flores, J.D., 2012. Topological plasticity increases robustness of mutualistic networks: Interaction rewiring in mutualistic networks. *Journal of Animal Ecology* 81, 896–904. <https://doi.org/10.1111/j.1365-2656.2012.01960.x>
- Schneider, F.D., Brose, U., Rall, B.C., Guill, C., 2016. Animal diversity and ecosystem functioning in dynamic food webs. *Nat Commun* 7, 12718. <https://doi.org/10.1038/ncomms12718>
- Schreiber, S.J., Moore, J.L., 2018. The structured demography of open populations in fluctuating environments. *Methods Ecol Evol* 9, 1569–1580. <https://doi.org/10.1111/2041-210X.12991>
- Teagle, H., Hawkins, S.J., Moore, P.J., Smale, D.A., 2017. The role of kelp species as biogenic habitat formers in coastal marine ecosystems. *Journal of Experimental Marine Biology and Ecology* 492, 81–98. <https://doi.org/10.1016/j.jembe.2017.01.017>
- Testa, G., Masotti, I., Farías, L., 2018. Temporal variability in net primary production in an upwelling area off central Chile (36°S). *Front. Mar. Sci.* 5, 179. <https://doi.org/10.3389/fmars.2018.00179>
- Thebault, E., Fontaine, C., 2010. Stability of Ecological Communities and the Architecture of Mutualistic and Trophic Networks. *Science* 329, 853–856. <https://doi.org/10.1126/science.1188321>

- Thiel, M., Macaya, E., Acuña, E., Arntz, W., Bastias, H., Brokordt, K., Camus, P., Castilla, J., Castro, L., Cortés, M., Dumont, C., Escribano, R., Fernandez, M., Gajardo, J., Gaymer, C., Gomez, I., González, A., González, H., Haye, P., Illanes, J.-E., Iriarte, J., Lancellotti, D., Luna-Jorquera, G., Luxoro, C., Manriquez, P., Marín, V., Muñoz, P., Navarrete, S., Perez, E., Poulin, E., Sellanes, J., Sepúlveda, H., Stotz, W., Tala, F., Thomas, A., Vargas, C., Vasquez, J., Vega, A., 2007. The Humboldt current system of northern and central Chile: oceanographic processes, ecological interactions and socioeconomic feedback, in: Gibson, R., Atkinson, R., Gordon, J. (Eds.), *Oceanography and Marine Biology*. CRC Press, pp. 195–344. <https://doi.org/10.1201/9781420050943.ch6>
- Thomsen, M., Byers, J., Schiel, D., Bruno, J., Olden, J., Wernberg, T., Silliman, B., 2014. Impacts of marine invaders on biodiversity depend on trophic position and functional similarity. *Mar. Ecol. Prog. Ser.* 495, 39–47. <https://doi.org/10.3354/meps10566>
- Vásquez, J.A., 2016. The Brown Seaweeds Fishery in Chile, in: Mikkola, H. (Ed.), *Fisheries and Aquaculture in the Modern World*. InTech. <https://doi.org/10.5772/62876>
- Villegas, M., Laudien, J., Sielfeld, W., Arntz, W., 2019. Effect of foresting barren ground with *Macrocystis pyrifera* (Linnaeus) C. Agardh on the occurrence of coastal fishes off northern Chile. *J Appl Phycol* 31, 2145–2157. <https://doi.org/10.1007/s10811-018-1657-1>
- Westermeier, R., Murúa, P., Patiño, D.J., Manoli, G., Müller, D.G., 2019. Evaluation of kelp harvest strategies: recovery of *Lessonia berteroana* (Phaeophyceae, Laminariales) in Pan de Azucar, Atacama, Chile. *J Appl Phycol* 31, 575–585. <https://doi.org/10.1007/s10811-018-1500-8>
- Williams, Rich J., 2010. *Network 3D: visualizing and modelling food webs and other complex networks*. Microsoft Research, Cambridge, UK.
- Worm, B., 2016. Averting a global fisheries disaster. *Proc Natl Acad Sci USA* 113, 4895–4897. <https://doi.org/10.1073/pnas.1604008113>
- Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S., Jackson, J.B.C., Lotze, H.K., Micheli, F., Palumbi, S.R., Sala, E., Selkoe, K.A., Stachowicz, J.J., Watson, R., 2006. Impacts of Biodiversity Loss on Ocean Ecosystem Services. *Science* 314, 787–790. <https://doi.org/10.1126/science.1132294>
- Yodzis, P., 2001. Must top predators be culled for the sake of fisheries? *Trends in Ecology & Evolution* 16, 78–84. [https://doi.org/10.1016/S0169-5347\(00\)02062-0](https://doi.org/10.1016/S0169-5347(00)02062-0)
- Yodzis, P., 1988. The Indeterminacy of Ecological Interactions as Perceived Through Perturbation Experiments. *Ecology* 69, 508–515. <https://doi.org/10.2307/1940449>
- Zabel, R., Harvey, C.J., Katz, S., Good, T.P., Levin, P.S., 2003. Ecologically Sustainable Yield. *Am. Sci.* 91, 150. <https://doi.org/10.1511/2003.2.150>

FIGURES

(A) Subtidal Food-web



(B) Intertidal Food-web

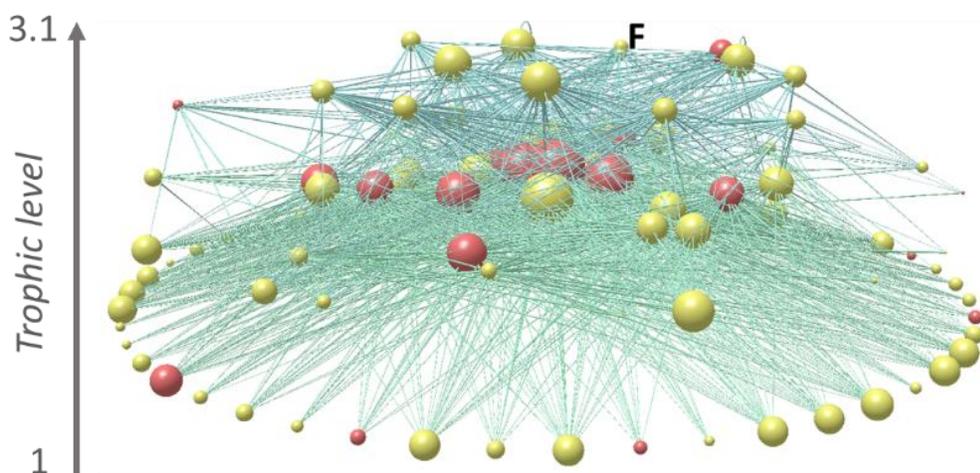


Figure 1. Subtidal (A) and Intertidal (B) food-webs. Node color represents the harvested (red) and non-harvested (yellow) species. Letter F represents the fisheries node. Node size represents the number of trophic interactions (degree) of each node. Bottom nodes represent basal species, and the nodes of the top represent top predators. The left axes represent the average trophic level (calculated as short weighted trophic level, SWTL) from the minimum to the maximum trophic level. Drawn using Network3D software (Williams, Rich J, 2010).

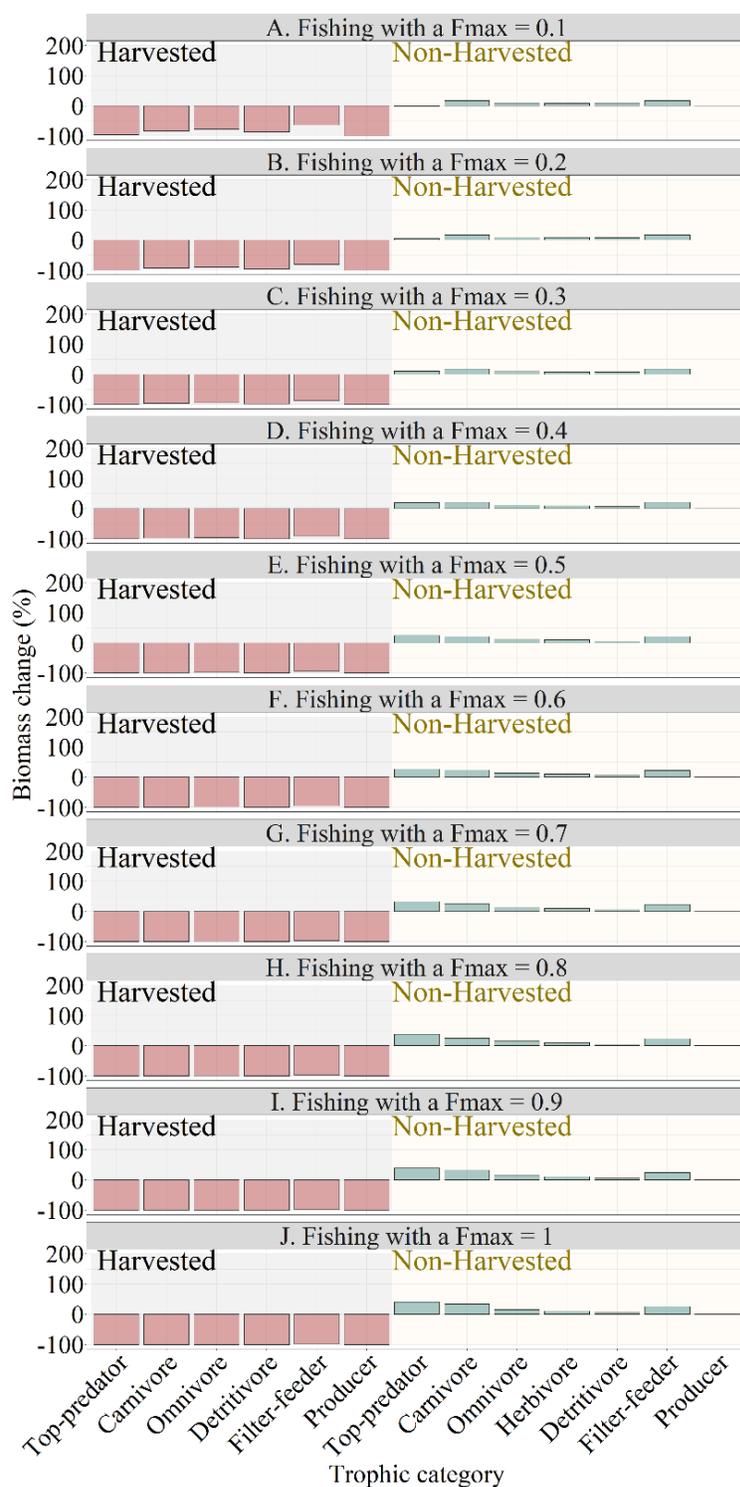


Figure 2. Total biomass change (y-axis) of each trophic category (x-axis) of the subtidal food-web after an increasing scenario of fisheries (from A to J). The red bar represents negative effects on species biomass, while green bars represent positive effects. The grey and yellow box represent the biomass change of harvested and non-harvested species, respectively.

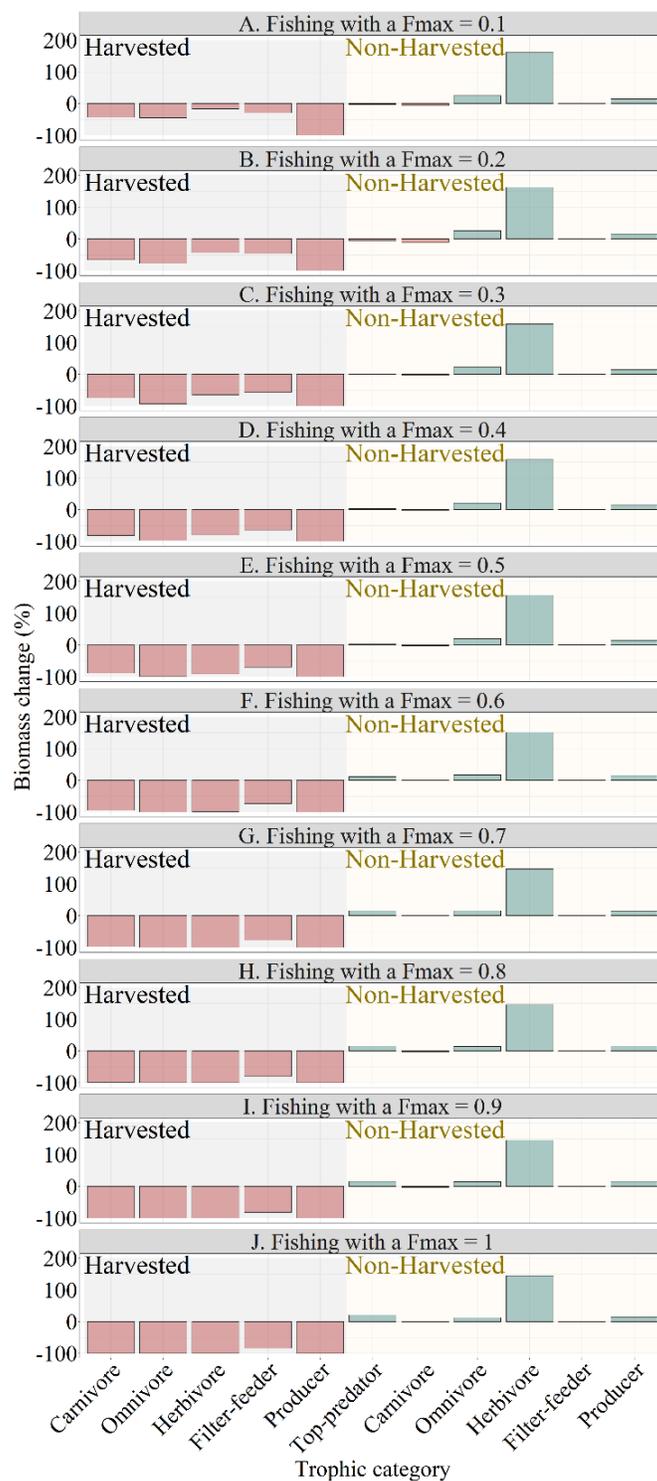


Figure 3. Total biomass change (y-axis) of each trophic category (x-axis) of the intertidal food-web after an increasing scenario of fisheries (from A to J). The red bar represents negative effects on species biomass, while green bars represent positive effects. The grey and yellow box represent the biomass change of harvested and non-harvested species, respectively.

INFORMACIÓN SUPPLEMENTARIA (CAPÍTULO 3)

KELPS ARE THE MOST SENSITIVE HARVESTED SPECIES TO SMALL-SCALE ARTISANAL FISHERIES.

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Intertidal

We used empirical measures of species body size, which was extracted from (Kéfi et al., 2015), to allometrically parameterize intrinsic growth rate of autotroph, metabolic rate, and maximum consumption rate of each species (used in equations 8, 9, and 10, respectively).

The initial biomass was estimated from density (mobile species + cnidaria) and the surface of cover (sessile species) recorded during six years of sampling in the Chilean marine reserve “Estacion Costera de Investigaciones Marinas” (ECIM) at the central-south of Chile. The density of mobile species was multiplied by the species body size. For sessile species, the surface of cover was multiplied by the weight of each species per unit of cover.

We calculated the community-level carrying capacity, K , by dividing all the primary producers into six functional groups (microalgae, ephemerals, corticates, crust, corallines, and kelps) (Boit et al., 2012). In each functional group, we multiplied the biomass of the species exhibiting the highest growth rate with the number of species that compose its functional group. Finally, we summed the resulting biomass over all functional groups.

Based on empirical experiments in aquatic (Calbet and Saiz, 2013) and terrestrial ecosystems (Mulder and Hendriks, 2014), we assumed that the half-saturation density parameter (B_0) decreases while the trophic levels increase in 10^3 order of magnitude. We use the values of (Boit et al., 2012) as a reference value. To herbivores, we fit the B_0 to ensure their persistence.

For the other parameters, we used values from (Boit et al., 2012) (see parameters values in table S3)

Subtidal

For the species in the subtidal food-web that were also present in the intertidal food-web, we used the same values for body size and initial biomass that we used for the intertidal food-web (Table S3). For species that were only found in the subtidal food-web, we recompile values of body size and initial biomass from literature. Body size values were used to parametrize the parameters related to metabolism of each specie (growth rate, metabolic rate, and maximum consumption rate, used in equations 8, 9, and 10, respectively). We calculate the reference subtidal carrying capacity (K) based on the methodology we use for the intertidal food-web. We increase the reference K to ensure the persistence of the species in the network (Table S3).

As in the intertidal food-web, in the subtidal we assume that the parameter of the half saturation density of consumers (B_0) decreases as trophic levels increase by 10^3 orders of magnitude (Calbet and Saiz, 2013; Mulder and Hendriks, 2014), using as a reference the values previously parameterized in LC (Boit et al., 2012) (values of the initial conditions in Table S3).

- Boit, A., Martinez, N.D., Williams, R.J., Gaedke, U., 2012. Mechanistic theory and modelling of complex food-web dynamics in Lake Constance: Mechanistic modelling of complex food web dynamics. *Ecology Letters* 15, 594–602. <https://doi.org/10.1111/j.1461-0248.2012.01777.x>
- Brose, U., Williams, R.J., Martinez, N.D., 2006. Allometric scaling enhances stability in complex food webs. *Ecol Letters* 9, 1228–1236. <https://doi.org/10.1111/j.1461-0248.2006.00978.x>
- Calbet, A., Saiz, E., 2013. Effects of trophic cascades in dilution grazing experiments: from artificial saturated feeding responses to positive slopes. *Journal of Plankton Research* 35, 1183–1191. <https://doi.org/10.1093/plankt/fbt067>
- Gómez-Canchong, P., Quiñones, R.A., Brose, U., 2013. Robustness of size–structure across ecological networks in pelagic systems. *Theor Ecol* 6, 45–56. <https://doi.org/10.1007/s12080-011-0156-7>

- Kéfi, S., Berlow, E.L., Wieters, E.A., Joppa, L.N., Wood, S.A., Brose, U., Navarrete, S.A., 2015. Network structure beyond food webs: mapping non-trophic and trophic interactions on Chilean rocky shores. *Ecology* 96, 291–303. <https://doi.org/10.1890/13-1424.1>
- Mulder, C., Hendriks, A.J., 2014. Half-saturation constants in functional responses. *Global Ecology and Conservation* 2, 161–169. <https://doi.org/10.1016/j.gecco.2014.09.006>
- Richard, J.W., Brose, U., Martinez, N.D., 2006. Homage to Yodzis and Innes 1992: Scaling up feeding-based population dynamics to complex ecological networks, in: *From Energetics to Ecosystems: The Dynamics and Structure of Ecological Systems*. Springer Netherlands, pp. 37–51. https://doi.org/10.1007/978-1-4020-5337-5_2
- Testa, G., Masotti, I., Farías, L., 2018. Temporal variability in net primary production in an upwelling area off central Chile (36°S). *Front. Mar. Sci.* 5, 179. <https://doi.org/10.3389/fmars.2018.00179>
- Williams, R.J., 2008. Effects of network and dynamical model structure on species persistence in large model food webs. *Theor Ecol* 1, 141–151. <https://doi.org/10.1007/s12080-008-0013-5>

TABLES

Table S1. List of species name of the subtidal food-web species number that is represented in the x-axis of fig. 2.

Code	Specie Name	Code	Specie Name	Code	Specie Name
1	<i>Acanthistius pictus</i>	53	<i>Petrolisthes tuberculatus</i>	105	Ophiuroidea
	<i>Cheilodactylus</i>				
2	<i>variegatus</i>	54	<i>Pisoides edwardsii</i>	106	<i>Petrolisthes desmarestii</i>
3	<i>Paralabrax humeralis</i>	55	Polychaeta_carnivore	107	<i>Semimytilus algosus</i>
4	<i>Semicossyphus darwini</i>	56	Polychaeta_omnivore	108	<i>Turritella cingulata</i>
5	<i>Cancer plebejus</i>	57	<i>Robsonella fontaniana</i>	109	Amphipoda_detritivore
6	<i>Fissurella crassa</i>	58	<i>Tegula quadricostata</i>	110	<i>Liopetrolisthes mitra</i>
7	<i>Genypterus chilensis</i>	59	Isopoda_omnivore	111	<i>Nemertea</i>
8	<i>Paralichthys adspersus</i>	60	<i>Myxodes</i> sp.	112	<i>Tanaidacea</i>
			<i>Allopetrolisthes</i>		
9	<i>Paralichthys microps</i>	61	<i>angulosus</i>	113	<i>Tonicia chilensis</i>
10	<i>Pinguipes chilensis</i>	62	Amphipoda_herbivore	114	Vermetidae
					<i>Gaudichaudia</i>
11	<i>Sebastes oculatus</i>	63	Amphipoda_omnivore	115	<i>gaudichaudi</i>
12	<i>Aplodactylus punctatus</i>	64	<i>Anemonia alicemartinae</i>	116	Nematoda
	<i>Concholepas</i>				
13	<i>concholepas</i>	65	<i>Calyptraea trochiformis</i>	117	<i>Ahnfeltiopsis durvillei</i>
14	<i>Fissurella costata</i>	66	<i>Chiton cumingsii</i>	118	<i>Blidingia</i> sp.
15	<i>Fissurella cumingi</i>	67	<i>Chromis crusma</i>	119	<i>Bossiella chiloensis</i>
	<i>Fissurella</i>				
16	<i>latimarginata</i>	68	<i>Gobiesox marmoratus</i>	120	<i>Ceramium</i> spp.
17	<i>Fissurella limbata</i>	69	<i>Meyenaster gelatinosus</i>	121	<i>Chaetomorpha</i> spp.
					<i>Chondria</i>
18	<i>Fissurella maxima</i>	70	<i>Paraxanthus barbiger</i>	122	<i>acrorhizophora</i>
19	<i>Fissurella picta</i>	71	<i>Phymactis clematis</i>	123	<i>Chondrus canaliculatus</i>
20	<i>Graus nigra</i>	72	Polychaeta_depositivore	124	<i>Cladophora</i> spp.
	<i>Hemilutjanus</i>				
21	<i>macrophthalmos</i>	73	<i>Prisogaster niger</i>	125	<i>Codium</i> spp.
22	<i>Homalaspis plana</i>	74	<i>Rhynchocinetes typus</i>	126	<i>Colpomenia</i> spp.
23	<i>Isacia conceptionis</i>	75	<i>Scartichthys viridis</i>	127	<i>Corallina</i> spp.
			<i>Schroederichthys</i>		
24	<i>Loxechinus albus</i>	76	<i>chilensis</i>	128	<i>Dictyota kunthii</i>
	<i>Metacarcinus</i>				
25	<i>edwardsii</i>	77	<i>Siphonaria lessoni</i>	129	<i>Ectocarpus</i> sp.
26	<i>Romaleon setosus</i>	78	<i>Stichaster striatus</i>	130	<i>Gelidium</i> spp.
					<i>Heterosiphonia</i>
27	<i>Sicyases sanguineus</i>	79	<i>Taliepus dentatus</i>	131	<i>subsecundata</i>
	<i>Austromegabalanus</i>				<i>Plocamium</i>
28	<i>psittacus</i>	80	<i>Taliepus marginatus</i>	132	<i>cartilagineum</i>

29	<i>Choromytilus chorus</i>	81	<i>Tegula tridentata</i>	133	<i>Pterosiphonia</i> sp.
30	<i>Pyura chilensis</i>	82	<i>Tetrapygus niger</i>	134	<i>Ralfsia</i> spp.
31	<i>Aulacomya atra</i>	83	<i>Alia unifasciata</i>	135	<i>Rhodymenia skottsbergii</i>
32	<i>Athyonidium chilensis</i>	84	<i>Eulithidium umbilicatum</i>	136	<i>Schottera nicaeensis</i>
33	<i>Lessonia trabeculata</i>	85	<i>Girella laevifrons</i>	137	<i>Ulva</i> spp.
34	<i>Macrocystis pyrifera</i>	86	<i>Heliaster helianthus</i>	138	<i>Halopteris</i> spp. <i>Hildenbrandia</i>
35	<i>Labrisomus philippii</i>	87	<i>Hypsoblennius sordidus</i>	139	<i>lecannellieri</i>
36	<i>Lutra felina</i>	88	Bryozoa	140	<i>Laurencia</i> sp.
37	Alpheidae	89	Isopoda_herbivore	141	<i>Lithophyllum</i> sp.
38	<i>Antholoba achates</i>	90	Lottiidae	142	<i>Eatoniella</i> sp.
	<i>Auchenionchus</i>				
39	<i>microcirrhis</i>	91	<i>Pagurus comptus</i>	143	Biofilm
40	<i>Bovichtus chilensis</i>	92	<i>Pagurus edwardsii</i>	144	Detritus
	<i>Calliclinus</i>				
41	<i>geniguttatus</i>	93	<i>Pagurus vilosus</i>	145	Plankton
	<i>Crassilabrum</i>				
42	<i>crassilabrum</i>	94	<i>Pilumnoides perlatus</i>	146	<i>Polysiphonia</i> spp.
43	<i>Eptatretus polytrema</i>	95	<i>Polychaeta_herbivore</i>		
	<i>Helcogrammoides</i>		<i>Allopetrolisthes</i>		
44	<i>cunninghami</i>	96	<i>spinifrons</i>		
45	<i>Nassarius gayii</i>	97	Amphipoda_depositivore		
46	<i>Odontaster penicillatus</i>	98	Amphipoda_suspensivore		
47	Opisthobranchia	99	<i>Anthothoe chilensis</i>		
48	<i>Oulactis concinnata</i>	100	<i>Balanus</i> spp.		
49	<i>Patiria chilensis</i>	101	<i>Brachidontes granulatus</i>		
50	<i>Cycethra verrucosa</i>	102	Demospongiae		
51	<i>Petrolisthes laevigatus</i>	103	Hydrozoa		
	<i>Petrolisthes</i>				
52	<i>tuberculatus</i>	104	<i>Mytilus edulis platensis</i>		

Table S2. List of species name of the intertidal food-web species number that is represented in the x-axis of fig. 3.

Code	Specie Name	Code	Specie Name	Code	Specie Name
1	<i>Acanthina monodon</i>	47	<i>Scurria viridula</i>	93	<i>Peysonella</i> spp.
	<i>Concholepas</i>				<i>Plocamium</i>
2	<i>concholepas</i>	48	<i>Scurria zebrina</i>	94	<i>cartilagineum</i>
	<i>Acanthopleura</i>				
3	<i>echinata</i>	49	<i>Siphonaria lessoni</i>	95	<i>Prionitis</i> spp.
			<i>Echinolittorina</i>		<i>Gastroclonium</i>
4	<i>Chiton granosus</i>	50	<i>peruviana</i>	96	<i>cylindricum</i>
			<i>Austrolittorina</i>		
5	<i>Fissurella costata</i>	51	<i>araucana</i>	97	<i>Rhodymenia</i> sp.
6	<i>Fissurella crassa</i>	52	<i>Onchidella</i> sp.	98	<i>Schottera nicaensis</i>
7	<i>Fissurella cummingi</i>	53	<i>Balanus laevis</i>	99	<i>Schyzimonia doryophora</i>
8	<i>Fissurella limbata</i>	54	<i>Jhelius cirratus</i>	100	<i>Trematocarpus</i> spp.
					<i>Corallina officinalis</i> var.
9	<i>Fissurella maxima</i>	55	<i>Nothobalanus flosculus</i>	101	Chilensis
			<i>Nothochthamalus</i>		<i>Hildenbrandia</i>
10	<i>Fissurella picta</i>	56	<i>scabrosus</i>	102	<i>lecanelierii</i>
			<i>Brachidontes</i>		
11	<i>Fissurella puhlcra</i>	57	<i>granulata</i>	103	<i>Lithothamnion</i> spp.
			<i>Perumytilus</i>		
12	<i>Scurria scurra</i>	58	<i>purpuratus</i>	104	<i>Ralfsia californica</i>
13	<i>Tegula atra</i>	59	<i>Semimytilus algosus</i>	105	Benthic diatoms
	<i>Austromegabalanus</i>		<i>Allelopetrolisthes</i>		
14	<i>psittacus</i>	60	<i>punctatus</i>	106	Plankton
15	<i>Pyura chilensis</i>	61	<i>Petrolisthes spinifrons</i>		
16	<i>Durvillaea antarctica</i>	62	<i>Petrolisthes angulosus</i>		
			<i>Petrolisthes</i>		
17	<i>Lessonia nigrescens</i>	63	<i>tuberculatus</i>		
			<i>Petrolisthes</i>		
18	<i>Gelidium rex</i>	64	<i>tuberculosis</i>		
19	<i>Sarcothalia</i> spp.	65	<i>Phragmatopoma</i> spp.		
	<i>Mazzaella</i>				
20	<i>laminarioides</i>	66	<i>Bryopsis</i> spp.		
21	<i>Pyropia</i> spp.	67	<i>Centroceras</i> spp.		
22	<i>Ulva rigida</i>	68	<i>Ceramium</i> spp.		
23	Gulls	69	<i>Chaetomorpha</i> spp.		
	<i>Cinclodes</i>				
24	<i>nigrofumosus</i>	70	<i>Cladophora</i> spp.		
25	<i>Anthotoe</i> spp.	71	<i>Ectocarpus silicosus</i>		
			<i>Enteromorpha</i>		
26	<i>Bunodactis</i> spp.	72	<i>compressa</i>		
27	<i>Oulactis concinnata</i>	73	<i>Halopteris funicularis</i>		
28	<i>Parantheopsis</i> spp.	74	<i>Polysiphonia</i> spp.		

29	<i>Phymactis</i> spp.	75	<i>Rhizoclonium</i>
	<i>Trimusculus</i>		<i>ambiguum</i>
30	<i>peruvianus</i>	76	<i>Scythosiphon</i>
31	<i>Heliaster helianthus</i>	77	<i>lomentaria</i>
32	<i>Stichaster striatus</i>	78	<i>Ulvella</i> spp.
33	<i>Acanthocyclus gayi</i>	79	<i>Adenocystis utricularis</i>
			<i>Ahnfeltiopsis</i> spp.
			<i>Chondrus</i>
34	<i>Acanthocyclus hassleri</i>	80	<i>canaliculatus</i>
	<i>Chaetopleura</i>		
35	<i>peruviana</i>	81	<i>Codium dimorpha</i>
			<i>Colpomenia</i>
36	<i>Chiton cummingsi</i>	82	<i>phaeodactyla</i>
37	<i>Chiton latus</i>	83	<i>Colpomenia sinuosa</i>
38	<i>Enoplochiton niger</i>	84	<i>Gelidium</i> spp.
39	<i>Tonicia lineolata</i>	85	<i>Glossophora kunthii</i>
40	<i>Tonicia chilensis</i>	86	<i>Grateloupia</i> spp.
			<i>Gymnogongrus</i>
41	<i>Tonicia elegans</i>	87	<i>furcellatus</i>
42	<i>Lottia orbignyi</i>	88	<i>Laurencia chilensis</i>
43	<i>Scurria araucana</i>	89	<i>Montemaria horridula</i>
44	<i>Scurria ceciliana</i>	90	<i>Nothogenia</i> spp.
45	<i>Scurria plana</i>	91	<i>Petalonia Fascia</i>
46	<i>Scurria variabilis</i>	92	<i>Petroglossum</i> spp.

Table S3. Summary of the parameters used in the ATN model for the subtidal and intertidal food-web of central Chile.

Parameter	Unit of measurement	Definition	Initial values min., max	Data sources
B	g/m ²	Population abundance	<p>Intertidal: 1.3 x 10⁻⁴, 112107</p> <p>Subtidal: 0.03, 112107</p>	<p>Intertidal: Empirical data obtained in ECIM. For plankton and benthic diatoms, data was extracted from (Gómez-Canchong et al., 2013)</p> <p>Subtidal: For the species present in both food-webs, we assume that the abundance of the species in the subtidal is the same as that obtained empirically for the intertidal. For species present only in the subtidal, abundance values were obtained from the literature.</p>
M	g	Body mass	<p>Intertidal: 1 x 10⁻⁵, 500</p> <p>Subtidal: 3.8 x 10⁻⁸, 4500</p>	<p>Intertidal: Base on empirical data from (Kéfi et al., 2015)</p> <p>Subtidal: For the species present in both food-webs, we assume that the body size of the species in the subtidal is the same as that obtained empirically for the intertidal. For species present only in the subtidal, abundance values were obtained from the literature.</p>

r_i	1/day	Mass-specific growth rate for basal species	Intertidal: 0.12, 3.74 Subtidal: 0.01, 1.6	(Brose et al., 2006)
x_i	1/day	Mass-specific metabolic rate	Intertidal: 0.72, 61.4 Subtidal: 0.17, 50.2	(Brose et al., 2006)
y_i	1/day	Maximum ingestion rate	Intertidal: 1.63, 5.82 Subtidal: 0.7, 5.82	(Brose et al., 2006)
K	g/m^2	Basal species carrying capacity	Intertidal: 176299 Subtidal: 5381136	(Boit et al., 2012)
C		Basal species inter-specific competition coefficient	1	(Boit et al., 2012)
f_a		Activity metabolism coefficient	0.4	(Boit et al., 2012)
f_m		Maintenance respiration coefficient	0.1	(Boit et al., 2012)

e_{ij}		Assimilation efficiency	Herbivores: 0.45 Carnivores: 0.85	(Richard et al., 2006)
d_{ij}	m^2/g	Feeding interference coefficient	0.5	(Boit et al., 2012)
q_{ij}		Functional response shape parameter	1.2	(Williams, 2008)
w_{ij}		Relative prey preference	$1/n_{\text{available resources}}$	(Boit et al., 2012)
p_{ij}		Fraction of resource species shared	0, 1	(Boit et al., 2012)
BO_{ij}	g/m^2	Half-saturation densities	Intertidal: 50, 15000 Subtidal: 1500, 15000	(Boit et al., 2012)
s	g/m^2	Plancton (both food-webs) and detritus (subtidal food-web) subsidy biomass	12% of initial biomass	(Testa et al., 2018)

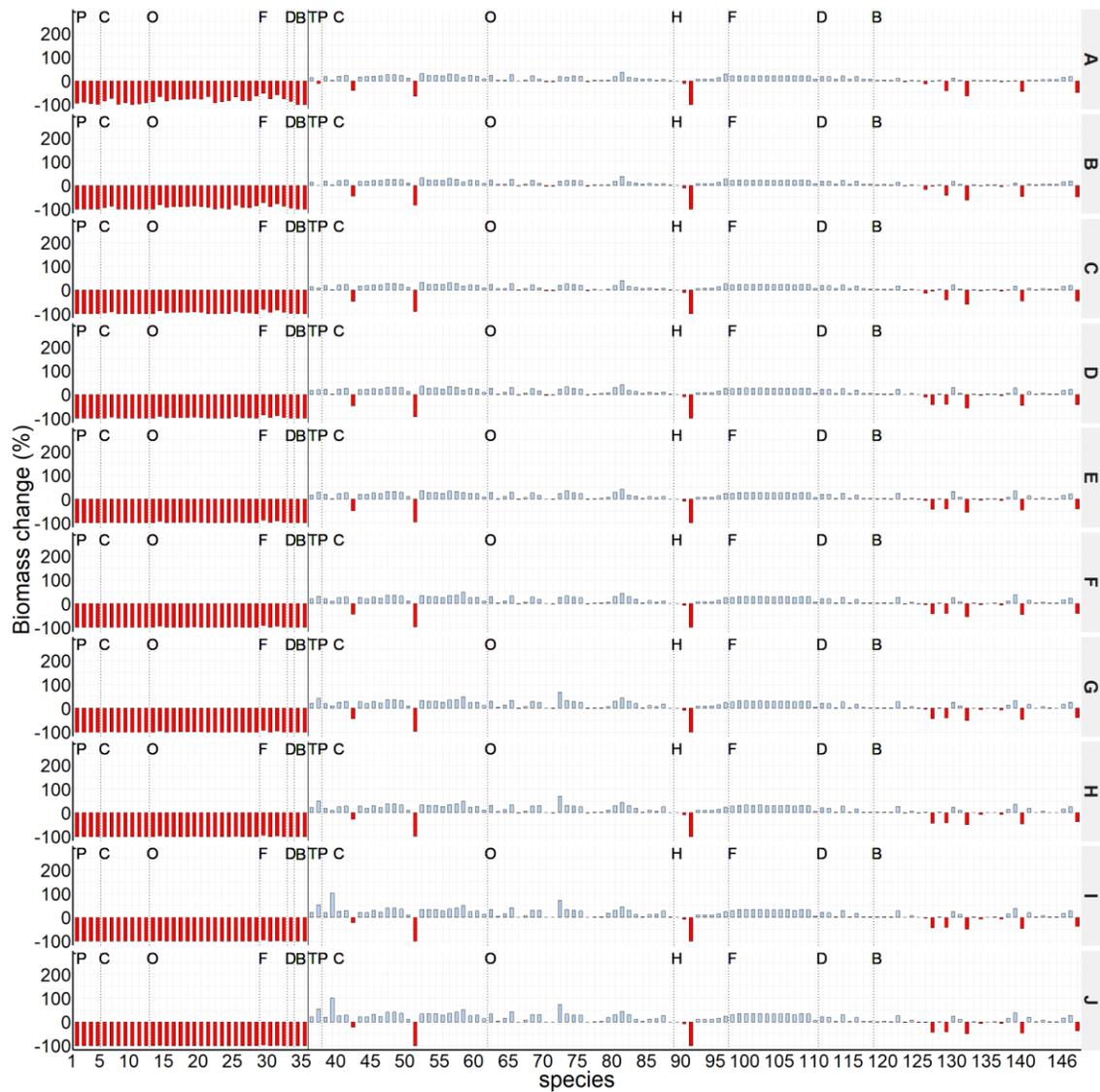


Figure S1. Biomass change (y-axis) of each species (x-axis) of the subtidal food-web after an increasing scenario of fisheries (from A to J). The red bar represents negative effects on species biomass, while blue bars represent positive effects. From the bold vertical line to the left, the figure shows all the harvested species. From the bold line to the right, the figure shows all the non-harvested species. Species are organized by trophic level (TP: top-predators, C: carnivores, O: omnivores, H: herbivores, F: filter-feeders, D: detritus, B: basal species) and their identity can be found by matching their number id with the numbers in Table S1 of the appendix.

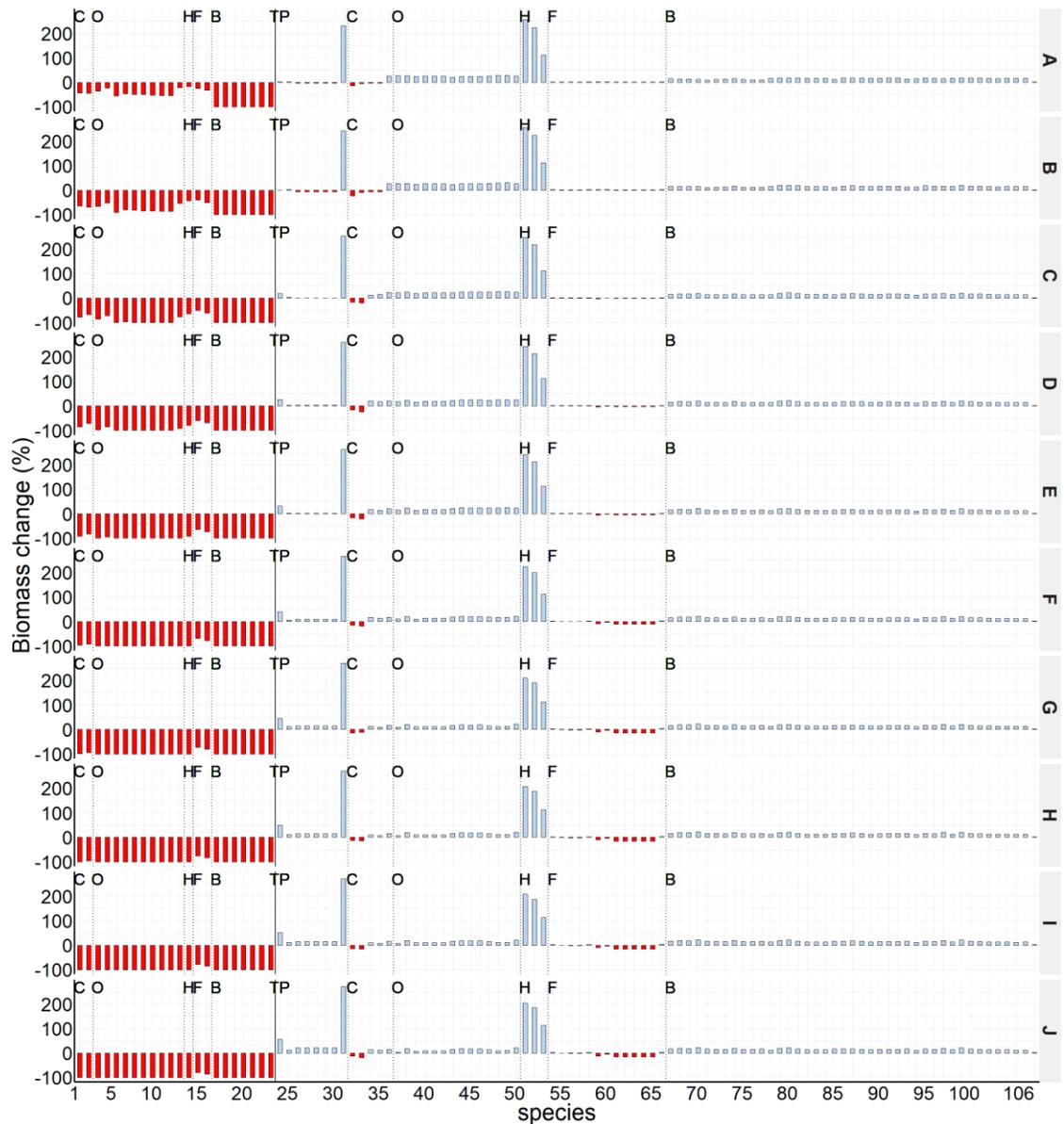


Figure. S2. Biomass change (y-axis) of each species (x-axis) of the intertidal food-web after an increasing scenario of fisheries (from A to J). The red bar represents negative effects on species biomass, while blue bars represent positive effects. From the bold vertical line to the left, the figure shows all the harvested species. From the bold line to the right, the figure shows all the non-harvested species. Species are organized by trophic level (TP: top-predators, C: carnivores, O: omnivores, H: herbivores, F: filter-feeders, B: basal species) and their identity can be found by matching their number id with the numbers in Table S2 of the appendix

CAPÍTULO 4.

EXPLORING THE EFFECTS OF SPACE COMPETITION TO UNDERSTAND THE IMPACTS OF FISHERIES ON BENTONIC FOOD WEBS.

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Abstract

Space competition is one of the most limiting non-trophic resources to sessile species in marine benthic ecosystems. Recent studies revealed that non-trophic interactions, especially those of competition for space, play a relevant role in understanding the dynamic of trophic networks. However, the research on ecological networks is mainly focused on trophic interactions. Here, we went further and assessed the role of space competition to understand the impacts of small-scale artisanal fisheries on benthic intertidal rocky-shore food-webs of central Chile. We simulated the food-web dynamics with and without space competition between sessile species. In both treatments, we simulated different fishing scenarios, and we compared their subsequent

impact on the biomass of all the species in the food-web. We found that considering the competition for space between sessile species generates opposite results at the higher non-harvested trophic levels, while in the rest of the non-harvested species, it only intensifies the effects found when space competition is not considered. Regardless of whether the competition for space is present, we find that the harvested macroalgae always were the most sensitive harvested species to fishing, while the filter-feeders were the most resistant to fishing. However, with space competition, the sensitivity to the fishing of harvested carnivores decreased, while the sensitivity to the fishing of omnivores and herbivores increased. Therefore, our results suggest that space-competition is a not trivial non-trophic interaction that should be considered to understand fisheries' impacts on benthic ecosystems. Finally, we believe that future work should incorporate other key non-trophic interactions, such as facilitation, to understand the impacts of fishing.

INTRODUCTION

In benthic marine ecosystems, space as a limiting resource promotes the space competition between sessile species (Connell, 1961; Dayton, 1971; Santelices, 1990; Svensson and Marshall, 2015; Swierts and Vermeij, 2016). Competition for space is a negative non-trophic interaction that affects, to a greater or lesser extent, all sessile species in benthic communities (Chadwick and Morrow, 2011; Kéfi et al., 2016, 2015), altering their abundance and spatial dominance (Castilla, 1999; Chadwick and Morrow, 2011). In consequence, space competition plays an important role in the structure and dynamics of biological communities (Alexandridis et al., 2017; Kéfi et al., 2016, 2012; Miele et al., 2019).

The intertidal rocky shore food-web of central Chile is a perfect model ecosystem to analyze the impact of space competition in food-web dynamics. Previous studies have been revealed that non-trophic interactions can be more than twice as trophic interactions (Kéfi et al., 2015), which promotes species persistence and abundance in this ecosystem (Kéfi et al., 2016). Among non-trophic interactions, the negative ones prevail over the positive ones (Kéfi et al., 2015), and competition for space between sessile is one of the most influential in the stability of the food-web (Miele et al., 2019). On the other hand, this ecosystem is not exempt from humans' perturbations, such as fishing exploitation. In the Chilean intertidal rocky shore, small-scale artisanal fishers (Castilla and Defeo, 2001) remove species from all trophic levels, including several sessile species (Ávila-Thieme et al., unpublished data) and can induce important changes in the structure of the community and the abundance of the dominant competitor for space (Castilla & Durán 1985, Castilla & Bustamante 1989, Castilla 1999, Manriquez et al. 2016). Therefore, artisanal fisheries could be altering the space competition between sessile species, as removing biomass of sessile species by fishing can relax the intensity of competition for space and change the strength of competition among those who remain there. However, the role of fishing in the abundance of species and the structure and dynamics of benthic communities has been mainly focused in their trophic relationships (Ávila-Thieme et al., unpublished data; Dunn et al., 2017; Dunne et al., 2016; Ortiz, 2008; Ortiz et al., 2015; Pérez-Matus et al., 2017).

In this work, we evaluated the role that competition for space has on understanding the effects of artisanal fisheries on the dynamics of a comprehensive intertidal rocky shore food-web of central-Chile (hereafter referred as intertidal food-web). We used the allometric trophic network model (Kuparinen et al., 2016; Richard et al., 2006) to simulate the simultaneous

fishing of all harvested species in the intertidal network when the competition for space is and is not considered. Particularly, we assessed the changes that different exploitation rates produce in the biomass of all the species in the intertidal network (harvested and non-harvested species) between before and after fisheries simulation.

METHODS

Food-web description and its robustness to species extinctions

We study a well-resolved food-web in the intertidal rocky shore of the central coast of Chile. This food-web is influenced by the highly productive Humboldt Current System (HCS) (Thiel et al., 2007) and harvested exclusively by small scale artisanal fisheries (Gelcich et al., 2010). The intertidal food-web has 107 species, 1381 trophic interactions, and connectance of 0.12, with 44% of its species corresponding to primary producers, 53% to invertebrates, 3% to endotherm vertebrates 46% to mobile species, and 56% to sessile species (primary producers + sessile filter-feeders). Fisheries harvest on 22 (21%) of the species including numerous species of macroalgae (including kelps) and sessile and mobile invertebrates (Fig. 1), harvest on highly connected species and harvest at least one predator and one prey of several species in the food-web (Ávila-Thieme et al., unpublished data).

The dynamic model without space competition between sessile species

In this model, all primary producers and plankton were considered as a basal species. The ATN model consists of two sets of equations, one describing the biomass changes of primary producers (eq. 1) and the other describing that of consumers (eq. 2), where \mathbf{B} is the biomass vector with the biomasses of every population in the food-web and B_i is the biomass of the population i , as follows

$$\frac{dB_i}{dt} = \overbrace{r_i B_i G_i(\mathbf{B})}^{\text{Autotrophic growth gain}} - \overbrace{\sum_j \frac{x_j y_{ji} B_j F_{ji}(\mathbf{B})}{e_{ji}}}^{\text{Herbivory loss}} - \overbrace{F_{\max i} B_i}^{\text{Fisheries loss}} \quad (\text{eq. 1})$$

$$\frac{dB_i}{dt} = \overbrace{f_a x_i B_i \sum_j y_{ij} F_{ij}(\mathbf{B})}^{\text{Resources consumption gain}} - \overbrace{f_m x_i B_i}^{\text{Maintenance loss}} - \overbrace{\sum_j \frac{x_j y_{ji} B_j F_{ji}(\mathbf{B})}{e_{ji}}}^{\text{Predation loss}} - \overbrace{F_{\max i} B_i}^{\text{Fisheries loss}} \quad (\text{eq. 2})$$

The biomass of producer i changes according to the balance of autotrophic growth gain and predation loss. The net autotrophic growth is determined by the logistic growth function $G_i(B) = 1 - (\sum_{j=\text{productores}} c_{ij} B_j)/K$, where r_i is the intrinsic growth rate of producer i , c_{ij} is the inter-specific competition coefficient between producer i and j , and K is the total carrying capacity of primary producers in the system. The biomass loss of producer i by herbivory (caused by herbivores or omnivores) increases with the mass-specific metabolic (x_j) and attack (y_j) rates of consumer i , and decreases with the assimilation efficiency of consumer i for resource j (e_{ij}). The consumers' population dynamics (eq. 2) depend on its mass-specific metabolic rate (x_j) and on the balance between biomass gain by resource consumption, biomass loss by metabolic maintenance, and biomass loss by predation. From the total amount of resources ingested by the consumer population i , $\sum_j y_{ij} F_{ij}(\mathbf{B})$, only a fraction f_a is assimilated into consumer biomass. The functional response $F_{ij}(\mathbf{B})$ determines the consumption rate of each consumer i for each resource j , defined by:

$$F_{ij}(\mathbf{B}) = \frac{\omega_{ij} B_j^q}{B_0_{ij}^q + d_i B_i B_0_{ij} + \sum_{l=\text{resources}} \omega_{il} B_l^q} \quad (\text{eq. 3})$$

where ω_{ij} is the relative preference of consumer i for resource j , q controls the shape of eq. 3 which becomes an intermediate functional response between type II and type III when $q=1.2$ (Williams, 2008). $B0_{ij}$ is the biomass of resource j at which the consumer i achieves half of its maximum consumption rate on resource j , and d_i is the intra-specific interference of consumer i when it forages resource j . In eq. 2, f_m defines the fraction of the consumer biomass that is respired as maintenance. F_{max} defines the fraction of biomass i that is removed by small-scale artisanal fisheries.

The biological rates of production, R , metabolism, X , and maximum consumption, Y , follow a negative power law with the species body size, with an exponent -1.4:

$$R_P = a_r M_P^{-0.25} \quad (\text{eq. 4})$$

$$X_C = a_x M_C^{-0.25} \quad (\text{eq. 5})$$

$$Y_c = a_y M_C^{-0.25} \quad (\text{eq. 6})$$

Where a_r , a_x , and a_y are allometric constant and the subscripts P and C stand for producers and consumer, respectively. The time scale is defined based on the primary producer with highest mass-specific growth rate (reference species). The mass-specific growth rate and the metabolic rate of each species were normalized by the growth rate of the reference species, and the maximum consumption rate was normalized each species' metabolic rate (Brose et al., 2006). These assumptions translate to the following expressions of intrinsic growth rate (r_i), metabolic rate (x_i), and maximum consumption rate (y_i) of each species i :

$$r_i = \frac{R_P}{R_{Pref}} = 1 \left(\frac{M_P}{M_{Pref}} \right)^{-0.25} \quad (\text{eq. 7})$$

$$x_i = \frac{X_C}{R_{Pref}} = \frac{a_x}{a_r} \left(\frac{M_C}{M_{Pref}} \right)^{-0.25} \quad (\text{eq. 8})$$

$$y_i = \frac{Y_C}{X_C} = \frac{a_y}{a_x} \quad (\text{eq. 9})$$

The dynamic model with space competition between sessile species

In this model, we considered all primary producers and all sessile filter-feeders as a basal species. Therefore, we modified the way to simulate the dynamic of basal species in the ATN model that we previously described. The eq. 1 of the dynamic model, instead of describing the biomass changes of primary producers, describes the biomass changes of all sessile species. Thus, the growth of basal species is also determined by the logistic growth function $G_i(B) = 1 - (\sum_{j=\text{basal species}} c_{ij} B_j) / K$, where r_i is the intrinsic growth rate of species i , c_{ij} is the inter-specific space competition coefficient between specie i and j , and K is the total space carrying capacity of basal species in the system. We maintained the plankton node as a basal specie to ensure the energy input to mobile filter-feeders. Due to plankton is available in the seawater rather than settled in the substrate, we do not consider it as a competitor for space. The biomass loss of basal species by predation and fisheries, as well as the rest of the model remained as we described in the previous section.

Implementation of the dynamic model

In Chilean benthic ecosystems, fisheries harvest on keystone species that are highly recognized by their trophic preference over the mussel *Perumitylus purpuratus* (Castilla, 1999). Therefore, we incorporate this trophic preferences (parameter ω_{ij} in the eq. 3) into the following consumers: *Acanthina monodon* (Soto et al., 2004), *Concholepas concholepas* (Serra et al., 1997), and *Heliaster heliantus* (Navarrete and Manzur, 2008).

Chilean marine ecosystems are one of the most productive ecosystems on the planet, mainly because of the nutrient enrichment caused by the Humboldt Current and upwelling systems (Thiel et al., 2007). This enrichment subsidizes most of the basal species (Testa et al., 2018), especially in plankton. To account for this phenomenon, our implementation of the ATN model assumes that the coastal currents and waves are permanently subsidizing the biomass of plankton. However, depending on the model, we modeled the plankton differently. In the model without space competition, due to all sessile and mobile filter-feeders depend trophically on plankton, we incorporated a constant of subsidy s (Pascual and Caswell, 1991; Schreiber and Moore, 2018) into the plankton dynamics as:

$$\frac{dB_i}{dt'} = d_{local} + s, \quad (\text{eq. 10})$$

where d_{local} represents plankton local dynamics (i.e., the right hand of eq. 1). While in the model with space competition, due to just mobile filter-feeders depend trophically on plankton, we kept the plankton biomass constant throughout the simulations.

Understanding the effects of fisheries on food-webs dynamics.

We assessed the impacts of small-scale artisanal fisheries on intertidal food-web dynamic, fishing simultaneously over all harvested species, and evaluate its subsequent effect on the biomass of all the species in the food-web. Separately, we coupled both allometric trophic network models (ATN) (with and without space competition) to the food-web (see model description above and parametrization in appendix section), simulated the simultaneous fishing of all the species that are naturally harvested by artisanal fishing (22 species), and

assessed its subsequent impact on the biomass of all the species in the food-web. In each model, we simulate ten fishing scenarios, each one with a different exploitation rate (F_{\max} parameter in the ATN model). The exploitation rate varied between the values 0.1 to 1. A value of $F_{\max} = 0.1$ means that the fisheries harvest 10% of the fishing stock; while a value of $F_{\max} = 1$ means that fisheries harvest 100% of the fishing stock. Within each fishing scenario, we simulated the simultaneously fishing of all harvested species with the same exploitation rate. We use these exploitation rates due to the high uncertainty the exists in the official landings as artisanal fishers lie, over- or underestimating their landings (Oyanedel et al., 2018).

Simulations.

In each model (with and without space competition) and each fishing scenario, we first run the model for 3650 time-steps (equivalent to 10 years) to ensure that the system reached a dynamic equilibrium, and the final species biomasses obtained were considered “before fishing” state ($F_{\max} = 0$). Then, we run the food-web dynamic for another 3650 time-steps to reach a post perturbation equilibrium, and final biomasses were considered “after fishing” state ($F_{\max} > 0$). Species were considered extinct if their biomasses diminished below 10^{-6} (Schneider et al., 2016)

In each model and in each fishing scenario and for each species i , we evaluated the effects of artisanal fisheries as:

$$Biomass\ change_i = \left[\left(\frac{after\ fishing}{before\ fishing} \right) - 1 \right] \quad (eq. 11)$$

The harvested species that after fishing had the highest biomass declines, were considered the most sensitive species in the food-web.

RESULTS

Assessing the effect of competition for species after fishing on non-harvested species

The total biomass of top predator's species responded differentially after fishing when the competition for space was present and absent into the model. With space competition, the total biomass of top predators decreased after fishing (Fig. 2). Without space competition, the biomass of top predators hardly decreased after our lower exploitation rates (Fig. 2A); while increased at higher exploitation rates (Fig. 2B to D and Fig. S1D to J). Conversely, the competition for space did not alter the direction in which the total biomass of the rest of the non-harvested trophic levels changes after fishing, only affected the magnitude of their responses. Therefore, fishing over all harvested species produced negative effects on the total biomass of carnivores and positive effects on the total biomass of the lower trophic (Fig. 2).

Fig. 2. Total biomass changes (y-axis) of each trophic (x-axis) after simulating a subset of the different fishing scenarios (from A to D) when space competition between sessile species is (red bars) and is not (green bars). The grey and yellow box represent the total biomass change of harvested and non-harvested trophic levels, respectively.

Assessing the effect of competition for species after fishing on harvested species

Regardless of the competition for space, harvested macroalgae and harvested filter-feeders were the most sensitive and tolerant species to fishing, respectively. In both space competition scenarios, harvested macroalgae do not tolerate our lower simulated exploitation

rates (Fig. 2A), while filter-feeders were not extinguished with our maximum exploitation rate (Fig. 2D).

Conversely, space competition has effects on the sensitivity to the fishing of the rest of the harvested species. With space competition, harvested carnivores tolerated lower exploitation rates before going extinct than without space competition, while harvested omnivores and herbivores tolerated higher exploitation rates (Fig. 3). Particularly, the harvested carnivores went from being the most to the least tolerant non-algal resources to fishing when space competition was absent and present, respectively (Fig. 3).

DISCUSSION

In this work, we assessed the role of considering space competition to understand the impacts of small-scale artisanal fisheries on benthic intertidal rocky-shore food-webs of central Chile. We simulated the food-web dynamics with and without space competition. In both treatments, we simulated different fishing scenarios, and we compared their impact on the biomass of all the species in the food-web. Our results suggest that space-competition is a not trivial non-trophic interaction that should be considered to understand fisheries' impacts on benthic ecosystems.

The relevance of non-trophic interactions for the coexistence, production, and stability of biological communities is increasingly evident (Berlow et al., 2004; Kéfi et al., 2016, 2015; Lurgi et al., 2016; Miele et al., 2019; Sauve et al., 2014), within which competition for space is one of the greatest influences (Miele et al., 2019). Here, we find that competition for space also influences how biological communities can respond to anthropogenic perturbations, such as small-scale artisanal fisheries. On the one hand, we found that the sensibility of harvested

macroalgae and harvested filters-feeders and the effects of fisheries on lower non-harvested trophic levels was independent of whether competition for space is considered. But, on the other hand, we found that the sensibility to fishing of harvested higher trophic levels and the biomass of higher non-harvested trophic levels respond differentially if the competition for space is considered or not in the model.

Long-term human-exclusion natural experiments produced on the Coastal Marine Research Station (ECIM) of central Chile, suggested that humans harvest over keystone species that control the abundance of dominant sessile competitors, which qualitatively and quantitatively affects the abundance of the main species as well as the dominance of strong sessile space competitors of the intertidal rocky-shore when humans are present/absent (Castilla, 1999). Despite this, the works that have been assessed the impacts of fisheries through a multi-species perspective in Chilean intertidal rocky-shores ecosystems of the north (Ortiz, 2008; Ortiz et al., 2015) and central-south of Chile (the area that our study covers) (Ávila-Thieme et al., unpublished data) have only focused on trophic interactions. Here, we found that although some impacts of fishing are independent of whether competition for space is considered, others are not. On the one hand, regardless of competition for space the macroalgae and harvested filter-feeders are the most sensitive harvested species to fishing and fisheries produce positive impacts of fishing in the abundance of lower non-harvested trophic levels (the discussion of these impacts are developed in (Ávila-Thieme et al., unpublished data A, unpublished data B). On the other hand, the sensitivity of carnivores, omnivores and herbivores harvested species and the effects of fisheries over the non-harvested higher trophic levels depends on whether competition for space is considered.

The controversy caused by competition for space in our results could have several implications for the management of benthic resources. For example, one of the most valuable benthic resources to Chilean benthic fisheries is the Chilean abalone *Choncolepas concholepas*, locally known as “el loco” (Castilla et al., 2007; Castilla and Defeo, 2001; Gelcich et al., 2010). This resource is under a permanent band and has strong enforcement due to its collapse in the late 1980s (Gelcich et al., 2010). In our simulation, we found that without considering space competition el loco is a highly resistant harvested specie to fishing, while, with space competition, it is highly sensitive. In the first case, the results could be interpreted as the exploitation of the loco could intensify, while in the second, the results suggest that the el loco exportation should be produced under strong precautions. This is key, since a recent study revealed that despite all the el loco enforcement, by illegal fishing, the el loco landings can be up to six times more than what fishermen’s declare as extracted. Therefore, do not consider the trophic and non-trophic mechanisms of these ecosystems could generate undesired effects in this valuable resource.

Here, we assessed the role of space competition due to is one of the most influential non-trophic interactions in benthic ecosystems (Miele et al., 2019). However, other non-trophic interactions also occur in these ecosystems, such as refuge provisioning from predation, facilitation on recruitment, and positive and negative effects in survival (Kéfi et al., 2015), which were not considered in this work. Previous studies have revealed that considering these interactions in isolation and jointly affects species diversity and community functioning (biomass and production) (Kéfi et al., 2016; Miele et al., 2019). Therefore, we can infer that it should also have an effect on how the effects of fishing propagate through food-webs. For example, fisheries strongly harvest on kelps (de Juan et al., 2018; Vásquez, 2016), which are

widely recognized for their role in promoting the biodiversity of ecosystems since they provide refuge, a nesting area and facilitate the recruitment of many species (Miller and Rudolf, 2011; Villegas et al., 2019). Therefore, not incorporating these other trophic interactions does not allow us to visualize the real impact that kelp fisheries could have on the food-web, and it is undoubtedly an important next step to evaluate.

Finally, our study is a step toward getting a better understanding of the impacts of fisheries on food-web dynamic from a multi-species as well as from a multiplex ecological network (i.e., including several interaction types among a set of species) perspective. Our results suggest that space competition produces non-trivial results in the abundance of both harvested and non-harvested species, and these results have important consequences for predicting the consequences of fisheries on the food-web dynamics.

REFERENCES

- Alexandridis, N., Dambacher, J.M., Jean, F., Desroy, N., Bacher, C., 2017. Qualitative modelling of functional relationships in marine benthic communities. *Ecological Modelling* 360, 300–312. <https://doi.org/10.1016/j.ecolmodel.2017.07.021>
- Ávila-Thieme, M.I., Corcoran, D., Pérez-Matus, A., Navarrete, S.A., Marquet, P.A., Valdovinos, F.S., unpublished data. Plankton biomass changes would negatively affect coastal South Pacific food-webs more strongly than artisanal fisheries.
- Berlow, E.L., Neutel, A.-M., Cohen, J.E., de Ruiter, P.C., Ebenman, B., Emmerson, M., Fox, J.W., Jansen, V.A.A., Iwan Jones, J., Kokkoris, G.D., Logofet, D.O., McKane, A.J., Montoya, J.M., Petchey, O., 2004. Interaction strengths in food webs: issues and opportunities. *J Anim Ecology* 73, 585–598. <https://doi.org/10.1111/j.0021-8790.2004.00833.x>
- Brose, U., Williams, R.J., Martinez, N.D., 2006. Allometric scaling enhances stability in complex food webs. *Ecol Letters* 9, 1228–1236. <https://doi.org/10.1111/j.1461-0248.2006.00978.x>
- Castilla, J.C., 1999. Coastal marine communities: trends and perspectives from human-exclusion experiments. *Trends in Ecology & Evolution* 14, 280–283. [https://doi.org/10.1016/S0169-5347\(99\)01602-X](https://doi.org/10.1016/S0169-5347(99)01602-X)

- Castilla, J.C., Defeo, O., 2001. Latin American benthic shellfisheries: Emphasis on co-management and experimental practices. *Reviews in Fish Biology and Fisheries* 11, 1–30. <https://doi.org/10.1023/A:1014235924952>
- Castilla, J.C., Gelcich, S., Defeo, O., 2007. Successes, Lessons, and Projections from Experience in Marine Benthic Invertebrate Artisanal Fisheries in Chile, in: McClanahan, T.R., Castilla, J.C. (Eds.), *Fisheries Management*. Blackwell Publishing Ltd, Oxford, UK, pp. 23–42. <https://doi.org/10.1002/9780470996072.ch2>
- Chadwick, N.E., Morrow, K.M., 2011. Competition Among Sessile Organisms on Coral Reefs, in: Dubinsky, Z., Stambler, N. (Eds.), *Coral Reefs: An Ecosystem in Transition*. Springer Netherlands, Dordrecht, pp. 347–371. https://doi.org/10.1007/978-94-007-0114-4_20
- Connell, J.H., 1961. Effects of Competition, Predation by *Thais lapillus*, and Other Factors on Natural Populations of the Barnacle *Balanus balanoides*. *Ecological Monographs* 31, 61–104. <https://doi.org/10.2307/1950746>
- Dayton, P.K., 1971. Competition, Disturbance, and Community Organization: The Provision and Subsequent Utilization of Space in a Rocky Intertidal Community. *Ecological Monographs* 41, 351–389. <https://doi.org/10.2307/1948498>
- de Juan, S., Subida, M.D., Gelcich, S., Fernandez, M., 2018. Ecosystem health in coastal areas targeted by small-scale artisanal fisheries: Insights on monitoring and assessment. *Ecological Indicators* 88, 361–371. <https://doi.org/10.1016/j.ecolind.2018.01.054>
- Dunn, R.P., Baskett, M.L., Hovel, K.A., 2017. Interactive effects of predator and prey harvest on ecological resilience of rocky reefs. *Ecol Appl* 27, 1718–1730. <https://doi.org/10.1002/eap.1581>
- Dunne, J.A., Maschner, H., Betts, M.W., Huntly, N., Russell, R., Williams, R.J., Wood, S.A., 2016. The roles and impacts of human hunter-gatherers in North Pacific marine food webs. *Sci Rep* 6, 21179. <https://doi.org/10.1038/srep21179>
- Gelcich, S., Hughes, T.P., Olsson, P., Folke, C., Defeo, O., Fernandez, M., Foale, S., Gunderson, L.H., Rodriguez-Sickert, C., Scheffer, M., Steneck, R.S., Castilla, J.C., 2010. Navigating transformations in governance of Chilean marine coastal resources. *Proceedings of the National Academy of Sciences* 107, 16794–16799. <https://doi.org/10.1073/pnas.1012021107>
- Kéfi, S., Berlow, E.L., Wieters, E.A., Joppa, L.N., Wood, S.A., Brose, U., Navarrete, S.A., 2015. Network structure beyond food webs: mapping non-trophic and trophic interactions on Chilean rocky shores. *Ecology* 96, 291–303. <https://doi.org/10.1890/13-1424.1>
- Kéfi, S., Berlow, E.L., Wieters, E.A., Navarrete, S.A., Petchey, O.L., Wood, S.A., Boit, A., Joppa, L.N., Lafferty, K.D., Williams, R.J., Martinez, N.D., Menge, B.A., Blanchette, C.A., Iles, A.C., Brose, U., 2012. More than a meal... integrating non-feeding interactions into food webs: More than a meal *Ecology Letters* 15, 291–300. <https://doi.org/10.1111/j.1461-0248.2011.01732.x>
- Kéfi, S., Miele, V., Wieters, E.A., Navarrete, S.A., Berlow, E.L., 2016. How Structured Is the Entangled Bank? The Surprisingly Simple Organization of Multiplex Ecological Networks Leads to Increased Persistence and Resilience. *PLoS Biol* 14, e1002527. <https://doi.org/10.1371/journal.pbio.1002527>

- Kuparinen, A., Boit, A., Valdovinos, F.S., Lassaux, H., Martinez, N.D., 2016. Fishing-induced life-history changes degrade and destabilize harvested ecosystems. *Sci Rep* 6, 22245. <https://doi.org/10.1038/srep22245>
- Lurgi, M., Montoya, D., Montoya, J.M., 2016. The effects of space and diversity of interaction types on the stability of complex ecological networks. *Theor Ecol* 9, 3–13. <https://doi.org/10.1007/s12080-015-0264-x>
- Miele, V., Guill, C., Ramos-Jiliberto, R., Kéfi, S., 2019. Non-trophic interactions strengthen the diversity—functioning relationship in an ecological bioenergetic network model. *PLoS Comput Biol* 15, e1007269. <https://doi.org/10.1371/journal.pcbi.1007269>
- Miller, T.E.X., Rudolf, V.H.W., 2011. Thinking inside the box: community-level consequences of stage-structured populations. *Trends in Ecology & Evolution* 26, 457–466. <https://doi.org/10.1016/j.tree.2011.05.005>
- Navarrete, S.A., Manzur, T., 2008. INDIVIDUAL- AND POPULATION-LEVEL RESPONSES OF A KEYSTONE PREDATOR TO GEOGRAPHIC VARIATION IN PREY. *Ecology* 89, 2005–2018. <https://doi.org/10.1890/07-1231.1>
- Ortiz, M., 2008. Mass balanced and dynamic simulations of trophic models of kelp ecosystems near the Mejillones Peninsula of northern Chile (SE Pacific): Comparative network structure and assessment of harvest strategies. *Ecological Modelling* 216, 31–46. <https://doi.org/10.1016/j.ecolmodel.2008.04.006>
- Ortiz, M., Berrios, F., Campos, L., Uribe, R., Ramirez, A., Hermosillo-Núñez, B., González, J., Rodríguez-Zaragoza, F., 2015. Mass balanced trophic models and short-term dynamical simulations for benthic ecological systems of Mejillones and Antofagasta bays (SE Pacific): Comparative network structure and assessment of human impacts. *Ecological Modelling* 309–310, 153–162. <https://doi.org/10.1016/j.ecolmodel.2015.04.006>
- Oyanedel, R., Keim, A., Castilla, J.C., Gelcich, S., 2018. Illegal fishing and territorial user rights in Chile: Illegal Fishing. *Conservation Biology* 32, 619–627. <https://doi.org/10.1111/cobi.13048>
- Pascual, M., Caswell, H., 1991. The dynamics of a size-classified benthic population with reproductive subsidy. *Theoretical Population Biology* 39, 129–147. [https://doi.org/10.1016/0040-5809\(91\)90032-B](https://doi.org/10.1016/0040-5809(91)90032-B)
- Pérez-Matus, A., Ospina-Alvarez, A., Camus, P., Carrasco, S., Fernandez, M., Gelcich, S., Godoy, N., Ojeda, F., Pardo, L., Rozbaczylo, N., Subida, M., Thiel, M., Wieters, E., Navarrete, S., 2017. Temperate rocky subtidal reef community reveals human impacts across the entire food web. *Mar. Ecol. Prog. Ser.* 567, 1–16. <https://doi.org/10.3354/meps12057>
- Richard, J.W., Brose, U., Martinez, N.D., 2006. Homage to Yodzis and Innes 1992: Scaling up feeding-based population dynamics to complex ecological networks, in: *From Energetics to Ecosystems: The Dynamics and Structure of Ecological Systems*. Springer Netherlands, pp. 37–51. https://doi.org/10.1007/978-1-4020-5337-5_2
- Santelices, B., 1990. Patterns of organizations of intertidal and shallow subtidal vegetation in wave exposed habitats of central Chile. *Hydrobiologia* 192, 35–57. <https://doi.org/10.1007/BF00006226>
- Sauve, A.M.C., Fontaine, C., Thébault, E., 2014. Structure-stability relationships in networks combining mutualistic and antagonistic interactions. *Oikos* 123, 378–384. <https://doi.org/10.1111/j.1600-0706.2013.00743.x>

- Schneider, F.D., Brose, U., Rall, B.C., Guill, C., 2016. Animal diversity and ecosystem functioning in dynamic food webs. *Nat Commun* 7, 12718. <https://doi.org/10.1038/ncomms12718>
- Schreiber, S.J., Moore, J.L., 2018. The structured demography of open populations in fluctuating environments. *Methods Ecol Evol* 9, 1569–1580. <https://doi.org/10.1111/2041-210X.12991>
- Serra, G., Chelazzi, G., Castilla, J.C., 1997. Effects of Experience and Risk of Predation on the Foraging Behaviour of the South-Eastern Pacific Muricid *Concholepas concholepas* (Mollusca: Gastropoda). *The Journal of Animal Ecology* 66, 876. <https://doi.org/10.2307/6003>
- Soto, R.E., Castilla, J.C., Bozinovic, F., 2004. Conducta de forrajeo del gastrópodo *Acanthina monodon* Pallas, 1774 (Gastropoda: Muricidae) en el intermareal rocoso de Chile central. *Rev. chil. hist. nat.* 77. <https://doi.org/10.4067/S0716-078X2004000100012>
- Svensson, J.R., Marshall, D.J., 2015. Limiting resources in sessile systems: food enhances diversity and growth of suspension feeders despite available space. *Ecology* 96, 819–827. <https://doi.org/10.1890/14-0665.1>
- Swierts, T., Vermeij, M.J., 2016. Competitive interactions between corals and turf algae depend on coral colony form. *PeerJ* 4, e1984. <https://doi.org/10.7717/peerj.1984>
- Testa, G., Masotti, I., Fariás, L., 2018. Temporal variability in net primary production in an upwelling area off central Chile (36°S). *Front. Mar. Sci.* 5, 179. <https://doi.org/10.3389/fmars.2018.00179>
- Thiel, M., Macaya, E., Acuña, E., Arntz, W., Bastias, H., Brokordt, K., Camus, P., Castilla, J., Castro, L., Cortés, M., Dumont, C., Escribano, R., Fernandez, M., Gajardo, J., Gaymer, C., Gomez, I., González, A., González, H., Haye, P., Illanes, J.-E., Iriarte, J., Lancellotti, D., Luna-Jorquera, G., Luxoro, C., Manriquez, P., Marín, V., Muñoz, P., Navarrete, S., Perez, E., Poulin, E., Sellanes, J., Sepúlveda, H., Stotz, W., Tala, F., Thomas, A., Vargas, C., Vasquez, J., Vega, A., 2007. The Humboldt current system of northern and central Chile: oceanographic processes, ecological interactions and socioeconomic feedback, in: Gibson, R., Atkinson, R., Gordon, J. (Eds.), *Oceanography and Marine Biology*. CRC Press, pp. 195–344. <https://doi.org/10.1201/9781420050943.ch6>
- Vásquez, J.A., 2016. The Brown Seaweeds Fishery in Chile, in: Mikkola, H. (Ed.), *Fisheries and Aquaculture in the Modern World*. InTech. <https://doi.org/10.5772/62876>
- Villegas, M., Laudien, J., Sielfeld, W., Arntz, W., 2019. Effect of foresting barren ground with *Macrocystis pyrifera* (Linnaeus) C. Agardh on the occurrence of coastal fishes off northern Chile. *J Appl Phycol* 31, 2145–2157. <https://doi.org/10.1007/s10811-018-1657-1>
- Williams, Rich J, 2010. *Network 3D: visualizing and modelling food webs and other complex networks*. Microsoft Research, Cambridge, UK.
- Williams, R.J., 2008. Effects of network and dynamical model structure on species persistence in large model food webs. *Theor Ecol* 1, 141–151. <https://doi.org/10.1007/s12080-008-0013-5>

FIGURES

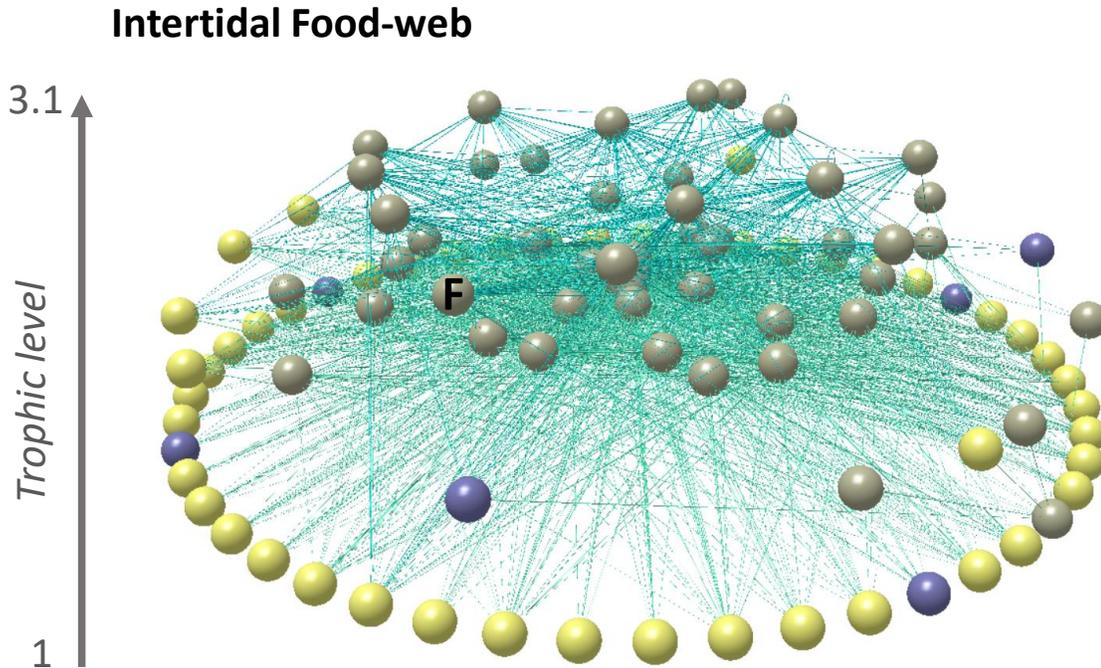


Figure 1. Intertidal food-web. Color node represents the sessile non-harvested (yellow), sessile harvested (blue) and mobile (grey) species. Letter F represents the fisheries node. Bottom nodes represent basal species, and the nodes of the top represent top predators. The left axes represent the trophic level (SWTL) from the minimum to the maximum trophic level. Drawn using Network3D software (Williams, Rich J, 2010)

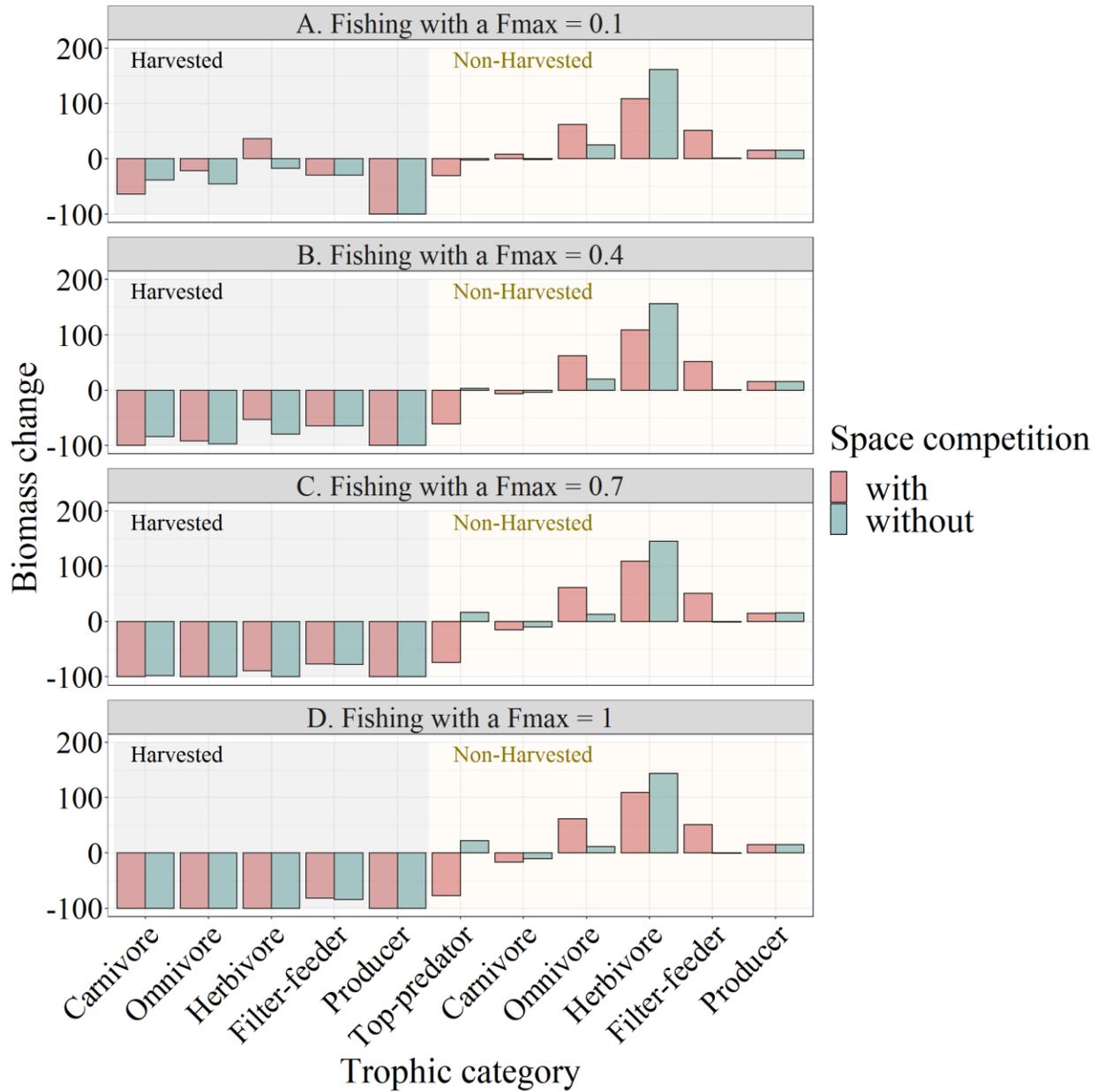


Figure 2. Total biomass changes (y-axis) of each trophic (x-axis) after simulating a subset of the different fishing scenarios (from A to D) when space competition between sessile species is (red bars) and is not (green bars). The grey and yellow box represent the total biomass change of harvested and non-harvested trophic levels, respectively.

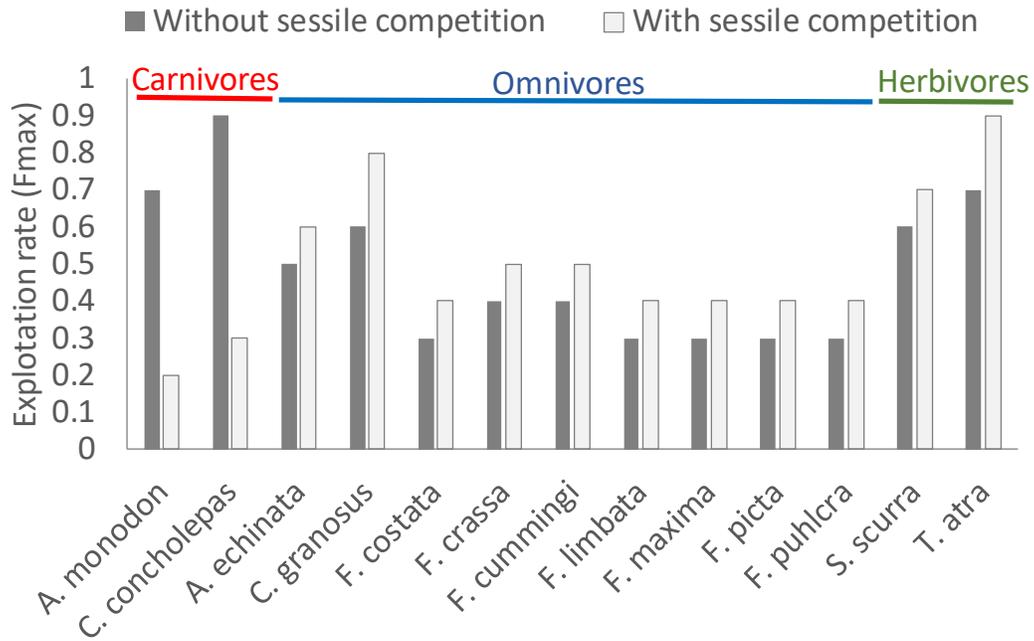


Figure 3. Exploitation rate at which non-algal species become extinct after fishing when space competition is (grey bars) as is not (light bars) considered in the model. We do not incorporate the filter-feeders in the figure since in no fishing scenario they were extinguished.

INFORMACIÓN SUPPLEMENTARIA (CAPÍTULO 4)

EXPLORING THE EFFECTS OF SPACE COMPETITION TO UNDERSTAND THE IMPACTS OF FISHERIES ON BENTONIC FOOD WEBS.

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Parametrization of the dynamic model

Supplementary Table S1 shows all the model parameters with their initial values and descriptions. We used empirical measures of species body size, which was extracted from (Kéfi et al., 2015), to allometrically parameterize intrinsic growth rate of autotroph, as well as metabolic rate, and maximum consumption rate of each species.

The initial biomass was estimated from density (mobile species + cnidaria) and the surface of cover (sessile species) recorded during six years of sampling in the Chilean marine reserve “Estacion Costera de Investigaciones Marinas” (ECIM) at the central-south of Chile. The density of mobile species was multiplied by the species body size. For sessile species, the surface of cover was multiplied by the weight of each species per unit of cover.

We calculated the community-level carrying capacity, K , by dividing all the primary producers into six functional groups (microalgae, ephemerals, corticates, crust, corallines, and kelps) (Boit et al., 2012). In each functional group, we multiplied the biomass of the species exhibiting the highest growth rate with the number of species that compose its functional group. Finally, we summed the resulting biomass over all functional groups.

Based on empirical experiments in aquatic (Calbet and Saiz, 2013) and terrestrial ecosystems (Mulder and Hendriks, 2014), we assumed that the half-saturation density parameter (B_0) decreases while the trophic levels increase in 10^3 order of magnitude. We use the values of (Boit

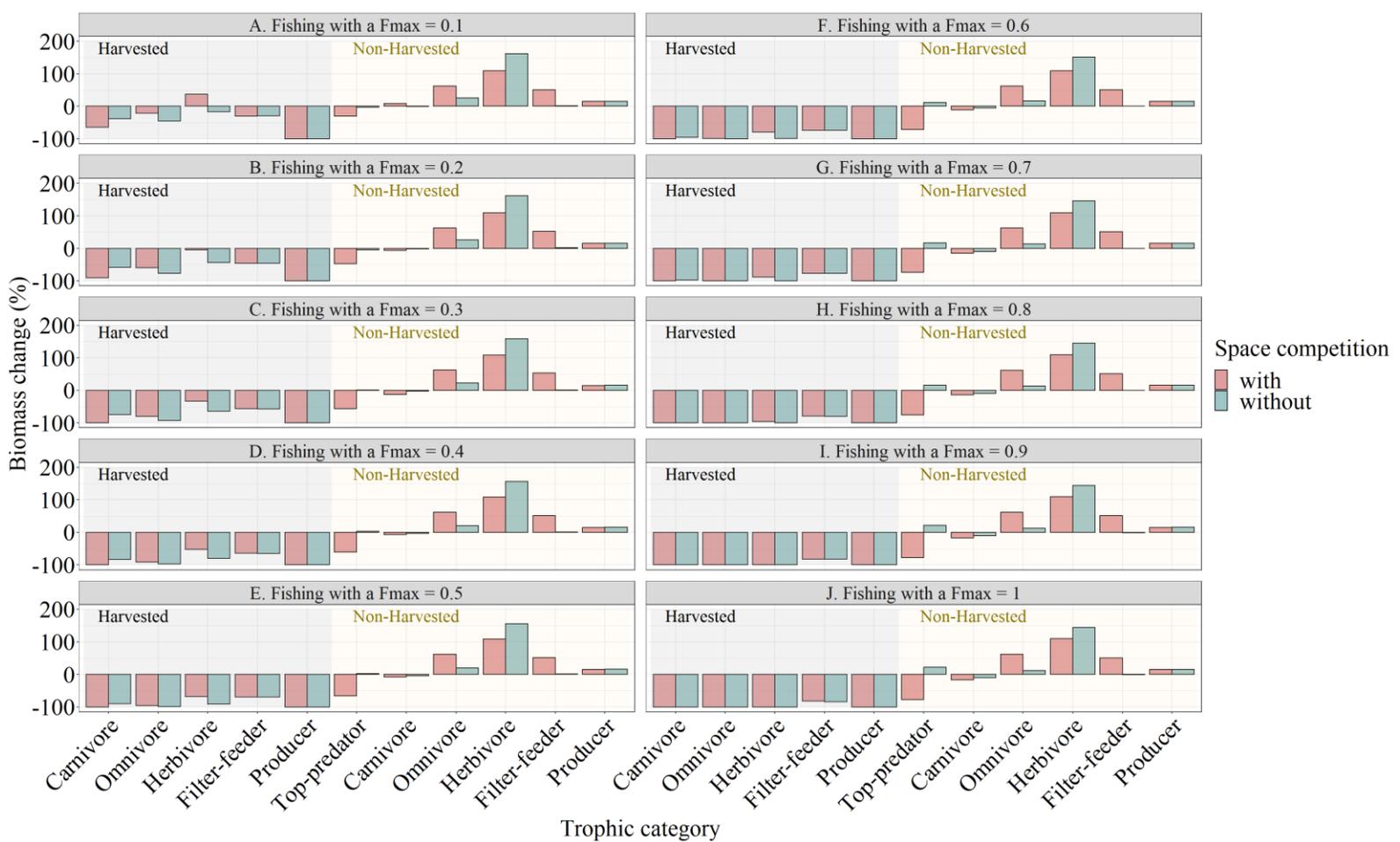
et al., 2012) as a reference value. To herbivores, we fit the B_0 to ensure their persistence. For the other parameters, we used values from (Boit et al., 2012) (see parameters values in table S1).

1 **Table S1.** Summary of the parameters and their initial values used in the ATN model for intertidal food-web of central Chile. Detailed
 2 values by species and interaction can be found in the additional information.

Parameter	Unit of measurement	Definition	Initial values min., max.	References
B_i	g/m^2	Population abundance	1.3×10^{-4} , 112107	Empirical data obtained in ECIM. For plankton and benthic diatoms, data was extracted from (Gómez-Canchong et al., 2013)
M_i	G	Body mass	1×10^{-5} , 500	Based on empirical data from (Kéfi et al., 2015)
r_i	1/day	Mass-specific growth rate for basal species	0.12, 3.74	(Brose et al., 2006)
x_i	1/day	Mass-specific metabolic rate	0.72, 61.4	(Brose et al., 2006)
y_i	1/day	Maximum ingestion rate	1.63, 5.82	(Brose et al., 2006)
K	g/m^2	Basal species carrying capacity	176299	(Boit et al., 2012)
C		Inter-specific competition coefficient.	1	(Boit et al., 2012)
		Without space competition: competition by resources.		

With space competition:			
competition for space			
space			
f_a		Activity metabolism coefficient	0.4 (Boit et al., 2012)
f_m		Maintenance respiration coefficient	0.1 (Boit et al., 2012)
e_{ij}		Assimilation efficiency	Herbivores: 0.45 Carnivores: 0.85 (Richard et al., 2006)
d_{ij}	m^2/g	Feeding interference coefficient	0.5 (Boit et al., 2012)
q_{ij}		Functional response shape parameter	1.2 (Williams, 2008)
w_{ij}		Relative prey preference	For <i>Acanthina monodon</i> , <i>Concholepas concholepas</i> , and <i>Helister heliantus</i> feeding on <i>Perumitylus purpuratus</i> : 0.9. For the rest of their resources: $0.1/n_{\text{available resources}}$ For the rest of the consumers: $1/n_{\text{available resources}}$ (Boit et al., 2012; Navarrete and Manzur, 2008; Serra et al., 1997; Soto et al., 2004)

				(Boit et al., 2012)
p_{ij}		Fraction of resource species shared	0, 1	(Boit et al., 2012)
B_{0ij}	g/m^2	Half-saturation densities	50, 15000	(Boit et al., 2012)
S	g/m^2	Plankton subsidy biomass	12% of initial biomass	(Testa et al., 2018)



15 **Figure S1.** Total biomass changes (y-axis) of each trophic level (x-axis) after simulating different fishing scenarios (from A to J) with
 16 (red bars) and without (green bars) space competition between sessile species. The grey and yellow box represent the total biomass
 17 change of harvested and non-harvested trophic levels, respectively.

REFERENCES

- Boit, A., Martinez, N.D., Williams, R.J., Gaedke, U., 2012. Mechanistic theory and modelling of complex food-web dynamics in Lake Constance: Mechanistic modelling of complex food web dynamics. *Ecology Letters* 15, 594–602. <https://doi.org/10.1111/j.1461-0248.2012.01777.x>
- Brose, U., Williams, R.J., Martinez, N.D., 2006. Allometric scaling enhances stability in complex food webs. *Ecol Letters* 9, 1228–1236. <https://doi.org/10.1111/j.1461-0248.2006.00978.x>
- Calbet, A., Saiz, E., 2013. Effects of trophic cascades in dilution grazing experiments: from artificial saturated feeding responses to positive slopes. *Journal of Plankton Research* 35, 1183–1191. <https://doi.org/10.1093/plankt/fbt067>
- Gómez-Canchong, P., Quiñones, R.A., Brose, U., 2013. Robustness of size–structure across ecological networks in pelagic systems. *Theor Ecol* 6, 45–56. <https://doi.org/10.1007/s12080-011-0156-7>
- Kéfi, S., Berlow, E.L., Wieters, E.A., Joppa, L.N., Wood, S.A., Brose, U., Navarrete, S.A., 2015. Network structure beyond food webs: mapping non-trophic and trophic interactions on Chilean rocky shores. *Ecology* 96, 291–303. <https://doi.org/10.1890/13-1424.1>
- Mulder, C., Hendriks, A.J., 2014. Half-saturation constants in functional responses. *Global Ecology and Conservation* 2, 161–169. <https://doi.org/10.1016/j.gecco.2014.09.006>
- Navarrete, S.A., Manzur, T., 2008. INDIVIDUAL- AND POPULATION-LEVEL RESPONSES OF A KEYSTONE PREDATOR TO GEOGRAPHIC VARIATION IN PREY. *Ecology* 89, 2005–2018. <https://doi.org/10.1890/07-1231.1>
- Richard, J.W., Brose, U., Martinez, N.D., 2006. Homage to Yodzis and Innes 1992: Scaling up feeding-based population dynamics to complex ecological networks, in: *From Energetics to Ecosystems: The Dynamics and Structure of Ecological Systems*. Springer Netherlands, pp. 37–51. https://doi.org/10.1007/978-1-4020-5337-5_2
- Serra, G., Chelazzi, G., Castilla, J.C., 1997. Effects of Experience and Risk of Predation on the Foraging Behaviour of the South-Eastern Pacific Muricid *Concholepas concholepas* (Mollusca: Gastropoda). *The Journal of Animal Ecology* 66, 876. <https://doi.org/10.2307/6003>
- Soto, R.E., Castilla, J.C., Bozinovic, F., 2004. Conducta de forrajeo del gastrópodo *Acanthina monodon* Pallas, 1774 (Gastropoda: Muricidae) en el intermareal rocoso de Chile central. *Rev. chil. hist. nat.* 77. <https://doi.org/10.4067/S0716-078X2004000100012>
- Testa, G., Masotti, I., Farías, L., 2018. Temporal variability in net primary production in an upwelling area off central Chile (36°S). *Front. Mar. Sci.* 5, 179. <https://doi.org/10.3389/fmars.2018.00179>
- Williams, R.J., 2008. Effects of network and dynamical model structure on species persistence in large model food webs. *Theor Ecol* 1, 141–151. <https://doi.org/10.1007/s12080-008-0013-5>

DISCUSIÓN Y CONCLUSIÓN GENERAL

La crisis pesquera global y la consecuente degradación de los ecosistemas marinos es evidencia suficiente para demostrar que el manejo y la administración pesquera y en particular el uso de modelos de una sola especie, ha sido ineficiente en la evaluación de los stocks y manejo sustentable de las pesquerías. Uno de los problemas críticos se deriva de la inevitable propagación trófica de los impactos sobre las especies capturadas por la actividad pesquera hacia todo el ecosistema. Por lo anterior, se han hecho llamados por enfoques más holísticos, en los que el ecosistema es considerado, para entender los efectos tanto directos e indirectos de la pesca (Collie et al., 2016; García, 2003; Plagányi, 2007). Sin embargo, los modelos basados en una sola especie continúan siendo el principal método aplicado (Skern-Mauritzen et al., 2016). Esta tesis tuvo como objetivo avanzar hacia el uso de modelos más holísticos, analizando los efectos de la pesca a través de enfoques de múltiples especies, y así, entender cómo dichos efectos se propagan por la red y afectan la abundancia de las especies que la componen. En particular, se evaluó la importancia relativa de las especies de importancia comercial para la conectividad, estructura, robustez y dinámica de la red trófica empírica del intermareal rocoso y submareal somero de Chile central. Con esto, esta tesis contribuyó con información relevante, que hubiese sido imposible de obtener si es que nos hubiésemos basado en modelos de una sola especie. Así, los resultados de esta tesis pueden ser útiles para futuros planes de manejo de las pesquerías en Chile.

La pesca comúnmente extrae especies altamente conectadas (Dunne et al., 2002; Pérez-Matus et al., 2017) y muchas veces a través de todos los niveles tróficos (Pauly, 1998). También es común que la pesquería se enfoque en especies que a su vez son recursos y/o depredadores de otras especies de otras o de la misma pesquería. Así, la pesca puede competir por recursos, o

bien liberar de depredación a múltiples especies que pueden o no tener importancia comercial. En consecuencia, los efectos directos de la pesca pueden propagarse vía cascada tróficas, alterar la abundancia de múltiples otras especies en la red (Crowder et al., 2008; Yodzis, 2001) y degradar las propiedades estructurales de las redes tróficas (Coll et al., 2008; Lotze et al., 2011; Pauly, 1998). En esta tesis, el uso de análisis de múltiples especies permitió reconocer la identidad de las especies que están involucradas en interacciones críticas con la pesquería artesanal, así como también identificar a las especies más sensibles y aquellas que son importantes para la persistencia de estas comunidades. Toda esta información es relevante ya que puede ser de gran utilidad para futuras gestiones pesqueras.

Con el enfoque tanto estático como dinámico se encontró que ambas redes son altamente robustas a la extinción de todas las especies de importancia comercial. Esto sugiere que las especies de importancia comercial son generalistas y por lo tanto que tienen otras alternativas de recursos. Pero además, con el enfoque dinámico se puede observar que si bien pescar sobre las especies de importancia comercial alteró la biomasa de todas las especies en ambas redes (III), las redes fueron altamente robustas porque la biomasa de las especies no cosechadas aumentó después de la pesca (capítulo II y III), sugiriendo que la liberación de depredación que produce la pesca artesanal y el relajo en la competencia inter-específica entre las especies basales actúa con mayor intensidad que la competencia por recursos. Discutimos el rol positivo de la pesca sobre las especies que no son cosechadas desde dos perspectivas contrastantes: (1) asociando el rol positivo de la pesca artesanal con el rol positivo que se le ha otorgado a los cazadores recolectores para la persistencia de redes tróficas del pacífico norte (Dunne et al., 2016), sugiriendo que bajo un manejo adecuado de los recursos, la pesca podría llegar a ser necesaria para aumentar la productividad de estos ecosistemas y contribuir hacia una economía

azul (Pauly, 2018), y (2) se discute a la pesca artesanal como un agente liberador de nicho, lo cual podría dejar propenso a estos ecosistemas a la llegada de nuevas especies, degradarlas (Bradley et al., 2019; Ponisio et al., 2019) y producir trayectorias que no fueron observadas en esta tesis ya que este mecanismo no estuvo permitido en nuestras simulaciones.

A pesar de la alta robustez de las redes ante la extinción de las especies de importancia comercial (capítulo II) y de los efectos positivos que la pesca produce en las especies sin importancia comercial (capítulo III), encontramos que la pesquería generó efectos negativos en las propiedades estructurales de las redes, especialmente en la disminución del número de enlaces tróficos (capítulo II). Por lo tanto, se discuten las consecuencias de esta degradación ante futuras perturbaciones (capítulo II). Esto, es particularmente relevante bajo el contexto de los potenciales efectos del cambio climático en la productividad de los océanos (Weidberg et al. 2020). Nosotros encontramos que el plancton resultó ser un nodo clave para la persistencia de ambas redes (ya que es el único recurso de un alto número de filtradores presentes en las redes tróficas), y además, encontramos que la variabilidad en la productividad del plancton puede acentuar los impactos negativos de las pesquerías (capítulo II). Por lo tanto, sugerimos que monitorear y/o considerar los cambios en la productividad costera podría contribuir al desarrollo de mejores estrategias de manejo.

Los enfoques de múltiples especies también permitieron identificar en cada red a las especies que fueron más sensibles a la pesca, así como también los mecanismos biológicos y tróficos que explican dicha sensibilidad. Además, permitieron comparar la sensibilidad a la pesca entre las dos redes tróficas (capítulo III), lo cual hubiese sido imposible de obtener con modelos de una sola especie. Por ejemplo, en esta tesis se encontró que, solo considerando las

interacciones tróficas, las macroalgas de importancia comercial fueron las especies más sensibles a la pesca, ya que fueron las especies que toleraron las menores tasas de explotación. La alta sensibilidad de las algas de importancia comercial se explica porque su tasa intrínseca de crecimiento es 3 veces menor que el de las otras especies basales que no son cosechadas y porque tienen 2.5 más depredadores que el resto de las especies cosechadas. En consecuencia, los efectos positivos que la pesca produjo en la biomasa de sus consumidores que no son cosechados por la pesca intensifican los impactos negativos que la pesca produce directamente sobre las macroalgas. Si bien, la tasa de crecimiento es un mecanismo biológico que puede ser inferido a partir de los modelos de una sola especie, la propagación de los efectos de la pesca sobre los consumidores de las macroalgas sólo puede ser observados a través de enfoques de múltiples especies.

Reconocer que en ambas redes las macroalgas de importancia comercial son las especies más sensibles a la pesca es útil y relevante para el manejo pesquero, ya que permite direccionar hacia donde debiese priorizarse el manejo. Entre las algas se encuentran los kelps, los cuales son claves para promover la diversidad de estos ecosistemas (Vásquez, 2016; Villegas et al., 2019) pero la intensidad de extracción (Vásquez, 2016), la lenta tasa de recuperación (Parada et al., 2016; Teagle et al., 2017) y el bajo o nulo manejo y control de su cosecha (Frangoudes, 2011; Westermeier et al., 2019), está dejando a los kelps vulnerables a sobreexplotación. De esta manera, esta tesis sugiere que es urgente que se establezcan mejores medidas de fiscalización y manejo sobre estas algas. Por otra parte, reconocer que la red del submareal fue más sensible a la pesca que la del intermareal, ya que las especies de importancia comercial del submareal toleraron menores tasas de explotación que las del intermareal (capítulo III), es interesante porque en el submareal es donde predominan la mayor diversidad de artes de pesca

(Castilla and Defeo, 2001) y es de desde donde se obtienen mayores desembarques (Pérez-Matus et al., 2017) en comparación con el intermareal, lo que sugiere que el ecosistema que tolera menores intensidades de pesca podría ser el que recibe los mayores esfuerzos de pesca y del cual los pescadores tienen mayor dependencia.

Las redes tróficas analizadas en esta tesis representan a ecosistemas bentónicos en los que la competencia por el espacio juega un rol fundamental para la estructura (Connell, 1961; Kéfi et al., 2015; Santelices, 1990) y estabilidad de las redes (Kéfi et al. 2016, Miele et al., 2019). Estudios previos han demostrado que la extracción de depredadores clave por parte de la pesca artesanal puede alterar la competencia por el espacio entre especies sésiles y generar cambios tanto cualitativos como cuantitativos en la abundancia de las especies a nivel local (Castilla & Bustamante, 1989; Castilla & Durán, 1985; Castilla, 1999; Durán & Castilla 1989). En el cuarto capítulo, evidenciamos que la competencia por el espacio juega un rol importante para entender la propagación de los efectos de la pesca artesanal en la red del intermareal. Si bien, la fuerte sensibilidad de las macroalgas de importancia comercial se mantuvo, encontramos que considerar la competencia por el espacio genera tendencias contrastantes en la sensibilidad a la pesca de los consumidores de importancia comercial y en la tendencia de las especies no cosechadas que conforman los niveles tróficos superiores. Lo anterior se puede explicar porque la pesquería remueve especies basales que son competidores por el espacio, lo cual relaja la competencia por el espacio entre las especies basales que no son cosechadas. A diferencia del modelo sin competencia por el espacio, con competencia por el espacio los filtradores sésiles pasaron a ser especies basales. Por lo tanto, después de la pesca los filtradores aumentaron su biomasa, efecto que no se observó sin competencia por el espacio. Esto produjo que, a pesar de que los depredadores topos, los carnívoros y los omnívoros son depredadores de

los filtradores, el aumento en la biomasa de los filtradores solo se propagó positivamente sobre la biomasa de los omnívoros (quienes también aumentaron en mayor proporción a lo observado sin competencia por el espacio), mientras que la biomasa de los carnívoros y depredadores tope disminuyó. Lo anterior sugiere que la pesquería intensifica la competencia interespecífica entre los omnívoros, carnívoros y depredadores tope cuando se considera la competencia por espacio entre especies sésiles. Por lo tanto, la competencia interespecífica por espacio que ocurre a niveles tróficos inferiores afecta la sensibilidad a la pesquería de los niveles tróficos superiores y de las especies de importancia comercial.

Los modelos de múltiples especies son los primeros pasos para moverse hacia perspectivas más amplias como lo es el manejo de la pesca desde un enfoque ecosistémico, en el cual no solo las especies cosechas e interactuantes son relevantes, sino que también la relación e interdependencia entre el ambiente físico y climático, la sociedad y el desarrollo pesquero (Christensen & Walter, 2004; Garcia, 2003; Plagányi, 2007). Sin duda, la integración de todos estos componentes es un importante siguiente paso. Sin embargo, aumentar el nivel de complejidad también aumenta el nivel de incertidumbre (Espinoza-Tenorio et al., 2012), por lo que entender cada subsistema antes de integrarlo permite entender los mecanismos que están actuando detrás de los resultados observados. Por ejemplo, antes de integrar nuevos componentes es necesario profundizar la complejidad de cómo actúa ya que en las simulaciones de pesquería desarrolladas en esta tesis no se incluyen la existencia de vedas ni medidas finas de extracción de cada especie o su estacionalidad.

BIBLIOGRAFÍA GENERAL

- Ávila-Thieme, M.I., Corcoran, D., Pérez-Matus, A., Navarrete, S.A., Marquet, P.A., Valdovinos, F.S., In preparation. Plankton biomass changes would negatively affect coastal South Pacific food-webs more strongly than artisanal fisheries.
- Boit, A., Martinez, N.D., Williams, R.J., Gaedke, U., 2012. Mechanistic theory and modelling of complex food-web dynamics in Lake Constance: Mechanistic modelling of complex food web dynamics. *Ecology Letters* 15, 594–602. <https://doi.org/10.1111/j.1461-0248.2012.01777.x>
- Bradley, B.A., Laginhas, B.B., Whitlock, R., Allen, J.M., Bates, A.E., Bernatchez, G., Diez, J.M., Early, R., Lenoir, J., Vilà, M., Sorte, C.J.B., 2019. Disentangling the abundance–impact relationship for invasive species. *Proc Natl Acad Sci USA* 116, 9919–9924. <https://doi.org/10.1073/pnas.1818081116>
- Castilla, J.C., 1999. Coastal marine communities: trends and perspectives from human-exclusion experiments. *Trends in Ecology & Evolution* 14, 280–283. [https://doi.org/10.1016/S0169-5347\(99\)01602-X](https://doi.org/10.1016/S0169-5347(99)01602-X)
- Castilla, J.C., Defeo, O., 2001. Latin American benthic shellfisheries: Emphasis on co-management and experimental practices. *Reviews in Fish Biology and Fisheries* 11, 1–30. <https://doi.org/10.1023/A:1014235924952>
- Castilla, J. C., & Duran, L. R. (1985). Human exclusion from the rocky intertidal zone of central Chile: the effects on *Concholepas concholepas* (Gastropoda). *Oikos*, 391-399.
- Christensen, V., & Walters, C. J. (2004). Ecopath with Ecosim: methods, capabilities and limitations. *Ecological modelling*, 172(2-4), 109-139.
- Coll, M., Libralato, S., Tudela, S., Palomera, I., Pranovi, F., 2008. Ecosystem Overfishing in the Ocean. *PLoS ONE* 3, e3881. <https://doi.org/10.1371/journal.pone.0003881>
- Colléter, M., Valls, A., Guitton, J., Gascuel, D., Pauly, D., & Christensen, V. (2015). Global overview of the applications of the Ecopath with Ecosim modeling approach using the EcoBase models repository. *Ecological Modelling*, 302, 42-53.
- Collie, J.S., Botsford, L.W., Hastings, A., Kaplan, I.C., Largier, J.L., Livingston, P.A., Plagányi, É., Rose, K.A., Wells, B.K., Werner, F.E., 2016. Ecosystem models for fisheries management: finding the sweet spot. *Fish Fish* 17, 101–125. <https://doi.org/10.1111/faf.12093>
- Connell, J.H., 1961. Effects of Competition, Predation by *Thais lapillus*, and Other Factors on Natural Populations of the Barnacle *Balanus balanoides*. *Ecological Monographs* 31, 61–104. <https://doi.org/10.2307/1950746>
- Costello, C., Ovando, D., Clavelle, T., Strauss, C.K., Hilborn, R., Melnychuk, M.C., Branch, T.A., Gaines, S.D., Szuwalski, C.S., Cabral, R.B., Rader, D.N., Leland, A., 2016. Global fishery prospects under contrasting management regimes. *Proc Natl Acad Sci USA* 113, 5125–5129. <https://doi.org/10.1073/pnas.1520420113>
- Crowder, L.B., Hazen, E.L., Avissar, N., Bjorkland, R., Latanich, C., Ogburn, M.B., 2008. The Impacts of Fisheries on Marine Ecosystems and the Transition to Ecosystem-Based Management. *Annu. Rev. Ecol. Evol. Syst.* 39, 259–278. <https://doi.org/10.1146/annurev.ecolsys.39.110707.173406>
- Defeo, O., Castilla, J.C., 2005. More than One Bag for the World Fishery Crisis and Keys for Co-management Successes in Selected Artisanal Latin American Shellfisheries. *Rev Fish Biol Fisheries* 15, 265–283. <https://doi.org/10.1007/s11160-005-4865-0>

- Dunn, R.P., Baskett, M.L., Hovel, K.A., 2017. Interactive effects of predator and prey harvest on ecological resilience of rocky reefs. *Ecol Appl* 27, 1718–1730. <https://doi.org/10.1002/eap.1581>
- Dunne, J.A., Maschner, H., Betts, M.W., Huntly, N., Russell, R., Williams, R.J., Wood, S.A., 2016. The roles and impacts of human hunter-gatherers in North Pacific marine food webs. *Sci Rep* 6, 21179. <https://doi.org/10.1038/srep21179>
- Dunne, J.A., Williams, R.J., Martinez, N.D., 2002. Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecol Letters* 5, 558–567. <https://doi.org/10.1046/j.1461-0248.2002.00354.x>
- Duran, L. R., & Castilla, J. C. (1989). Variation and persistence of the middle rocky intertidal community of central Chile, with and without human harvesting. *Marine Biology*, 103(4), 555-562.
- Espinoza-Tenorio, A., Wolff, M., Taylor, M.H., Espejel, I., 2012. What model suits ecosystem-based fisheries management? A plea for a structured modeling process. *Rev Fish Biol Fisheries* 22, 81–94. <https://doi.org/10.1007/s11160-011-9224-8>
- FAO (Ed.), 2018. Meeting the sustainable development goals, The state of world fisheries and aquaculture. Rome.
- Frangoudes, K., 2011. Seaweeds Fisheries Management in France, Japan, Chile and Norway 9.
- Fulton, E. A., Link, J. S., Kaplan, I. C., Savina-Rolland, M., Johnson, P., Ainsworth, C., ... & Smith, D. C. (2011). Lessons in modelling and management of marine ecosystems: the Atlantis experience. *Fish and fisheries*, 12(2), 171-188.
- Garcia, S.M., 2003. The ecosystem approach to fisheries: issues, terminology, principles, institutional foundations, implementation and outlook. Food & Agriculture Org.
- Glaum, P., Cocco, V., Valdovinos, F.S., 2019. Integrating Economic dynamics into Ecological Networks: The case of 1 fishery sustainability. *bioRxiv*.
- Gomez, P., Quinones, R., Neira, S., Arancibia, H., 2017. Modelling fishery induced impacts on the food web of the continental shelf off central south Chile using a size based network approach. *IJAR* 45, 748–765. <https://doi.org/10.3856/vol45-issue4-fulltext-11>
- Gómez-Canchong, P., Quiñones, R.A., Brose, U., 2013. Robustness of size–structure across ecological networks in pelagic systems. *Theor Ecol* 6, 45–56. <https://doi.org/10.1007/s12080-011-0156-7>
- Kéfi, S., Berlow, E.L., Wieters, E.A., Joppa, L.N., Wood, S.A., Brose, U., Navarrete, S.A., 2015. Network structure beyond food webs: mapping non-trophic and trophic interactions on Chilean rocky shores. *Ecology* 96, 291–303. <https://doi.org/10.1890/13-1424.1>
- Kéfi, S., Miele, V., Wieters, E.A., Navarrete, S.A., Berlow, E.L., 2016. How Structured Is the Entangled Bank? The Surprisingly Simple Organization of Multiplex Ecological Networks Leads to Increased Persistence and Resilience. *PLoS Biol* 14, e1002527. <https://doi.org/10.1371/journal.pbio.1002527>
- Kuparinen, A., Boit, A., Valdovinos, F.S., Lassaux, H., Martinez, N.D., 2016. Fishing-induced life-history changes degrade and destabilize harvested ecosystems. *Sci Rep* 6, 22245. <https://doi.org/10.1038/srep22245>
- Lotze, H.K., Coll, M., Dunne, J.A., 2011. Historical Changes in Marine Resources, Food-web Structure and Ecosystem Functioning in the Adriatic Sea, Mediterranean. *Ecosystems* 14, 198–222. <https://doi.org/10.1007/s10021-010-9404-8>

- Lurgi, N. Galiana¹, B.R Broitman, S. Kéfi, E. A. Wieters and S.A Navarrete. 2020. Geographical variation of multiplex ecological networks in marine intertidal communities. *Ecology*, *in press*
- Miele, V., Guill, C., Ramos-Jiliberto, R., Kéfi, S., 2019. Non-trophic interactions strengthen the diversity—functioning relationship in an ecological bioenergetic network model. *PLoS Comput Biol* 15, e1007269. <https://doi.org/10.1371/journal.pcbi.1007269>
- Neira, S., Arancibia, H., & Cubillos, L. (2004). Comparative analysis of trophic structure of commercial fishery species off Central Chile in 1992 and 1998. *Ecological Modelling*, 172(2-4), 233-248.
- Ortiz, M., Berrios, F., Campos, L., Uribe, R., Ramirez, A., Hermsillo-Núñez, B., González, J., Rodríguez-Zaragoza, F., 2015. Mass balanced trophic models and short-term dynamical simulations for benthic ecological systems of Mejillones and Antofagasta bays (SE Pacific): Comparative network structure and assessment of human impacts. *Ecological Modelling* 309–310, 153–162. <https://doi.org/10.1016/j.ecolmodel.2015.04.006>
- Oyanedel, R., Keim, A., Castilla, J.C., Gelcich, S., 2018. Illegal fishing and territorial user rights in Chile: Illegal Fishing. *Conservation Biology* 32, 619–627. <https://doi.org/10.1111/cobi.13048>
- Parada, G.M., Tellier, F., Martínez, E.A., 2016. Spore dispersal in the intertidal kelp *Lessonia spicata*: macrochallenges for the harvested *Lessonia* species complex at microscales of space and time 7.
- Pascual, M., Dunne, J.A., 2006. *Ecological Networks: Linking Structure to Dynamics in Food Webs* (Santa Fe Institute Studies on the Sciences of Complexity). Oxford University Press.
- Pauly, D., 2018. A vision for marine fisheries in a global blue economy. *Marine Policy* 87, 371–374. <https://doi.org/10.1016/j.marpol.2017.11.010>
- Pauly, D., 1998. Fishing Down Marine Food Webs. *Science* 279, 860–863. <https://doi.org/10.1126/science.279.5352.860>
- Pauly, D., Zeller, D., 2016. Catch reconstructions reveal that global marine fisheries catches are higher than reported and declining. *Nat Commun* 7, 10244. <https://doi.org/10.1038/ncomms10244>
- Pérez-Matus, Alejandro, Carrasco, S.A., Gelcich, S., Fernandez, M., Wieters, E.A., 2017. Exploring the effects of fishing pressure and upwelling intensity over subtidal kelp forest communities in Central Chile. *Ecosphere* 8, e01808. <https://doi.org/10.1002/ecs2.1808>
- Pérez-Matus, A, Ospina-Alvarez, A., Camus, P., Carrasco, S., Fernandez, M., Gelcich, S., Godoy, N., Ojeda, F., Pardo, L., Rozbaczylo, N., Subida, M., Thiel, M., Wieters, E., Navarrete, S., 2017. Temperate rocky subtidal reef community reveals human impacts across the entire food web. *Mar. Ecol. Prog. Ser.* 567, 1–16. <https://doi.org/10.3354/meps12057>
- Pikitch, E.K., 2004. *ECOLOGY: Ecosystem-Based Fishery Management*. *Science* 305, 346–347. <https://doi.org/10.1126/science.1098222>
- Plagányi, É.E., 2007. *Models for an ecosystem approach to fisheries*, FAO fisheries technical paper. Food and Agriculture Organization of the United Nations, Rome.

- Plagányi, É. E., & Butterworth, D. S. (2004). A critical look at the potential of Ecopath with Ecosim to assist in practical fisheries management. *African Journal of Marine Science*, 26, 261-287.
- Ponisio, L.C., Valdovinos, F.S., Allhoff, K.T., Gaiarsa, M.P., Barner, A., Guimarães, P.R., Hembry, D.H., Morrison, B., Gillespie, R., 2019. A Network Perspective for Community Assembly. *Front. Ecol. Evol.* 7, 103.
<https://doi.org/10.3389/fevo.2019.00103>
- Santelices, B., 1990. Patterns of organizations of intertidal and shallow subtidal vegetation in wave exposed habitats of central Chile. *Hydrobiologia* 192, 35–57.
<https://doi.org/10.1007/BF00006226>
- Skern-Mauritzen, M., Ottersen, G., Handegard, N.O., Huse, G., Dingsør, G.E., Stenseth, N.C., Kjesbu, O.S., 2016. Ecosystem processes are rarely included in tactical fisheries management. *Fish Fish* 17, 165–175. <https://doi.org/10.1111/faf.12111>
- Sutherland, W.J., Freckleton, R.P., Godfray, H.C.J., Beissinger, S.R., Benton, T., Cameron, D.D., Carmel, Y., Coomes, D.A., Coulson, T., Emmerson, M.C., Hails, R.S., Hays, G.C., Hodgson, D.J., Hutchings, M.J., Johnson, D., Jones, J.P.G., Keeling, M.J., Kokko, H., Kunin, W.E., Lambin, X., Lewis, O.T., Malhi, Y., Mieszkowska, N., Milner-Gulland, E.J., Norris, K., Phillimore, A.B., Purves, D.W., Reid, J.M., Reuman, D.C., Thompson, K., Travis, J.M.J., Turnbull, L.A., Wardle, D.A., Wiegand, T., 2013. Identification of 100 fundamental ecological questions. *J Ecol* 101, 58–67.
<https://doi.org/10.1111/1365-2745.12025>
- Teagle, H., Hawkins, S.J., Moore, P.J., Smale, D.A., 2017. The role of kelp species as biogenic habitat formers in coastal marine ecosystems. *Journal of Experimental Marine Biology and Ecology* 492, 81–98. <https://doi.org/10.1016/j.jembe.2017.01.017>
- Travis, J., Coleman, F.C., Auster, P.J., Cury, P.M., Estes, J.A., Orensanz, J., Peterson, C.H., Power, M.E., Steneck, R.S., Wootton, J.T., 2014. Integrating the invisible fabric of nature into fisheries management. *PNAS* 111.
- Vásquez, J.A., 2016. The Brown Seaweeds Fishery in Chile, in: Mikkola, H. (Ed.), *Fisheries and Aquaculture in the Modern World*. InTech. <https://doi.org/10.5772/62876>
- Villegas, M., Laudien, J., Sielfeld, W., Arntz, W., 2019. Effect of foresting barren ground with *Macrocystis pyrifera* (Linnaeus) C. Agardh on the occurrence of coastal fishes off northern Chile. *J Appl Phycol* 31, 2145–2157. <https://doi.org/10.1007/s10811-018-1657-1>
- Westermeier, R., Murúa, P., Patiño, D.J., Manoli, G., Müller, D.G., 2019. Evaluation of kelp harvest strategies: recovery of *Lessonia berteroa* (Phaeophyceae, Laminariales) in Pan de Azucar, Atacama, Chile. *J Appl Phycol* 31, 575–585.
<https://doi.org/10.1007/s10811-018-1500-8>.
- Weidberg, N., Ospina-Alvarez, A., Bonicelli, J., Barahona, M., Aiken, C. M., Broitman, B. R., & Navarrete, S. A. (2020). Spatial shifts in productivity of the coastal ocean over the past two decades induced by migration of the Pacific Anticyclone and Bakun effect in the Humboldt Upwelling Ecosystem. *Global and Planetary Change*, 103259.
- Worm, B., 2016. Averting a global fisheries disaster. *Proc Natl Acad Sci USA* 113, 4895–4897. <https://doi.org/10.1073/pnas.1604008113>
- Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S., Jackson, J.B.C., Lotze, H.K., Micheli, F., Palumbi, S.R., Sala, E., Selkoe, K.A., Stachowicz, J.J.,

- Watson, R., 2006. Impacts of Biodiversity Loss on Ocean Ecosystem Services. *Science* 314, 787–790. <https://doi.org/10.1126/science.1132294>
- Worm, B., Hilborn, R., Baum, J.K., Branch, T.A., Collie, J.S., Costello, C., Fogarty, M.J., Fulton, E.A., Hutchings, J.A., Jennings, S., Jensen, O.P., Lotze, H.K., Mace, P.M., McClanahan, T.R., Minto, C., Palumbi, S.R., Parma, A.M., Ricard, D., Rosenberg, A.A., Watson, R., Zeller, D., 2009. Rebuilding Global Fisheries. *Science* 325, 578–585. <https://doi.org/10.1126/science.1173146>
- WWF, 2018. Living planet report. WWF, Gland, Switzerland.
- Yodzis, P., 2001. Must top predators be culled for the sake of fisheries? *Trends in Ecology & Evolution* 16, 78–84. [https://doi.org/10.1016/S0169-5347\(00\)02062-0](https://doi.org/10.1016/S0169-5347(00)02062-0)