



## Diversity of small-scale fisheries in Chile: Environmental patterns and biogeography can inform fisheries management

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### ABSTRACT

Small-scale fisheries are major contributors to global fishing catch and to the livelihoods of many coastal communities. However, little is known about these fisheries, the spatial heterogeneity in which they are found, and the factors that explain this heterogeneity. In Chile, the distinct environmental regimes driven by the Humboldt Current System can contribute to a high diversity in the species targeted by small-scale fisheries. Through a Chilean case-study, we aimed to characterize how environmental and socio-economic conditions influence small-scale benthic fisheries in 15 coves, straddling two biogeographic regions along 24 degrees of latitude (*ca.* 2600 km) and administered by a nation-wide management framework. We compiled and analyzed a long-term database generated by a standardized monitoring protocol in order to determine how fishing techniques, benthic resource diversity, effort and fishers' income vary along the coastline. Our results highlighted that small-scale fisheries are strongly influenced by the variations in the environmental conditions, which determine variations in landings along the coast. Our analyses also illustrated how fishers seek to ensure their livelihoods by dealing with regional and local environmental conditions, ecology of marine resources, socio-economic context and a management system that is not able to accommodate fisheries' heterogeneity. Our results suggest that future changes to the Chilean management system should integrate the spatial variation observed among small-scale fisheries to ensure sustainable livelihoods of the fishers and conservation of the marine resources. Fishery management rules should be shaped according to the region where they are applied, moving from homogeneous nation-wide systems, or systems adapted from administrative divisions to differentiated co-management systems based on biogeographic units.

### 1. Introduction

Small-scale fisheries (SSFs) are a highly dynamic and diversified sector. It involves the exploitation of coastal and inland hydrobiological resources by fishers employing labor intensive technologies, working from land or using boats of minimal tonnage (<50 gross tonnes) and low-power engine (<400 HP) for short-term fishing trips (World Bank, 2012; Smith and Basurto, 2019). The SSF sector employs about 90 percent of all workers that depend directly on commercial capture fisheries value chains, and contributes to about a quarter of the fishing captures worldwide, representing the majority of catches in many

developing countries (World Bank, 2012; Pauly and Zeller, 2020). Despite the substantial contribution of SSFs for socio-economic well-being in coastal communities worldwide, their local functioning and sustainability have received relatively little attention (FAO, 2019).

There is a worldwide paucity of information about SSFs, particularly in developing countries (Salas et al., 2007; Mills et al., 2011; Guyader et al., 2013). SSFs have received limited attention when compared to industrial fisheries (Teh and Pauly, 2018) and are often neglected by policymakers and researchers, mostly because of an underestimation of their socioeconomic value and contribution to societal well-being (e.g., Garcia et al., 2008; Béné et al., 2016). On a broad scale, catch and effort

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estimations of SSFs have consistently helped to fill this information gap, providing reliable information to managers and decision-makers (Zeller et al., 2011; Le Manach et al., 2012; Pauly and Zeller, 2016). However, the feasibility of obtaining such reliable indicators at the local level is more limited. Technical difficulties are found in building reliable long-term databases on SSFs, which are generally multi-gear and multi-species, operating at a very local scale, with remote landing sites, sporadic fishing efforts, decentralized post-harvest and marketing systems, with under-resourced data systems and often with a substantial amount of illegal fishing. Despite these challenges, reliable SSF monitoring programs can contribute to the implementation of strategies that both improve sustainable incomes for fishers and facilitate fisheries recovery and resilience (Berkes et al., 2001; Salas et al., 2007; McIlgorm et al., 2010).

The sustainability of the social-ecological systems (SESs) centered around SSFs relies in part on the adequacy between the management institutions, the socioenvironmental problems they are designed to address, and the contexts in which they operate (Kalikoski et al., 2002; Cinner et al., 2009; Epstein et al., 2015). In particular, a mismatch between the scale of management and the scales of the ecological processes being managed may jeopardize fisheries sustainability and the livelihoods of those who depend on them (Cumming et al., 2006; Folke et al., 2007; Stotz, 2019). To date, fisheries management still tends to be implemented for a single species at a single large scale (e.g., Wilson, 2006; Johnson et al., 2012). However, it may be of greater benefit to fishers if management models consider the interdependence among exploited species as well as the heterogeneity of fisheries at a finer scale (e.g., Sanchirico et al., 2008; Pellowe and Leslie, 2017). Although a slow transition is undergoing from monospecific and off-scale management to other management approaches with promising long-term results, effective practices remain challenging (e.g., Gelcich et al., 2006; Walters, 2007; Westgate et al., 2013; Patrick and Link, 2015).

Chile is among the top ten fishing countries in the world and accounts for three percent of the world's marine production (FAO, 2020). SSFs currently generate over half of the national catch, of which about 30 % is landed by benthic fishers (SERNAPESCA, Servicio Nacional de Pesca y Acuicultura, 2019). Our work is focused exclusively on small-scale benthic fisheries in Chile, which have essentially a top-down management approach, from centralized government institutions to interregional and regional offices that are in contact with local fishers' organizations. Government institutions regulate access to SSFs based on administrative regions. Every benthic fisher is required to register in a national registry program managed in 16 administrative regions. Thus, fishers can only officially operate in one administrative region and new registrations have been almost permanently closed since 1995 to avoid overexploitation (Moreno et al., 2007). All along the Chilean coast, the management system combines benthic fisheries with very local and exclusive Territorial Use Rights (TURFs) and fisheries from "open access" areas that can exploit the marine resources of the entire administrative region except for TURF areas (Gelcich et al., 2010). The regulation of the Chilean benthic SSFs is carried out through a combination of administrative measures, such as yearly quotas, restrictions of the authorized fishing gears, minimum legal size and temporary bans on a species-by-species basis. Although the implementation of the TURF co-management regime has contributed to strengthening the territorial stewardship of Chilean small-scale fishers, power and decision-making remain largely concentrated in the national government, and TURF areas only provide in most cases a complementary income to small-scale fishers (Marín and Berkes, 2010; Gelcich et al., 2017; Romero and Melo, 2021). Since 2013, Chilean fishers' representatives, government institutions and other key actors have had the opportunity to form multi-sectoral Management Committees (MCs) that work within the legal structure of the fisheries Management Plans (Law 20.657, 2013). These management plans can be applied to any coastal fishery in "open access" areas of a given territory and allow the MCs to define the main objectives to be achieved, gather the necessary information, and

establish guidelines and rules to achieve these objectives. MCs are also directly involved in the implementation of this management framework within the designated territories. Unlike the top-down national management framework, this legal structure can promote a polycentric approach to governance in Chilean benthic SSFs (Gelcich, 2014; Estévez et al., 2020).

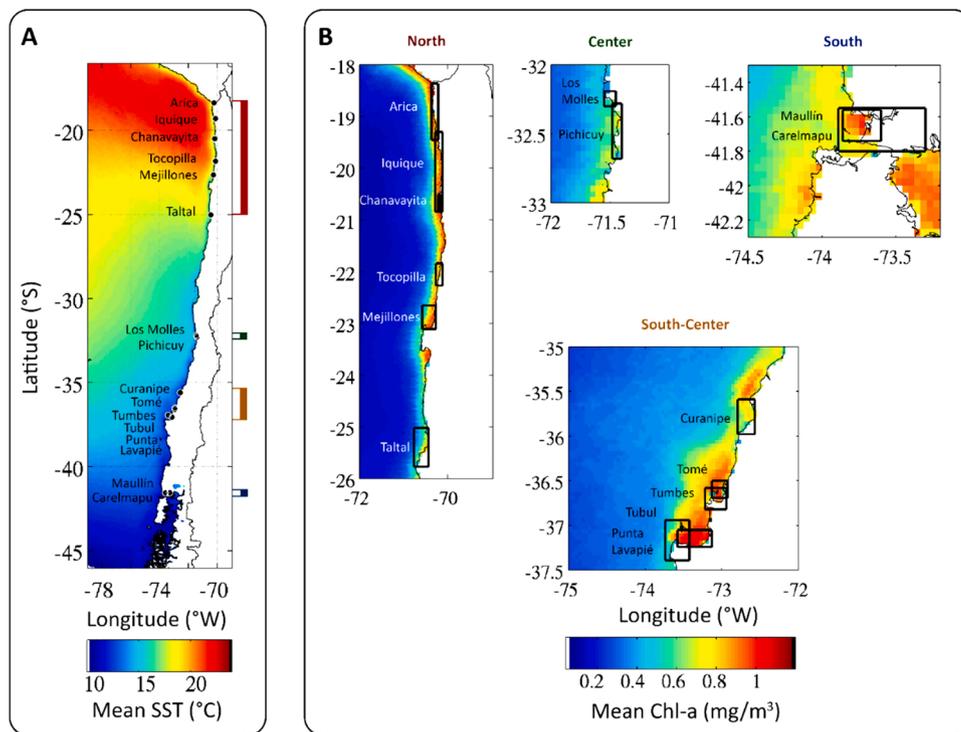
Small-scale benthic fishers work in coastal areas off to the first nautical mile using boats smaller than 12 m or directly from the shoreline around small-scale fishing coves. They use a variety of gears and fishing techniques, ranging from manual seaweed harvest to semi-autonomous diving, to capture a diverse set of marine benthic organisms (*i.e.*, seaweeds, mollusks, crustaceans, echinoderms and tunicates). The diversity of resources, gears and techniques is not surprising considering the marine biogeography of Chile. From 18 °S to 42 °S, the Chilean coast extends linearly along a wide latitudinal gradient of temperature. There are no apparent geographic or environmental discontinuities along these 2600 km of coastline (Haye et al., 2014), except for a biogeographic break reported at 30 °S, which reflects a change in coastal upwelling regime (Hormazabal et al., 2004; Aguilera et al., 2019). Benthic coastal ecosystems are influenced by the Humboldt Current System (HCS), where coastal upwelling fuels one of the highest primary productions worldwide (Chavez and Messié, 2009). The frequency and intensity of upwelling events along the HCS exhibit strong spatial and temporal variation and so do fisheries landings (Anguita et al., 2020; Chevallier et al., 2021). Recent reviews showed that SSFs local efforts and yields respond mainly to a combination of multi-scale environmental and socio-economic drivers (e.g., Crona et al., 2015; Yáñez et al., 2017). Hence, both types of factors are expected to drive spatial heterogeneity in coastal benthic SSFs along the Chilean coast.

SSF management has generally focused on overall production together with other biological indicators (Andrew et al., 2007), paying little attention to the broad system in which SSFs are found. The multiple interactions among the socio-economic, oceanographic, and ecological components that shape coastal fisheries are rarely addressed, despite their relevance for management. With a rather homogeneous management framework and a few management alternatives, Chilean benthic SSFs are an ideal case study to illustrate how a diversity of SSFs can be found along a seemingly homogeneous coastline. Therefore, we examined how fishing techniques, resources diversity, efforts, landings and incomes vary along the coast using a large-scale (2600 km of coastline) and long-term (17 years) standardized database for 15 SSFs spread along the HCS, together with a satellite-based assessment of their local and regional patterns of environmental conditions. This assessment would help determine if the rather homogeneous management system in place takes into account the main components of Chilean SSFs or if it should be restructured to better accommodate the livelihoods of fishers and the diversity of environmental conditions along the coast. Our analysis could highlight possible inadequacies between the management scale, environmental regimes and the scales of the socio-ecological systems being managed.

## 2. Materials & methods

### 2.1. Study area

Scientific observers of the National Institute for Fisheries Support (Instituto de Fomento Pesquero – IFOP) monitored multi-specific benthic fisheries in "open access areas" (*i.e.*, in all fishing areas except TURFs) centered on 15 small-scale fishing coves using a standardized protocol. These fishing coves are distributed from Arica (18 °S) to Carelmapu (42 °S) along the continental coast of Chile, excluding the Patagonian islands and fjords (Fig. 1). We grouped these fishing coves into four clusters based on biogeographic boundary reviews (Camus, 2001; Spalding et al., 2007), species distribution and molecular taxonomic composition (e.g., Rivadeneira et al., 2011; Guillemin et al., 2016; Lara et al., 2019; Navarrete et al., 2020), and variation of environmental



**Fig. 1.** Location of the small-scale fishing coves monitored along the Chilean coast and spatial variation of the associated environmental conditions. A) Latitudinal gradient of mean sea surface temperature (SST) across our study area over the 2003–2018 period. B) Variation in mean chlorophyll-a concentration (Chl-a) for the four geographic clusters (North, Center, South-Center, South) and estimates of the total fishing area for each fishing cove (area inside each black outline rectangle).

conditions in the region (Carr and Kearns, 2003; Demarq et al., 2012; Lara et al., 2019). An IFOP geographic information system (GIS) manager estimated the total fishing area operated by fishers from each fishing cove, by cross-referencing information from GPS point surveys of the daily fishing sites with interviews with fishers.

2.2. Satellite environmental data

We calculated mean sea surface temperature (SST, °C) and mean chlorophyll-a concentration (Chl-a, mg/m<sup>3</sup>) from eight-day night-time composite data (2003–2018) from the MODIS spectroradiometer on

board NASA’s Aqua satellite with a spatial resolution of 4 × 4 km (<http://oceancolor.gsfc.nasa.gov/>). These variables were used as proxies of the spatial variation of the environmental conditions along the coast (e.g., Aravena et al., 2014; Lara et al., 2019), both on a regional scale (Fig. 1-A), and on a local scale (Fig. 1-B).

2.3. Characterization of Chilean small-scale fisheries

2.3.1. Landings and sale prices

IFOP scientific observers collected daily landings records in the 15 fishing coves within the framework of the Benthic Small-scale Fisheries

**Table 1**  
Main fishing coves’ attributes.

Fishing cove	Latitudinal range of the fishing area (°S)	Number of years sampled <sup>a</sup>	Interannual mean ± SD number of identified <sup>b</sup> fishers	Interannual mean ± SD total Catch (tonnes)	Interannual mean ± SD estimate of the total value per identified <sup>b</sup> fisher (2018 USD)	Interannual mean ± SD number of taxonomic families fished
Arica	18.4–19.5	17	78 ± 49	413 ± 195	2878 ± 836	11 ± 1
Iquique	19.3–20.8	17	44 ± 17	330 ± 210	3788 ± 1221	9 ± 1
Chanavayita	20.5–20.8	17	28 ± 9	180 ± 110	3265 ± 933	8 ± 1
Tocopilla	21.8–22.3	11	15 ± 6	139 ± 50	5569 ± 1882	6 ± 2
Mejillones	22.7–23.1	8	25 ± 11	160 ± 60	5131 ± 1836	10 ± 1
Taltal	25.0–25.8	10	26 ± 17	31 ± 24	3555 ± 2697	3 ± 1
Los Molles	32.2–32.3	7	23 ± 6	935 ± 270	5238 ± 1224	3 ± 2
Pichicuy	32.3–32.7	10	51 ± 23	1348 ± 1138	3236 ± 1834	4 ± 3
Curanipe	35.6–36.0	13	35 ± 30	79 ± 50	5085 ± 3955	4 ± 2
Tomé	36.5–36.7	17	33 ± 5	291 ± 91	5696 ± 2328	13 ± 1
Tumbes	36.6–36.8	17	356 ± 109	1158 ± 615	1516 ± 532	14 ± 4
Tubul	37.1–37.2	17	1210 ± 323	6082 ± 1553	3922 ± 1529	7 ± 2
Punta Lavapié	36.9–37.4	12	89 ± 45	263 ± 127	2483 ± 1746	6 ± 3
Mauilín	41.6–41.7	17	177 ± 48	1792 ± 678	1884 ± 702	3 ± 1
Caremapu	41.6–41.8 <sup>c</sup>	17	336 ± 69	4734 ± 1410	3961 ± 991	8 ± 1

<sup>a</sup> During certain months, scientific observers were not able to visit the fishing coves on a daily basis. We excluded from our analyses years that were monitored for less than nine months on a daily basis so as to analyze only representative periods of the fishers’ activities.

<sup>b</sup> When possible, scientific observers identified individually divers and seashore fishers during daily landings. However, crab fishers, vessel owners (commonly the managers-skippers), and eventually other crew members were not identified during landings.

<sup>c</sup> Fishers from Caremapu went further south to about 42.7°S, but fishing activities south of 41.8°S were not considered in this study.

Monitoring Program (Barahona et al., 2006). Scientific observers conducted surveys five days per week from 2002 to 2018, for eight fishing coves (Arica, Iquique, Chanavayita, Tomé, Tumbes, Tubul, Maullín and Carelmapu), and for seven to 13 years for seven other fishing coves, considering only the years that they monitored for at least nine months

on a daily basis (Table 1).

Scientific observers identified each benthic resource of the landings to the most accurate taxonomic level (Supplementary Material, Appendix A). They weighed the landings either on the fishing pier, or on the beach in the case of seashore fishers. We grouped by family closely

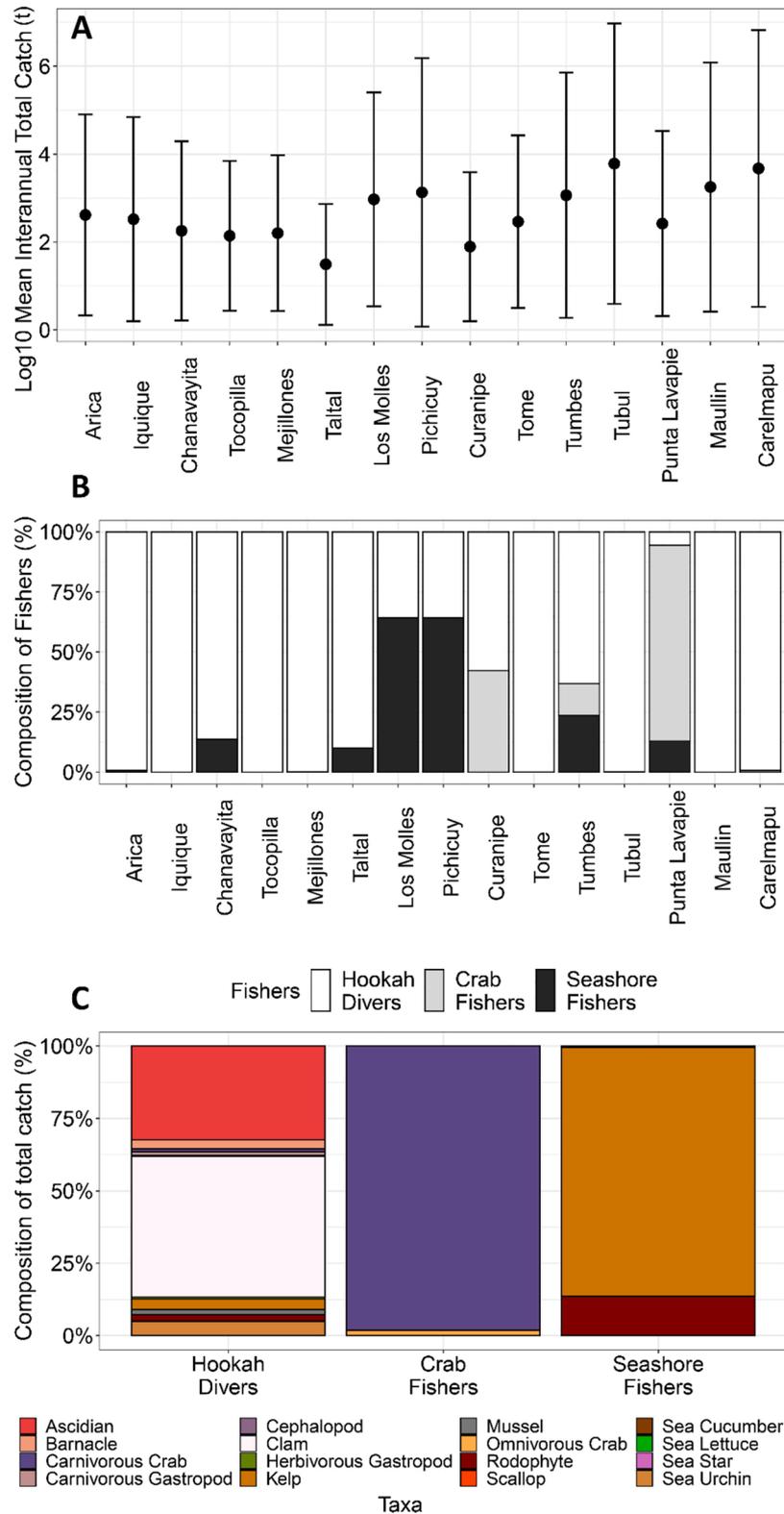


Fig. 2. Diversity in total catch among fishing coves and fishers' categories. A) Interannual mean and standard deviation of the total catch in biomass for each fishing cove. B) Proportion of the total catch in biomass landed by each fishers' category among fishing coves for all years. C) Proportion of the total catch in biomass landed by each fishers' category for all fishing coves and all years according to functional taxonomy.

related species whose identification to the species level was uncertain. These taxonomic uncertainties involved 14 species from the Epiplatidae, Fissurellidae and Veneridae families, namely omnivorous kelp crabs, herbivorous keyhole limpets and clams, respectively. Likewise, we grouped six species of carnivorous crabs into the ‘carnivorous brachyuran’ taxon. We assessed resource composition by fishers’ categories (Fig. 2C) and fishing coves (Fig. 3) using a classification by functional groups based on ecological guilds (Root, 1967). We defined each guild using a combination of taxonomic class and trophic level (Appendix A). Exceptions were made for eight species of Florideophyceae and one species of Bangiophyceae that we grouped as ‘Rodophyte’, and the suspension feeder bivalves that we separated in ‘Clam’ (12 species) and ‘Mussel’ (three species). It is worth mentioning that the monitoring program did not cover the TURF areas, and therefore did not include the landings of the highly valued carnivorous snail *Concholepas concholepas* (Gelcich et al., 2010). Current legislation does not officially authorize to fish *C. concholepas* in ‘open access’ areas. However, recent studies have shown that annual unauthorized landings of *C. concholepas* in ‘open access’ areas are an order of magnitude higher than in TURF areas, with significantly smaller median individual size (Fernández et al., 2020; Stotz et al., 2021).

Scientific observers recorded on-site sale prices either after the weighing during the sales, or by interviewing fishers or buyers after the sale was concluded. We estimated values of the total daily catch of each taxon by multiplying the total catch of the day by the average selling price of the day. We then normalized these economic values by deflating them relative to the Chilean Consumer Price Index (base 2018 = 100), calculated by the Chilean Institute of Statistics (Instituto Nacional de Estadísticas). Finally, we converted the deflated prices into 2018 US dollars using the historical value of the US dollar in Chilean pesos,

provided by the Chilean Central Bank (<https://www.bcentral.cl/>).

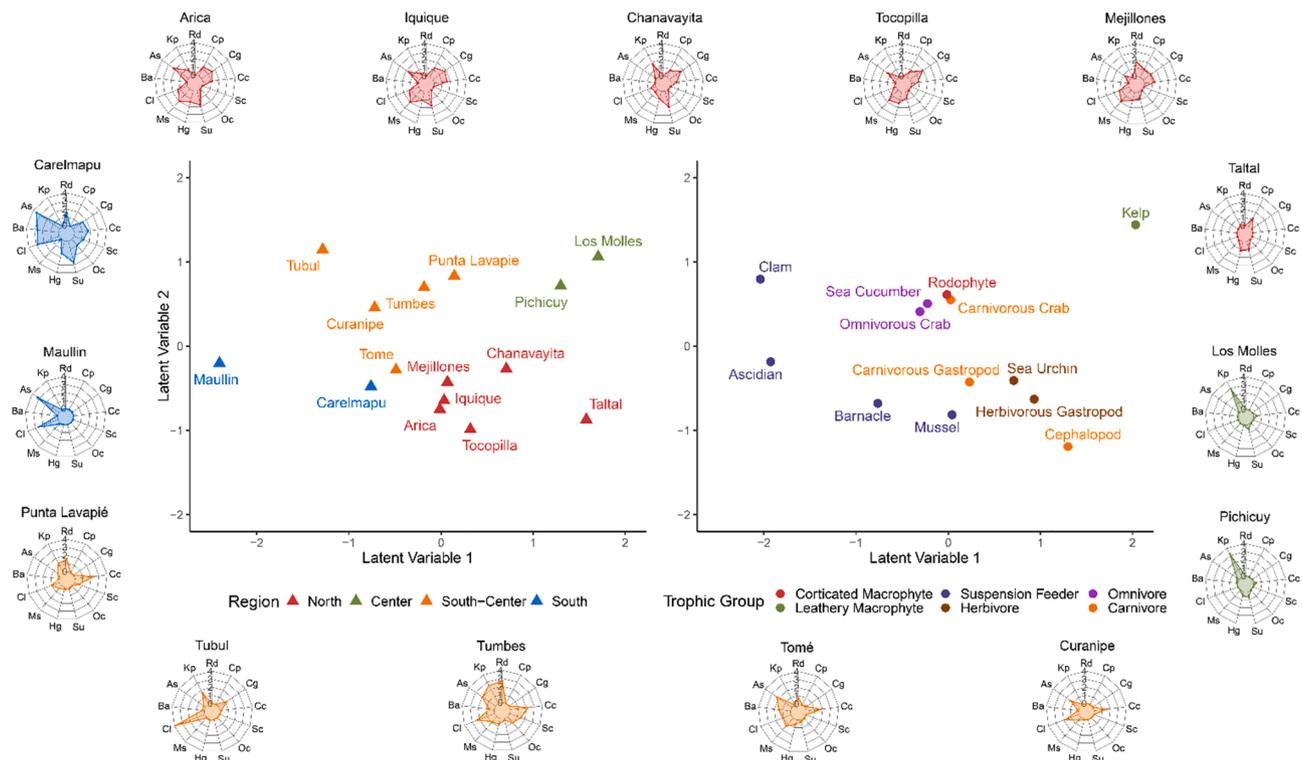
### 2.3.2. Fishing techniques

In each fishing cove, we grouped fishers into three categories: hookah divers, seashore fishers and crab fishers. Hookah divers go fishing on boats equipped with a collective air compressor to which hoses with pressure regulators (‘hookah’) are connected. Seashore fishers walk along the shore, and can also fish close to the coast, free dive, and gather algae from boats with a grappling hook. Finally, crab fishers mostly use boats to set baited traps. Scientific observers recorded the dates and times of departure and return to port for each boat. They also determined the number of fishers associated with each landing record as well as the extraction areas of the landings by direct observation and by interviewing the fishers during landings. We calculated the proportion of landings for each category of fishers for each fishing cove, and the proportion of each landed resource for each category of fishers, according to our established functional classification.

We summarized a set of the main quantitative attributes of the 15 monitored small-scale fishing coves in Table 1.

### 2.4. Diversity of fishing resources along the Chilean coast

We characterized the variation of the diversity of ecological guilds exploited between fishing coves and identified indicator taxa using a model-based approach of unconstrained ordination, which was applied to the interannual mean catch of all main taxa (Fig. 3A). We only excluded from the analysis the Peruvian scallop, sea lettuce and sea stars, whose total landings summed less than 100 tonnes for all sampled years and fishing coves combined. We fitted a latent variable model (LVM) using Bayesian Markov chain Monte Carlo (MCMC) estimation (Hui et al.,



**Fig. 3. Model-based unconstrained ordination of the interannual mean catch of all fishing coves for all main taxa according to a functional taxonomy combining class and trophic group.** We used a Tweedie distribution function with a log link function to model biomass responses and included random row effects to account for sampling variability between fishing coves. The resulting ordination is presented in a biplot of all fishing coves (center left) and corresponding taxa (center right), which is surrounded by a series of individual starplots showing the decimal logarithm of the interannual mean catch for each fishing cove according to functional taxonomy: Rodophytes (Rd) and Kelps (Kp) for the seaweeds, Ascidians (As), Barnacles (Ba), Clams (Cl) and Mussels (Ms) for the suspension feeders, Herbivorous gastropods (Hg) and Sea urchins (Su) for the herbivores, Omnivorous crabs (Oc) and Sea cucumbers (Sc) for the omnivores, and Carnivorous crabs (Cc), Carnivorous gastropods (Cg) and Cephalopods (Cp) for the carnivorous taxa.

2015; Warton et al., 2015) via the R package *boral* (Hui, 2016, 2020), where species' responses were assumed to follow a Tweedie distribution with a log link function connecting the linear predictor and the mean of the distribution. The model included random row intercepts for the fishing coves to account for the variability inherent to the monitoring design. This model-based ordination minimized the risk of confounding between location patterns and changes in dispersion, which is frequent in multivariate analyses (Warton et al., 2012; Warton and Hui, 2017). Model-based ordination using latent variables has become increasingly popular in community ecology (e.g., Björk et al., 2018; Brown and Hamilton, 2018; Høye et al., 2018), particularly given its capacity to incorporate a variety of features such as spatial and temporal correlations (Thorson et al., 2015), imperfect detection (Tobler et al., 2019), and different spatial resolutions (Ovaskainen et al., 2016). We chose the Tweedie distribution because of its suitability to model continuous, non-negative real variables with a non-negligible proportion of zero responses (63 % of our total catch matrix), as is characteristic of biomass data in fisheries ecology (Shono, 2008; Carvalho et al., 2010; Foster and Bravington, 2013). We validated our model's fit by analyzing Dunn-Smyth residuals (Dunn and Smyth, 2018), and by fitting a binary LVM with a binomial distribution and a probit link function using a presence-absence response rather than biomass data (Appendix C in Supplementary Material). We assessed the goodness-of-fit of our models using residual analyses (Appendices B and D).

### 3. Results

The 15 fishing coves were distributed along a latitudinal SST gradient spanning over 10 °C (Fig. 1-A). Most of the fishing sites were located in areas of high primary production (Fig. 1-B), with Chl-a ranging from more than 1 mg/m<sup>3</sup> at Tubul to less than 0.8 mg/m<sup>3</sup> at Los Molles and Pichicuy. We observed the highest values of Chl-a alongside prominent bays and coastal promontories (around 23 °S, 36.5 °S and 37 °S). Most of the coves were located on the lee side of these

headlands, on their equatorial face with a northwest orientation. The south-central and southern coves (35 °S - 42 °S) were associated with a wider coastal band of increased primary production when compared to the northern and central clusters. This coastal band of high primary production spread diffusely in the southern cluster (41 °S - 42 °S). The latitudinal extent of the total fished areas varied among coves with a mean and standard deviation of 0.5 ± 0.4° (Fig. 1-B and Table 1). Only fishers from Arica, Iquique and Carelmapu fished in coastal areas of more than one degree of latitude, considering the entire fishing area of Carelmapu fishers (41.6 °S - 42.7 °S). In this study, we did not consider fishing activities south of 41.8 °S because they correspond to another biogeographic region.

The number of benthic fishers identified was highly variable among the different fishing coves (Table 1). While on average the number of fishers varied slightly from Arica to Tomé (18.5 °S - 36.5 °S), it increased from Tumbes to Carelmapu (36.5 °S - 42 °S), where most fishing coves had more than a hundred fishers per year on average. Tubul was the only fishing cove with more than a thousand fishers per year on average. These estimations were less accurate in Punta Lavapié because scientific observers did not count the number of crab fishers during monitoring as crab fishers worked mainly with traps that they set and retrieved during two successive days.

The interannual average of the total catch varied by two orders of magnitude among the different fishing coves (illustrated in Fig. 2-A). On the one hand, some coves recorded a low fishing production such as Taltal (25 °S) and Curanipe (36 °S). On the other hand, we classified the highly productive coves in two groups: Los Molles and Pichicuy (32 °S - 33 °S), which were characterized by a reduced number of fishers highly specialized in kelp harvesting (Table 2), and Tumbes, Tubul, Maullín and Carelmapu in the south (36.5 °S - 42 °S), which had a much greater fishing effort.

The taxonomic richness of the landings also varied significantly among fishing coves. From Arica to Mejillones (18.5 °S - 23 °S), we recorded nine families on average during the year, while we recorded

**Table 2**

**The main taxa landed at each fishing cove.** We determined the most caught taxa by their total catch for all years monitored for a minimum of nine months, and estimated interannual mean and standard deviation for those years.

Fishing cove	Interannual Mean ± SD Catch of the most caught taxon (tonnes)	Interannual Mean ± SD Catch of the second most caught taxon (tonnes)	Interannual Mean ± SD Catch of the third most caught taxon (tonnes)	Interannual Mean ± SD Catch of the fourth most caught taxon (tonnes)
Arica	<i>Pyura chilensis</i> 155 ± 50	<i>Aulacomya atra</i> 69 ± 44	<i>Loxechinus albus</i> 61 ± 50	<i>Thaisella chocolata</i> 33 ± 32
Iquique	<i>Aulacomya atra</i> 80 ± 51	<i>Thaisella chocolata</i> 62 ± 45	<i>Loxechinus albus</i> 50 ± 75	<i>Pyura chilensis</i> 42 ± 22
Chanavayita	<i>Loxechinus albus</i> 95 ± 90	<i>Thaisella chocolata</i> 43 ± 55	<i>Lessonia berteroa</i> 30 ± 20	<i>Lessonia trabeculata</i> 189 (one year)
Tocopilla	<i>Aulacomya atra</i> 46 ± 17	<i>Thaisella chocolata</i> 66 ± 42	Fissurellidae 27 ± 27	<i>Pyura chilensis</i> 24 ± 10
Mejillones	<i>Aulacomya atra</i> 59 ± 32	<i>Agarophyton chilense</i> 55 ± 35	Carnivorous brachyuran 17 ± 7	Veneridae 11 ± 6
Taltal	Fissurellidae 14 ± 13	<i>Octopus mimus</i> 13 ± 8	<i>Loxechinus albus</i> 9 ± 10	<i>Lessonia berteroa</i> 0.49 (one year)
Los Molles	<i>Lessonia spicata</i> 578 ± 219	<i>Lessonia trabeculata</i> 376 ± 283	<i>Lessonia spp.</i> 101 (one year)	<i>Lessonia spp. or Macrocystis pyrifer</i> 93 (one year)
Pichicuy	<i>Lessonia spicata</i> 796 ± 622	<i>Lessonia trabeculata</i> 824 ± 496	<i>Macrocystis pyrifer</i> 193 ± 99	<i>Loxechinus albus</i> 3 ± 2
Curanipe	Carnivorous brachyuran 34 ± 11	<i>Ensis macha</i> 54 ± 60	<i>Pyura chilensis</i> 22 ± 24	<i>Aulacomya atra</i> 1 ± 1
Tomé	<i>Pyura chilensis</i> 164 ± 49 T	Carnivorous brachyuran 64 ± 58	<i>Austromegabalanus psittacus</i> 28 ± 15	<i>Aulacomya atra</i> 18 ± 19
Tumbes	<i>Sarcothalia crispata</i> 347 ± 324	Carnivorous brachyuran 159 ± 126	<i>Lessonia spicata</i> 265 ± 298	<i>Lessonia trabeculata</i> 271 ± 311
Tubul	<i>Tagelus dombeii</i> 3314 ± 1854	<i>Mulinia edulis</i> 1588 ± 1109	<i>Ensis macha</i> 1154 ± 617	<i>Chorus giganteus</i> 12 ± 9
Punta Lavapié	Carnivorous brachyuran 214 ± 122	<i>Sarcothalia crispata</i> 31 ± 29	<i>Lessonia spicata</i> 16 ± 20	<i>Ensis macha</i> 6 ± 7
Maullín	<i>Pyura chilensis</i> 1524 ± 765	Veneridae 281 ± 157	<i>Mulinia edulis</i> 289 ± 217	<i>Gari solida</i> 7 ± 7
Carelmapu	<i>Pyura chilensis</i> 2981 ± 1165	<i>Loxechinus albus</i> 519 ± 279	<i>Austromegabalanus psittacus</i> 446 ± 351	<i>Gari solida</i> 433 ± 152

only three to four families at Taltal, Los Molles, Pichicuy, Curanipe and Maullín. We observed the greatest taxonomic richness at Tomé and Tumbes (36.5 °S), with 13 and 14 families, respectively. At Tubul and Punta Lavapié (37 °S), and at Carelmapu (42 °S), we recorded seven families on average in the landings.

We estimated that each fisher generated on average a total interannual value of  $3642 \pm 1459$  standardized U.S. dollars (2018 USD) for the 15 fishing coves. The estimates of the total interannual economic value generated per fisher varied significantly among fishing coves. For example, although Tomé and Tumbes were located in the same bay and shared a large part of their fishing areas (Fig. 1), their interannual per capita incomes constituted the maximum (USD 5696) and minimum (USD 1516) incomes observed among all fishing coves, respectively. Furthermore, there was little interannual variation in the annual income per capita within the same fishing cove. On average, the interannual standard deviation represented less than 35% of the value of the interannual average across 13 sites, excluding Taltal, Curanipe and Punta Lavapié. The latter coves recorded a much greater interannual variation, with a standard deviation representing more than 70% of the average.

Hookah divers landed more than 85 % of the catch in all fishing coves other than Los Molles, Pichicuy, Curanipe, Tumbes and Punta Lavapié (Fig. 2-B). Overall, hookah divers' landings were diverse (Fig. 2-C), consisting of clams (48 %), ascidians (32 %), sea urchins (5%), barnacles (3%), kelp (4%), rodophytes (3%), mussels (2%), carnivorous and herbivorous gastropods (2%), and carnivorous crabs (1%). Aggregate landings of other resources, namely cephalopods, omnivorous crabs, Peruvian scallops, sea cucumbers, sea lettuce and sea stars, represented less than 1% of the total catch.

In the central cluster (32 °S - 33 °S), 64 % of the total catch was landed by seashore fishers and 36 % by hookah divers (Fig. 2-B), specializing for the most part in kelp harvesting (Table 2). Fishing techniques were more diversified in the south-central cluster (35.5 °S - 37.5 °S), where crab fishing accounted for a significant portion of the landings in Punta Lavapié (81 %), Curanipe (42 %) and Tumbes (13 %). Overall, crab fishers were highly specialized in carnivorous crabs, which represented 98 % of their catch (Fig. 2-C). Seashore fishers were also highly specialized in kelps (80 %) and rodophytes (19 %) with very low landings of ascidians, cephalopods, clams, and fissurellid herbivorous gastropods.

The ordination based on fishing resources diversity of each fishing cove distinguished the same four clusters of fishing coves previously grouped according to biogeography, species distribution and environmental conditions (Fig. 3). Northern fisheries were characterized by carnivorous gastropods, mussels, sea urchins and herbivore gastropods of the Fissurellidae family. Only Taltal was isolated from the northern cluster with much smaller landings (see the individual starplots in Fig. 3). The cephalopod *Octopus mimus* was an indicator species of the northern fisheries, as it exhibits a warm-temperate distribution. The central fisheries of Los Molles and Pichicuy specialized in kelp harvesting. South-central fisheries, except for Tubul, were characterized by high landings of carnivorous crabs and did not show any clear other common patterns. Finally, southern fishing coves were characterized by very productive fisheries, with several thousands of tonnes of ascidians and several hundreds of tonnes of clam species. Carelmapu was also very productive in fishing hundreds of tonnes of sea urchins and barnacles, had a much more diversified fishery in comparison to Maullín and in particular, various resources in common with the south-central fishing cove of Tomé. The low resource diversity of Maullín explained why the fishing cove was isolated in the ordination.

The residuals analysis largely validated the use of a model-based ordination approach (available as Supplementary Material, Appendix B), with no strong evidence of violations of the model assumptions, except in the plot of the residuals against the linear predictors which showed residuals tending to increase with the corresponding linear predictor. Further analyses revealed that this pattern was driven by the very heterogeneous fisheries data compiled, with an interannual

average of landings that differed by several orders of magnitude between fishing ports (See for example the ascidian, clams or kelp fisheries in Fig. 3). As a precautionary measure, we fitted a second model presented in the Supplementary Material section (Appendices C–D), which was based only on presence-absence instead of biomass data. This second ordination exhibited similar results to the model presented in the main text, distinguishing also the four geographical clusters by their resource composition, but with a lower precision as it did not account for the large differences in landings biomass observed from one cove to another. Furthermore, analysis of model residuals did not exhibit any noticeable evidence of issues with modeling assumptions. Overall, results confirmed that our model-based ordination on the biomass responses, and the conclusions arising from this, were reasonable and not an artifact of failing to account for the mean-variance relationship in the data.

## 4. Discussion

### 4.1. The strong influence of environmental conditions on small-scale fisheries

Sea surface temperature (SST) is a robust indicator of the variability of coastal oceanographic conditions of intertidal and shallow subtidal ecosystems (Hinojosa et al., 2006; Blanchette et al., 2008; Fenberg et al., 2015). Chlorophyll-a concentration is a complementary indicator of SST, reflecting primary production and nutrient supply (Demarcq et al., 2012), which provide a coherent prediction of the biogeographical structure of coastal ecosystems (Lara et al., 2019). In this study, the diversity of resources observed among the 15 fishing coves was consistent with the gradient of the long-term mean SST and the variation of the coastal band of high primary production along the Chilean coast. Moreover, the spatial structure of the diversity of the fishing resources and that of the environmental indicators are consistent with the grouping of fishing coves defined from the existing literature (please see Materials and Methods). In Chile, small-scale fishers are spatially confined to administrative regions. The observed correspondence of the observed resource diversity with the species distribution and taxonomic composition described in the existing literature, combined with the fact that fishers are spatially restricted, indicates that this diversity of resources is largely determined by marine biogeography. Our results thus support the hypothesis that the taxonomic diversity of SSFs landings varies greatly depending on environmental conditions and biogeography, regardless of the fishing effort and price attractiveness of these resources.

While many taxa are distributed and fished all along the Chilean coast, large variations in magnitude were observed in the landings among the different clusters of fishing coves. These variations may depend on the ecological and oceanographic context, as illustrated by the fisheries specializing in carnivorous crabs in the south-central cluster (35.5 °S - 37.5 °S). For instance, each of the highly productive fisheries of Tumbes and Punta Lavapié landed over 150 tonnes of carnivorous crabs per year, on average. These high landings were consistent with a large-scale experiment on bait consumption by intermediate predators (Musri et al., 2019), which suggested that carnivorous crabs are the main benthic predators in south-central Chile (around 30 °S - 42 °S). Carnivorous crabs play a major ecological role in shaping soft-bottom macrobenthic community structure, both as an abundant intermediate predator and a source of spatial heterogeneity of the benthic seascape (Wolff and Cerda, 1992; León and Stotz, 2004; Pacheco et al., 2013).

Spatial variations in the magnitude of resources' landings may also depend on other environmental variables, besides SST and local primary production. For instance, this applies to the Chilean kelp harvest between about 18 °S to 33 °S. Although kelp species are also distributed much further south, they are mainly harvested at these intermediate latitudes to benefit from high solar irradiation and low humidity. These drying conditions allow a significant cost reduction before the kelp

commercialization (Vásquez et al., 2012). It is worth noting that our monitoring covered the southern tip of the kelp harvesting area, represented by landings from two locations of the central cluster (32°S - 33°S). From the northern cluster (18.5°S - 25.5°S), significant landings of kelp were only reported in Chanavayita (20.5°S). Our monitoring data did not include other fishing coves in the northern region, where kelp harvest is very high (Tellier et al., 2011). However, a large part of the Chilean kelp landings is harvested either in TURFs or by illegal fishers, hence misreported at the fishing coves. The illegal kelp harvest is fostered by the high demand of the international alginate market and poor regulatory enforcement and surveillance, making its monitoring very difficult (Araya et al., 2018; Vásquez et al., 2018). In the context of our study, accounting for more kelp landings would have only further highlighted the differences between clusters of fishing coves from remote geographic regions.

On a local scale, our results showed that many fishing areas overlapped with the most productive coastal areas in terms of primary production: near coastal promontories and large bays which break the linearity of the coastline. A characteristic feature of mid-latitude eastern boundaries, such as our study region, is that the alongshore equatorward wind field is compressed around prominent bays and coastal promontories, which in turn intensifies coastal upwelling and generates local peaks of primary production visible in satellite imagery as squirts and plumes (Figueroa and Moffat, 2000; Lara et al., 2019). The topographical structure also plays a major role in larval supply and resulting species recruitment through the oceanographic interplay of upwelled waters and nearshore retention zones ('upwelling shadows'), cross-shore circulation and vertical migration of larvae (Graham and Largier, 1997; Morgan and Fisher, 2010; Satterthwaite et al., 2020). Our study shows that these productive areas can sustain high landings from a wide diversity of macrobenthic species over time.

Along the coast, the variation observed of the width of the coastal band of high primary production is related to the width and slope of the continental shelf. The shelf extends less than 25 km off the coast from 18°S to about 33°S with a very steep continental slope and extends more than 50 km between 35°S and about 42°S with a softer slope (Carr and Kearns, 2003). A wider continental shelf is associated with iron-rich sediments from the continent, which are deposited and then brought to the surface by upwelling (Messié and Chavez, 2015). Primary production along the Chilean coast is also locally fueled by the additional nutrient supply and increased mixing in the upper photic layer provided by turbid river plumes of major Andean rivers (Iriarte et al., 2012, 2017). In particular, many river mouths are located around the southern cluster (41°S - 42°S). The river outflow combined with the mixing pattern of the Inner Sea of Chiloé maintains strong primary production (e.g., Lara et al., 2016; Iriarte et al., 2017), supporting the large landings of macroinvertebrates in the southern region. Overall, the strong coupling between atmospheric forcing, ocean circulation, biogeochemical cycling and food web dynamics within the major Eastern Boundary Upwelling Ecosystems has been amply evidenced (Chavez and Messié, 2009; Chenillat et al., 2013). Our results illustrated how this strong coupling supports productive benthic fisheries in the HCS, and how this relationship varies along an extensive latitudinal gradient crossing several biogeographical regions.

#### 4.2. Diversity of fishers and fishing strategies within local contexts

Archaeological studies have shown that the spatial correspondence between small-scale fishing settlements and highly productive coastal ecosystems along the Chilean coast has existed for millennia (e.g., Salazar et al., 2018). Since the late 1990s, the coordinated implementation of Chile's TURF regime and a national registry program for all fishers has led to a decrease in fishers' mobility between fishing coves (Aburto et al., 2009). Our results showed that some fishers in the northern region (18°S - 21°S) fished within a long coastal strip, sometimes over consecutive days (A. Chevallier, personal observations), which allowed

them to exploit the narrow coastal strip of high primary production. They were mostly hookah divers and caught a wide variety of marine species. This strategy of diversification of the fishing resources has often proven to be successful in managing the risks that characterize the biological and economic environments where SSFs take place (McKelvey, 1983; Minnegal and Dwyer, 2008; Sanchirico et al., 2008). On the other hand, fishers of the central cluster (32°S - 33°S) have specialized in harvesting kelp in smaller areas, with a similar strategy to those of some southern fishing coves (36°S - 37°S), who also specialized in a single resource, in this case crabs. In the southernmost area (41°S - 42°S), hookah divers had high landings of various resources, taking advantage of the high primary productivity.

While there is a strong effect of environmental forcing on regional primary production and thus on landings, differences between nearby fishing coves also reflect local contexts. Among the 15 fishing coves, we observed high variation in the species targeted, fishing efforts, total catch and total income per capita. Within the same fishing cove, the low interannual variation of the income per capita highlighted that fishers tended to ensure a relative stability of their fishing income. However, this yearly income was very variable among fishing coves, ranging on average from USD 1500 to USD 5700 per capita each year, without deducting operating expenses. Considering that the minimum monthly wage in Chile was set at USD 439 in 2018 (Law 21.112, 2018), i.e., USD 5268 per year, the income earned from fishing seems insufficient to ensure fishers' livelihoods, which suggests the existence of other sources of income. For instance, the relatively high interannual variation in per capita income in the fishing coves of Taltal (25°S) and Curanipe (36°S), as well as the large interannual fluctuations in the number of active fishers, could be associated with the great importance of the pelagic and demersal fisheries in these two fishing coves (SERNAPESCA, Servicio Nacional de Pesca y Acuicultura, 2019). At the mouth of the Maullín river (42°S), fishers earned additional income by working in their designated TURF areas and some of them also worked targeting estuarine fish, cultivating crops, or working in salmon farming (A. Chevallier, personal observations). Some of them also moved seasonally in the neighboring cove of Carelmapu, fishing in very productive benthic areas.

#### 4.3. The need to consider heterogeneity in small-scale fisheries management

Our study is the first systematized assessment of the diversity of SSFs on a large spatial (2600 km of coastline) and temporal (17 years) scale. Chilean benthic SSFs are an ideal case study for assessing SSFs diversity and determining the drivers of this diversity because these multi-species fisheries are under a rather homogeneous management framework and we have benefited from the availability of a high-quality standardized monitoring made by scientific observers from the National Fisheries Support Institute (IFOP). Our results have shown that resource diversity is strongly influenced by climate forcing, the variation of primary production at the regional scale, and by small-scale topographic features fueling high biological production. At the local scale, other local factors co-determine the observed landings. They include socioeconomic factors such as price fluctuations, individual fishing behaviors, marketing circuits and complementary sources of income, and can include historical factors, e.g., which species were locally abundant enough to allow the development of a fishery. Overall, a great heterogeneity was observed between neighboring fishing coves in terms of fishing effort, biomass and composition of landings, and finally in terms of per capita income. Our results also suggest that, in most cases, fishers face insufficient income per capita for sustaining their livelihoods. These results are similar to the trends observed by Giron-Nava et al. (2021) for most fishers worldwide. On the other hand, our results contrast with the national trend they observed concerning the total catch of all Chilean fisheries, which included industrial fisheries (Giron-Nava et al., 2021), highlighting the importance of distinguishing small-scale from industrial

fisheries.

There seems to be a mismatch between the scale of the top-down "open access" management system of Chilean benthic fisheries and the scale of critical processes shaping the variations in landings and efforts in each fishing cove. Administrative measures are mostly designed at the national level and their application is very homogeneous among the different administrative regions of the country, and yet a strong spatial variation in SSFs is observed all along the coast, shaped by biophysical, ecological and socioeconomic factors, which are not taken into account by the management system. The current management system aims to regulate catch and fishing effort on a species-by-species basis without accounting for the diversity and interdependence of the marine resources exploited over thousands of kilometers of coastline. Moreover, it does not address the disparity of fishers' livelihoods. A given management measure may be appropriate somewhere, such as closing the fishery for a given resource, but it may be a serious problem in another region, which has no other fishery to maintain its income, or which may overfish other resources as a result. Overall, this mismatch is largely due to a lack of practical understanding of the social-ecological systems (SESS) associated with each SSF (Kittinger et al., 2013; Stotz, 2019). Slowly, the complexity of these systems is being understood (e.g., Basurto et al., 2013). Integrating social sciences into management institutions, as well as implementing a transdisciplinary approach, could go a long way toward establishing a more nuanced view of SSFs management (Symes and Hoefnagel, 2010).

From a practical perspective, we demonstrated that benthic SSFs can be grouped into consistent fishing units, based on the similarity of their resources composition and landings magnitude. We also emphasized the importance of considering local socio-economic conditions and fishers' strategies for management planning, as they generate a unique local context. Thus, our results can inform that the management of Chilean benthic SSFs should be implemented on two nested spatial scales: 1) on the scale of large territories where there is a high level of homogeneity of fishing resources, and 2) within these territories, on the local scale where fishers must be the centerpiece of a participatory decision-making process. Within such a management framework, fishers would still be allowed to work throughout a unique administered area, except that, this way, the area would exhibit cohesion within its key biophysical and ecological features, and the rules would be dynamically adapted to its features. For instance, a large-scale resource-based approach has been adopted in the United States and in Europe during the last decade, moving from homogeneous nation-wide systems to differentiated systems based firstly on biogeographic units (Giakoumi et al., 2013; Caldow et al., 2015; Froese et al., 2018; ICES, 2020).

Within each of these biogeographic units, additional regulations, specific to each locality, could be adopted by local communities under co-management regimes and supported by local authorities (Gelcich, 2014). The combination of adaptive and more specific measures emanating from co-management regimes could increase fishers' per capita income, allowing them to sustain their livelihoods and reduce illegal fishing (d'Armengol et al., 2018). To this end, in Chile, it has been possible for a few years now to set up co-management of multi-species fisheries within given territories, in accordance with the Management Plans legal structure (Law 20.657, 2013; Gelcich, 2014). To date, 15 Management Plans (MPs) for benthic SSFs are implemented along a large part of the Chilean coast. Among the 15 fishing coves presented in this study, Chanavayita is largely guided by a MP administering the kelp fishery within its entire administrative region. Tubul is also largely guided by a MP covering its three most abundant resources, the clams *Tagelus dombeii*, *Mulinia edulis* and *Ensis macha*. Co-managers and scientists have undertaken promising work with this MP built upon strong socioeconomic capital (Estévez et al., 2020). To a lesser extent, Maullín is also guided by a MP for the fishery of the surf clam *Mesodesma donacium*, although most of the landings of this species come from the TURF areas of this fishing cove and were not analyzed in the present study.

Poleward of our study area, it is worth mentioning two atypical MPs. First, there is a MP for clams, sea urchin and red algae of the only Chilean Contiguous Zone between two administrative regions, in which Carelmapu fishers regularly go fishing. Second, there is a very localized MP in Chiloé Island that integrates the administration of all benthic resources. In practice, MPs generally concern a very limited number of resources managed on a species-by-species basis and are limited to administrative regions or very localized areas. Our study suggests that the exception should become the norm, and that MPs should be drafted on an interactive multi-species basis integrating the different resources of the fisheries of a territory delimited by biogeographic limits.

Moreover, Management Committees are currently made up of a small number of stakeholders (fishers' representatives, representatives of processing plants, government institutions) with a low representation of local territories. Within each territory under management, local stakeholders should be constantly involved in the decision-making process from the local to the regional scale through the implementation of legally binding and effective participatory mechanisms (Estévez et al., 2020). This management framework would be highly appropriate for adopting two of the most promising approaches to fisheries management: ecosystem-based management (e.g., Fogarty, 2014; Collie et al., 2016), considering species interactions, environmental and anthropogenic factors, and the human consequences generated by these interactions, and adaptive management (e.g., Armitage, 2008; Berkes, 2010; Allen et al., 2011), promoting continuous learning to deal with the uncertainties related to overfishing, socio-economic crises and under-going climate change.

## 5. Conclusion

In this work, we analyzed a long-term standardized monitoring of benthic SSFs in order to assess the diversity of fishing techniques, resources, efforts, landings and incomes that can be found along 2600 km of coastline in Chile. This assessment would help determine if the rather homogeneous management system in place takes into account the main components of Chilean SSFs or if it needs to be modified to better accommodate the livelihoods of fishers and the diversity of environmental conditions along the coast. Our results highlighted that benthic SSFs are strongly influenced by the variations in the environmental conditions associated with marine biogeographic regions, which determine resources diversity and variations in landings along the coast. In addition, it illustrated how fishers' strategies adapted to environmental and socioeconomic contexts and can generate a high local heterogeneity. Our findings suggest that the top-down management system implemented does not consider the spatial variations in biophysical, ecological and socioeconomic conditions along the coast. Therefore, it can lead to very different outcomes from one fishery to another, ranging from insufficient incomes or overexploitation to socioeconomic and ecological sustainability. Fishery management rules should be shaped according to the region where they are applied, moving from homogeneous nation-wide systems, or systems adapted from administrative divisions to differentiated co-management systems based on biogeographic units. In order for the Chilean management system to adjust to the diversity of conditions and fisheries, we recommend that it be restructured along two nested spatial scales: from biogeographic regions to local fisheries. For this purpose, benthic SSFs Management Plans should be drafted on a multi-species basis, involving local stakeholders in the decision-making process.

## CRedit authorship contribution statement

**Adrien Chevallier:** Conceptualization, Investigation, Methodology, Data curation, Formal analysis, Writing - original draft, Writing - review & editing. **Bernardo R. Broitman:** Conceptualization, Formal analysis, Writing - review & editing. **Nancy Barahona:** Investigation, Data curation, Writing - review & editing. **Claudio Vicencio-Estay:** Data

curation. **Francis K.C. Hui**: Methodology, Formal analysis, Writing - review & editing. **Pablo Inchausti**: Methodology, Writing - review & editing. **Wolfgang B. Stotz**: Conceptualization, Writing - review & editing.

## Declaration of Competing Interest

The authors report no declarations of interest.

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## Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at: <https://doi.org/10.1016/j.envsci.2021.06.002>.

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