frontiers in Ecology and Evolution

TYPE Original Research
PUBLISHED 11 November 2026
DOI 10.3389/fevo.2026.1947989

Check for updates

OPEN ACCESS

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RECEIVED 24 July 2026
REVISED 29 September 2026
ACCEPTED 30 September 2026
PUBLISHED 11 November 2026

CITATION
Vera-Duarte J, Gonzalez-Aragon D, Núñez M, Estévez RA and Broitman BR (2026) Diversity and composition of benthic marine communities under contrasting management and temperature regimes.
Front. Ecol. Evol. 14:1947989.
doi: 10.3389/fevo.2026.1947989

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Diversity and composition of benthic marine communities under contrasting management and temperature regimes

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The sustainable management of small-scale fisheries is key for the well-being of coastal communities. Environmental conditions are known to influence the ecology of the coastal zone, yet their interactions with fisheries management regimes remains poorly understood. We examined spatial changes in the structure of benthic communities under distinct management regimes (TURF or Territorial Use Rights for Fisheries, and OA or open access areas) located in areas with different temperature patterns (warm and cold). Using underwater visual censuses, we assessed benthic community patterns across four locations in northern-central Chile and examined how species diversity and composition varied between management and environmental regimes. Our results showed that communities differed significantly between management and temperature regimes. In general, sessile community richness was 65% higher under cold regimes compared to warm regimes. For mobile invertebrates, richness and diversity were 42% and 41% greater in TURF areas than in OA areas, while both attributes were 4% and 5% higher under cold than warm temperature regimes. In the case of fish communities, species composition varied as a function of the interaction between management and temperature regimes. In cold sites, benthic communities within TURF areas were characterized by the kelp *Lessonia trabeculata*, the whelk *Concholepas concholepas*, and keyhole limpets (*Fissurella* spp.), whereas OA areas were dominated by kelp, the sea urchin *Arbacia nigra*, and the starfish *Meyenaster gelatinosus*. Benthic communities of TURF areas in warm sites were associated with anemones, sea urchins and kelps, whereas OA areas were dominated mainly by anemones and sea urchins. Overall, our results support the notion that the structure of benthic communities can be influenced by an interaction between management regime and environmental conditions. The two temperature regimes stem from the differential exposure to coastal upwelling between sites, which suggests that other environmental processes, such as productivity or wave exposure, are implicated. Overall, the marked

ecological differences between TURF and OA areas under contrasting temperature patterns suggest that environmental conditions should be incorporated into the design of novel fishery policies to promote the sustainable management of small-scale coastal fisheries.

KEYWORDS

Chile, coastal upwelling, fisheries management, small-scale fisheries, species richness, TURF, *Lessonia trabeculata*

1 Introduction

Small-scale fisheries account for half of the world's seafood, providing work and subsistence for millions (Short et al., 2021; FAO, 2024). In Chile, the sector accounts for close to half of landings by tonnage and employs over 100,000 people (Villanueva García Benítez and Flores-Nava, 2019; Servicio Nacional de Pesca y Acuicultura, 2026). The sector is governed through a polycentric management system that combines several institutional arrangements, including Territorial Use Rights for Fisheries (TURF) for benthic resources, Fishery Management Committees responsible for developing management plans for major fisheries, and open access (OA) areas (Estévez and Gelcich, 2020). TURF are areas administered, exploited, and monitored by local fisher organizations promoting the use of sustainable practices. On the other hand, OA areas are the fraction of benthic habitat that is not under management and only subject to broad and poorly enforced administrative mandates (Castilla and Fernandez, 1998; Castilla and Defeo, 2001; Castilla, 2010; Chevallier et al., 2021; González-Roca et al., 2023). The TURF system has been recognized as an important governance instrument that promotes sustainable resource use while enhancing biodiversity, supporting food provisioning, and maintaining multiple ecosystem services, including regulating and cultural services (Gelcich et al., 2008, 2019; Andreu-Cazenave et al., 2017; Pérez-Matus et al., 2017; Beckensteiner et al., 2020; Garmendia et al., 2021). However, productivity among TURF and OA areas is highly variable in space due to environmental or social factors (Gallardo et al., 2011; Anguita et al., 2020; Franco-Meléndez et al., 2021; Pérez-Matus et al., 2025; Ruz et al., 2026).

Along the coastline of northern-central Chile (~27-32°S), a weak, semipermanent upwelling regime north of 30°S transitions to a more seasonal regime poleward of around 32°S. The transitional region experiences strong, year-round and protracted upwelling events locked to the Punta Lengua de Vaca headland (PLV) (Strub et al., 1998; Hormazabal et al., 2004; Aguirre et al., 2012; Rahn et al., 2015). The spatial heterogeneity in environmental conditions has been associated with an ecological, phylogeographic and biogeographic discontinuity along this section of the coastline (Camus, 2001; Hormazabal et al., 2004; Navarrete et al., 2005; Thiel et al., 2007; Haye et al., 2014; Tapia et al., 2014; Broitman et al., 2018). The windward side of PLV is fully exposed to open–ocean swell and largely devoid of protected bays and major cities. To the north, the bay on the lee of PLV is protected from the prevailing equatorward wind and experiences a warmer regime with two large cities associated with its sheltered harbors (Thiel et al., 2007). Although the ecological benefits of TURFs have been widely documented, their outcomes vary substantially among locations also due to differences in environmental and social conditions (Vega et al., 2014; Chevallier et al., 2021; González et al., 2021; Ruz et al., 2026). Upwelling regime in the central-northern Chile have been shown to maintain distinct benthic communities (Navarrete et al., 2005). Similarly, the spatial differences in TURF landings have been shown to be influenced by local-to-regional differences in oceanographic processes (Anguita et al., 2020; Hernández et al., 2020). To this end, we hypothesized that community diversity and composition should differ between sites exposed to upwelling (cold) relative to protected (warm) sites, and that these environmental effects will interact with management regime (i.e., TURF vs OA areas). In this context, isolating the relative contribution of the environmental regime on the diversity and composition of benthic communities under contrasting management systems can improve current management strategies and support the design of novel regulatory instruments. Our study aimed to: (1) characterize the diversity and composition of marine communities across localities nested in the two contrasting environmental regimes found along the transitional region of north-central Chile, and (2) evaluate how these potential ecological attributes responded to different management regimes.

2 Methods

2.1 Study area and biodiversity assessments

This study was conducted at four coastal sites located between 29.5°S and 31.4°S, in the Coquimbo region, northern-central Chile. From north to south the selected sites were Chungungo, Guanaqueros, Punta de Talca and Puerto Oscuro encompassing approximately 72.25 ± 18.19 km of coastline. To compare the community structure of marine communities between management and temperature regimes, four sites were selected according to seawater temperature regimes (°C), specifically two sites exposed to the warm regime and two sites exposed to the cold regime. Those scenarios were supported by prior knowledge of upwelling or non-upwelling conditions (Aravena et al., 2014) and the long-term *in situ* records (2009-2024) presented in this study (see below). Hence, Chungungo and Guanaqueros were selected as sites with a warm temperature regime, whereas Puerto Oscuro and Punta de Talca were selected as sites with cold temperature regime. The northern and southern sites are separated by the PLV upwelling center (Figures 1a, b).

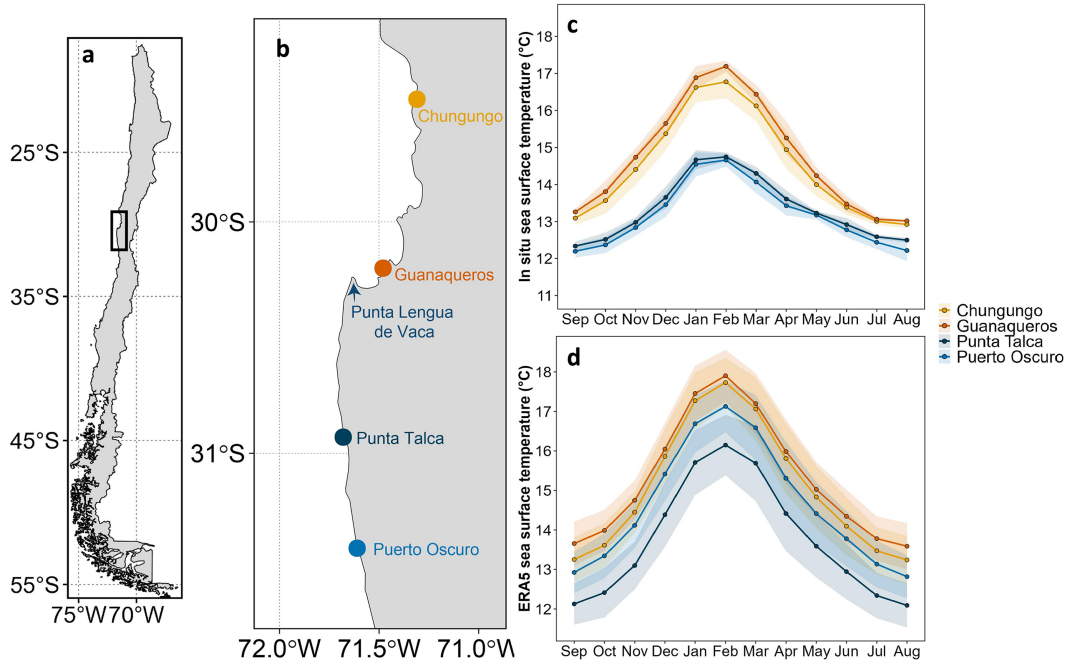


FIGURE 1
Study sites and environmental context along the Coquimbo coast, Chile. **(a)** General location of Chile, with the study area indicated by a black rectangle. **(b)** Location of the four study sites (Chungungo, Guanaqueros, Punta de Talca, and Puerto Oscuro) and the Punta Lengua de Vaca headland upwelling center. **(c)** Monthly climatology of seawater temperature (mean ± SD) recorded *in situ* in each study site. **(d)** Monthly sea surface temperature (mean ± SD) obtained from ERA5 for each site.

At each site, the structure of marine communities was assessed across management and temperature regimes, by evaluating both the diversity and composition (i.e., sessile, mobile invertebrates, and fish) through underwater visual censuses conducted via autonomous SCUBA diving. To this end, we haphazardly established eight transects of 50 m in length, each separated by ca. 100 m. Four transects were placed within TURF areas and four within open access (OA) areas at 10.34 ± 5.26 m depth. Along each transect, five stations of 100 x 100 cm (1 m^2) were defined, spaced at 10 m intervals. In each station, two divers counted the sessile and mobile invertebrates species densities. Fish were counted along the transects considering a two meter-wide strip that covered an area of 100 m^2. Fish counts were conducted exclusively when individuals were actively swimming within the area of transects, thereby excluding those that entered the transect from outside or appeared from behind the divers. In Chungungo and Puerto Oscuro, the number of stations was reduced primarily due to unfavorable environmental conditions during diving, including poor visibility, unexpected increases in wind and strong currents. The selection of individual transects and their placement inside or outside local TURF areas was determined using a handheld GPS when possible, and together with the local fishers responsible for the management regime, who provided direct support for the selection of habitats of similar substrate complexity inside and outside the TURF areas (Supplementary Figure S1).

2.2 Seawater temperature regimes

Seawater temperature in warm and cold regimes was calculated using the long-term average daily field temperature obtained from sensors along with satellite data that considered the period between 2009 and 2024. Field seawater temperature was obtained from time series (°C) recorded by HOBO sensors moored at depths of 1–2 m at each site, operating continuously and recording at 20 minutes intervals between 2009 and 2024 (Figure 1c) (Aravena et al., 2014). In parallel, Sea Surface Temperature (SST, °C) data sets were obtained from the ERA5 reanalysis for the period between 1980 and 2024 (Figure 1d) (Hersbach et al., 2020). ERA5 is the fifth-generation global atmospheric reanalysis produced by the European Center for Medium-Range Weather Forecasts (ECMWF). This model provided a consistent reconstruction of historical climate conditions. The seawater temperature data set considered a spatial resolution of 0.25° (~31 km) and an hourly temporal resolution. Those proxies allowed us to validate the characterization of the long-term thermal variability of sites located in the study region (Hersbach et al., 2020).

2.3 Statistical analyses

The total richness (y), the average richness (S) and the Shannon-Wiener diversity (H') were separately estimated for sessile species, mobile invertebrates and fish communities and subsequently classified according to management regimes (i.e., TURF and OA areas) and temperature regimes (i.e., warm and cold conditions). Prior to conducting the analyses, the assumptions of normality and homoscedasticity of variance for S and H' were evaluated using the Shapiro-Wilk test and Bartlett's test, respectively. Species richness accumulation curves (i.e., sessile species, mobile invertebrates, and fish) were estimated using the Chao 1 Index for each site (Chao and Jost, 2012; Chase and Knight, 2013).

Generalized Linear Models (GLMs) were fitted to evaluate the richness and diversity of sessile, mobile invertebrates and fish communities. For all models, management and temperature regimes were considered as fixed factors with two levels, TURF and OA areas and warm and cold regimes, respectively. We used gaussian distributions on untransformed data whenever possible and selected alternative data distributions for the GLMs models using the Akaike Information Criteria. Sessile richness was assessed with negative binomial distribution while sessile diversity with gamma distribution whereas mobile invertebrates richness and diversity were evaluated with gaussian distribution. For fish communities, richness was assessed with Poisson distribution while diversity with gaussian distribution. The fit of each model was assessed by examining error normality, dispersion values and residual diagnostics. Formulas are presented in Table 1. As we sampled two sites to represent each temperature regime and used multiple replicated transects within sites, our results should not be interpreted as independent site-level replicates of temperature regime.

To determine the contribution of species and their dissimilarity between communities, we compared the composition of species (i.e., sessile, mobile invertebrates, and fish) between management regimes and temperature regimes using percentage similarity analysis (SIMPER) (Clarke, 1993). Previously, for each assemblage, permutation tests for homogeneity of multivariate dispersions (i.e., PERMDISP) were done to compare potential differences in variability in group dispersion rather than the groups means. Thus, we performed three different two-way PERMANOVA to compare the composition of species (i.e., sessile, mobile invertebrates, and fish) between management and temperature regimes. For the PERMANOVA analyses, we considered management and temperature regimes as fixed factors, each with two levels: TURF and OA areas for management regimes, and warm or cold for temperature regimes, respectively. We ran the models using a type III design, while the F-value was obtained from permutations of the unrestricted residuals in an unreduced model. Before running multivariate analyses, sessile community composition was transformed to the fourth root, mobile invertebrates to the square root, and fish communities to the fourth root. Multivariate analyses were performed with a Bray–Curtis similarity matrix and 9999 permutations (Anderson, 2001). All statistical analyses were performed using RStudio (version 2026.05.0; R Core Team, 2026).

TABLE 1 Formulas (in the R programming language) used to calculate the Generalized linear models (GLMs) for assessing the richness and diversity of sessile and mobile invertebrates, as well as fish species.

Community response	Model formula
Sessile species	
Richness	MASS::glm.nb (sessile_richness ~ temp * regime, data=richness_div)
Diversity	glm (sessile_shannon+0.001 ~ temp * regime, family=Gamma (link="identity"), data=richness_div)
Mobile invertebrates	
Richness	glm (mobile_inv_richness ~ temp * regime, data=richness_div, family=gaussian())
Diversity	glm (mobile_inv_shannon ~ temp * regime, data=richness_div, family=gaussian())
Fishes	
Richness	glm (fish_richness ~ temp * regime, family=poisson, data=richness_div)
Diversity	glm (fish_shannon ~ temp * regime, data=richness_div, family=gaussian())

3 Results

3.1 Seawater temperature regime

In general, the non-overlapping standard deviations of in situ seawater temperatures observed between regimes confirmed the long-term persistence of seawater thermal regimes year-round. Temperature averaged 13.17 ± 0.86 °C (Mean ± SD) in the cold regimes and 14.50 ± 1.40 °C in the warm regimes during the austral spring months. The thermal differential increased to 3 °C during summer, with 16.49 ± 0.5 °C for the warm regimes and 13.38 ± 0.26 °C for the cold regimes (Figure 1).

3.2 Diversity and composition of sessile communities

We found significant differences only for sessile community richness between the temperature regimes (χ^2 = 31.395, P < 0.001), but not between management regimes (χ^2 = 0.648, P = 0.421) or in the interaction between management and temperature regimes (χ^2 = 0.034, P = 0.855) (Table 2a). Similarly, we did not find significant differences in sessile community diversity between management regimes (χ^2 = 11.034, P = 0.144), temperature regimes (χ^2 = 19.395, P = 0.052), nor in the interaction between management and temperature regimes (χ^2 = 1.677, P = 0.568) (Table 2b).

In cold sites, sessile community richness was two and 19 species in the TURF areas, and two and three species in the OA areas, corresponding to Puerto Oscuro and Punta de Talca, respectively. In warm sites, sessile community richness was three and two species in the TURF areas and one and four species in the OA areas of Chungungo and Guanaqueros, respectively (Supplementary Table S1). In cold sites, sessile communities richness exhibited a continuous increase until ca. 40 observations at Punta de Talca (Supplementary Figure S2).

Mean sessile community richness was 65% higher under cold regimes compared to warm regimes. In cold sites, mean richness was 1.12 ± 0.56 and 2.22 ± 1.79 in TURF areas and 1.05 ± 0.51 and 1.52 ± 0.75 in OA areas while mean sessile community diversity was 0.11 ± 0.22 and 0.31 ± 0.39 in TURF areas and 0.05 ± 0.14 and 0.17 ± 0.25 in OA areas of Puerto Oscuro and Punta de Talca, respectively (Figure 2). In warm sites, mean sessile community richness was 1.50 ± 0.50 and 0.24 ± 0.42 in TURF areas, and 0.23 ±

TABLE 2 Generalized linear models (GLMs) for the richness (*S*) and diversity (*H′*) of sessile communities recorded at four sites in northern-central Chile following their management (i.e., TURF and OA areas) and temperature regimes (i.e., warm and cold) presented in **Figure 2**.

a. Sessile *S*	Df	Deviance	Resid. Df	Res. dev	P
Management regimes	1	0.648	41	30.478	0.421
Temperature regimes	1	31.395	40	31.126	< **0.001**
Management*Temp.	1	0.034	39	30.455	0.855
b. Sessile *H′*	Df	Deviance	Resid. Df	Res. dev	P
Management regimes	1	11.034	41	170.070	0.144
Temperature regimes	1	19.395	40	181.104	0.052
Management*Temp.	1	1.677	39	168.394	0.568

Significant results are indicated by P-values in boldface.

0.42 and 0.29 ± 0.59 in the OA areas while mean sessile community diversity was 0.25 ± 0.26 and 0.00 ± 0.00 in TURF areas and 0.00 ± 0.00 and 0.01 ± 0.08 in OA areas of Guanaqueros and Chungungo, respectively (Figure 2).

Sessile communities composition differed significantly between management regimes (Pseudo-F = 3.619, P < 0.001) and temperature regimes (Pseudo-F = 33.200, P < 0.001). Furthermore, we found a significant interaction in the composition of sessile communities between management regimes and temperature regimes (Pseudo-F = 6.899, P < 0.001) (Supplementary Table S2). Nevertheless, significant differences in dispersion were detected between temperature regimes (Pseudo-F = 28.767, P < 0.001) suggesting that the PERMANOVA results may be partly driven by unequal within-group variability as well as compositional shifts.

In cold sites, sessile community composition showed lower differences ~32% particularly between the TURF and OA areas. However, sessile community composition exhibited higher differences ~94% between the TURF areas of cold sites and OA areas of warm sites. Similarly, sessile community composition differed ~95% between OA areas of cold and warm regimes. Conversely, sessile community composition of TURF areas of warm sites differed by 60-62% relative to OA areas across both temperature regimes and TURF areas from cold sites.

In cold sites, sessile communities composition was related to the kelp *Lessonia trabeculata* (~65-80%), the red algae *Bossiella chiloensis* (~6%), and the anemone *Phymanthea pluvia* (~5%) in TURF and OA areas. In warm sites, the composition of sessile communities was related to the anemone *Phymanthea pluvia* (~49%) and the kelp *L. trabeculata* (~48%) in the TURF areas and by the anemones *Anthothoe chilensis* (~46%) and *P. pluvia* (~42%) in the OA areas. Moreover, *L. trabeculata* was not observed in the OA areas of warm sites (Supplementary Table S3).

3.3 Diversity and composition of mobile invertebrates communities

We found significant differences in the richness of mobile invertebrates between management regimes (χ^2 = 111.363, P < 0.001). In addition, mobile invertebrates richness differed significantly between temperature regimes (χ^2 = 45.978, P = 0.010). Moreover, no significant interaction was detected in mobile invertebrates richness between management and temperature regimes (χ^2 = 10.922, P = 0.212) (Table 3a). Mobile invertebrates diversity also showed significant differences between the management regimes (χ^2 = 1.697, P = 0.012); moreover, significant differences were observed between the temperature regimes (χ^2 = 2.716, P = 0.001). Furthermore, mobile invertebrates diversity did not exhibit a significant interaction between management and temperature regimes (χ^2 = 0.141, P = 0.468) (Table 3b).

Mobile invertebrates richness was 14 and 25 in the TURF areas and 10 and 21 in the OA areas of cold sites of Puerto Oscuro and Punta de Talca, respectively. In warm sites, richness of mobile invertebrates was 14 and 19 in the TURF areas, and 10 and 22 in the OA areas of Chungungo and Guanaqueros, respectively (Supplementary Table S4). For mobile invertebrates, the richness saturation curve stabilized after approximately 20 observations, such as the case of Chungungo and Puerto Oscuro. In Guanaqueros, mobile invertebrates richness stabilized after 30 observations, while in Punta de Talca the accumulative mobile invertebrates richness continued to increase steadily until it reached 40 observations (Supplementary Figure S3).

The richness and diversity of mobile invertebrates were 42% and 41% higher in TURF areas compared to OA areas across both temperature regimes. In contrast, richness and diversity were only 4-5% higher in cold sites relative to warm sites. In cold sites, mean mobile invertebrates richness was 3.83 ± 2.69 and 2.90 ± 2.41 in the TURF areas and 1.23 ± 1.51 and 1.77 ± 1.56 in the OA areas while mean mobile invertebrates diversity was 0.85 ± 0.57 and 0.72 ± 0.63 in TURF areas and 0.22 ± 0.35 and 0.47 ± 0.49 in OA areas considering Puerto Oscuro and Punta de Talca, respectively (Figure 3). In warm sites, the mean mobile invertebrates richness was 3.85 ± 2.40 and 2.33 ± 1.47 in TURF areas and 1.25 ± 1.66 and 1.96 ± 1.17 in OA while mean mobile invertebrates diversity was 0.93 ± 0.55 and 0.42 ± 0.40 in TURF areas and 0.30 ± 0.45 and 0.33 ± 0.31 in OA areas of Chungungo and Guanaqueros, respectively (Figure 3).

Mobile invertebrates composition differed significantly between management regimes (Pseudo-F = 3.935, P < 0.001) and temperature regimes (Pseudo-F = 30.143, P < 0.001). Moreover, mobile invertebrate composition exhibited a significant interaction between management regimes and temperature regimes (Pseudo-F = 6.419, P < 0.001) (Supplementary Table S5). Nevertheless, dispersion differed

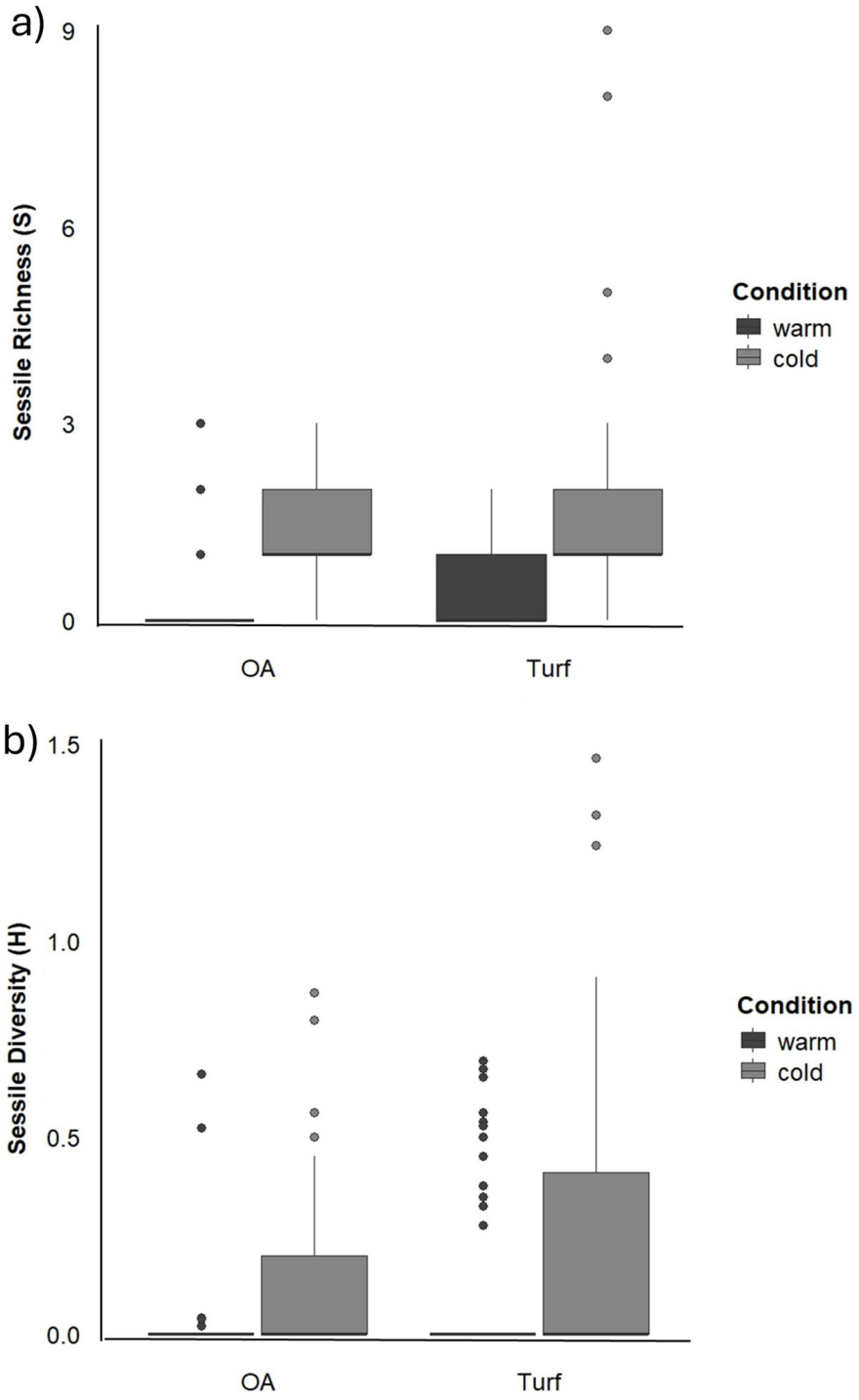


FIGURE 2
(a) Richness (*S*) and **(b)** diversity (*H'*) of sessile communities recorded at four sites in northern-central Chile according to their management regimes (i.e., TURF and OA areas) and temperature regimes (i.e., warm and cold). A GLM analysis presented in Table 2 showed significant differences only for *S* between temperature regimes.

significantly between temperature regimes (Pseudo-F = 27.762, P < 0.001) indicating that the PERMANOVA results may reflect not only composition shifts but also unequal within-group variability.

In general, mobile invertebrates composition differed ~72-88% across all comparison groups. In sites with cold regime, mobile invertebrate composition was related to the snail *Concholepas concholepas* (26%), the keyhole limpets *Fissurella* spp. (16%) and the sea urchin *Arbacia nigra* (9%) in the TURF area and related to *A. nigra* (25%), the starfish *Meyenaster gelatinosus* (12%) and the snail *Tegula atra* (8%) in OA areas. In warm sites, mobile

invertebrates composition was associated with the sea urchin *A. nigra* (34%), the snail *Incatella cingulata* (11%) and the shrimp *Rhinchocinetes tipus* (9%) in TURF areas. Similarly, mobile invertebrate composition in OA areas was related to *A. nigra* (37%), *I. cingulata* (15%) and the snail *Tegula luctuosa* (14%) (Supplementary Table S6).

3.4 Diversity and composition of fish communities

We did not find significant differences in fish richness between management regimes (χ^2 = 0.160, P = 0.690) and temperature regimes (χ^2 = 0.441, P = 0.507). In contrast, fish richness exhibited a significant interaction between management regimes and temperature regimes (χ^2 = 5.663, P = 0.017) (Table 4a). Regarding diversity, no significant differences were observed in fish diversity between management regimes (χ^2 = 0.246, P = 0.354) and temperature regimes (χ^2 = 0.431, P = 0.219). Furthermore, fish diversity did not show a significant interaction between management and temperature regimes (χ^2 = 0.814, P = 0.091) (Table 4b).

In cold sites, fish richness was 10 and 16 in the TURF areas, and 12 and 20 in the OA areas of Puerto Oscuro and Punta de Talca, respectively. At warm sites, fish richness was 16 and 19 in the TURF areas, and 12 and 26 in the OA areas of Chungungo and Guanaqueros, respectively (Supplementary Table S7). The species accumulation curves for fish species did not reach a plateau at the maximum number of observations (Supplementary Figure S4).

In cold sites, mean fish richness was 2.97 ± 1.06 and 3.68 ± 1.99 in the TURF areas and 3.60 ± 1.19 and 5.16 ± 2.84 in the OA areas while mean fish diversity was 0.78 ± 0.40 and 0.61 ± 0.44 in the TURF areas, and 1.15 ± 0.49 and 0.74 ± 0.33 in the OA areas corresponding to Puerto Oscuro and Punta de Talca, respectively (Figure 4). In warm sites, mean fish richness was 4.31 ± 1.79 and 4.21 ± 1.52 in TURF areas and 3.40 ± 1.72 and 3.74 ± 1.69 in OA areas while mean fish diversity was 1.14 ± 0.44 and 1.06 ± 0.33 in the TURF areas, and 0.83 ± 0.56 and 0.91 ± 0.43 in the OA areas of Chungungo and Guanaqueros, respectively (Figure 4).

Fish composition differed significantly between management regimes (Pseudo-F = 2.839, P = 0.018) and temperature regimes (Pseudo-F = 39.647, P < 0.001). Moreover, we found a significant interaction for fish composition between management and temperature regimes (Pseudo-F = 6.371, P < 0.001) (Supplementary Table S8). Similar to sessile and mobile invertebrates communities, we detected significant differences in the dispersion between temperature regimes (Pseudo-F = 8.180, P = 0.005) implying that the PERMANOVA outcomes may be influenced both by unequal within-group variability and compositional differences.

Fish composition differed 61-66% across all comparison groups. In cold sites, the composition of the fish was related to the damselfish *Chromis crusma* (~20%), the sandperch *Pinguipes chilensis* (~13%) and the drunk-blenny *Scartichthys* sp. (~13%) in both management regimes. Similarly, in warm sites, fish composition was related to *P. chilensis* (~18%), *C. crusma* (~17%), the morwong *Chirodactylus variegatus* (~14%) and *Scartichthys* sp.(~14%) in both management regimes (Supplementary Table S9).

4 Discussion

Coastal marine communities and small-scale fisheries in northern-central Chile straddle a major oceanographic transition associated with the Punta Lengua de Vaca (PLV) upwelling center (Hormazabal et al., 2004; Rahn et al., 2015). The environmental transition around PLV sustains persistent environmental heterogeneity, expressed through the cold and warm regimes at our study sites. Differential exposure to coastal upwelling has been linked to different ecological and organismal patterns among sites located north and south of the PLV headland (Broitman et al., 2001; Navarrete et al., 2005; Valdivia et al., 2015; Broitman et al., 2018). Furthermore, the presence of both biogeographic and phylogeographic breaks around PLV has been attributed to the persistent oceanographic processes operating along the transition zone (Camus, 2001; Haye et al., 2014; Parada et al., 2026). In this context, our observational results evidenced that species diversity and composition differed between management and temperature regimes across the PLV transition. Overall, sessile community richness was approximately 65% higher at sites under the cold

TABLE 3 Generalized linear models (GLM) for the richness (*S*) and diversity (*H′*) of mobile invertebrates communities recorded at four sites in northern-central Chile according to their management regimes (i.e., TURF and OA areas) and temperature regimes (i.e., warm and cold) presented in **Figure 3**.

a. Mobile invertebrates *S*	Df	Deviance	Resid. Df	Res. dev	P
Management regimes	1	111.363	42	291.386	**< 0.001**
Temperature regimes	1	45.978	41	402.750	**0.010**
Management*Temp.	1	10.922	40	280.464	0.212
b. Mobile invertebrates *H′*	**Df**	**Deviance**	**Resid. Df**	**Res. dev**	**P**
Management regimes	1	1.697	42	10.864	**0.012**
Temperature regimes	1	2.716	41	12.560	**0.001**
Management*Temp.	1	0.141	40	10.723	0.468

Significant results are indicated by P-values in boldface.

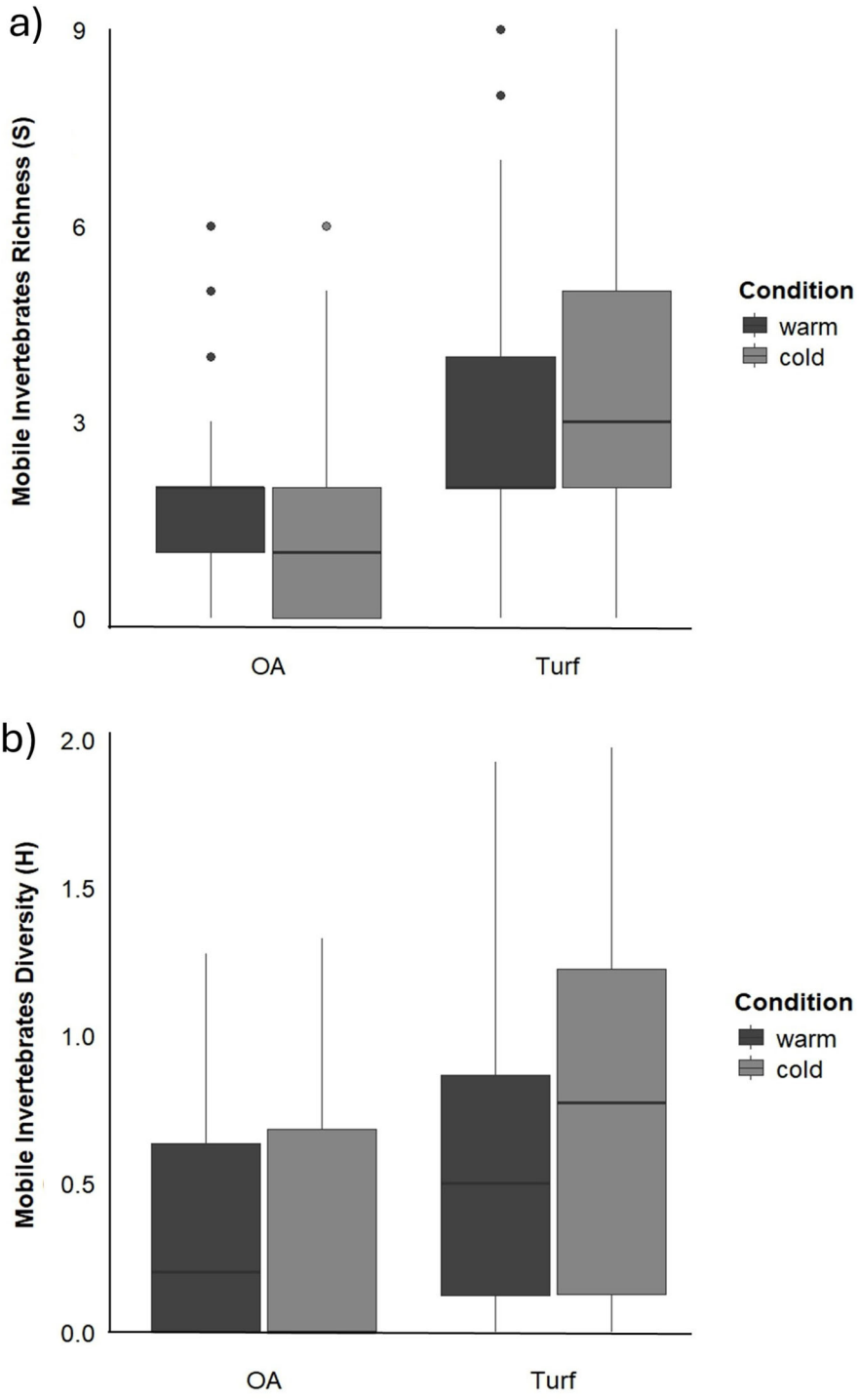


FIGURE 3
(a) Richness (*S*) and **(b)** diversity (*H'*) of mobile invertebrates recorded at four sites in northern-central Chile according to their management (i.e., TURF and OA areas) and temperature regimes (i.e., warm and cold). A GLM analysis presented in Table 3 showed significant differences between management and temperature regimes for both *S* and *H'*, but not for their interaction.

regime compared to those under the warm regime, whereas mobile invertebrates richness and diversity were 42% and 41% greater, respectively, in TURF relative to OA areas, and both attributes were 4% and 5% higher under cold than warm temperature regimes. In addition, the composition of sessile and mobile invertebrates along with benthic fish, also varied across management and temperature regimes. Our thermal classification was driven by variation in exposure to recently upwelled waters and potentially other environmental characteristics, such as wave exposure, together with processes such as fishing history. Hence, our results should not be

TABLE 4 Generalized linear models (GLMs) for richness (*S*) and diversity (*H′*) of fish recorded at four sites in northern-central Chile according to their management (i.e., TURF and OA areas) and temperature regimes (i.e., warm and cold) presented in **Figure 4**.

a. Fish *S*	df	Deviance	Resid. Df	Res. dev	P
Management regimes	1	0.160	26	39.047	0.690
Temperature regimes	1	0.441	25	39.207	0.507
Management*Temp.	1	5.663	24	33.384	**0.017**
b. Fish *H′*	Df	Deviance	Resid. Df	Res. dev	P
Management regimes	1	0.246	26	7.669	0.354
Temperature regimes	1	0.431	25	7.914	0.219
Management*Temp.	1	0.814	24	6.854	0.091

Significant results are indicated by P-values in boldface.

interpreted as effects of temperature alone. Since our transects were replicated within sites they are not independent site-level replicates of temperature regime, so temperature-regime effects should be interpreted cautiously and primarily in the context of the four sites examined in this study. Coastal upwelling brings deep, cold and nutrient–rich waters to the surface layers (Strub et al., 1998). On the one hand, exposure to recently upwelled waters and topographic sheltering can drive differences in the structure of subtidal benthic communities within management areas in southern-central Chile (Hernández et al., 2020). Exposure to coastal upwelling, for example, has been related to faster recovery of kelp stands following harvest (Pérez-Matus et al., 2025). On the other hand, the structure of benthic communities inside and outside of TURF areas consistently differ in the diversity and abundance of species (Gelcich et al., 2008, 2012). Although environmental variability has been shown to impact TURFs (González et al., 2021), the interaction of environmental and management regimes had never been examined for the extensive Chilean TURF system. Below we discuss some of the potential mechanisms and implications of this social-ecological interaction.

The dominance of the kelp *L. trabeculata* and the sea urchin *A. nigra* under contrasting oceanographic conditions (i.e., upwelling and non-upwelling conditions) has been shown before in sites located in northern and central Chile. In those studies, coastal marine communities in TURF areas were associated with *L. trabeculata* whereas communities in OA areas were characterized by the presence of *A. nigra* (Pérez-Matus et al., 2017, 2025; Riquelme-Pérez et al., 2019). In our study, the higher richness of sessile organisms in colder sites may be related to the persistent presence of *L. trabeculata*, a species that maintains complex habitats for other organisms (Pérez-Matus et al., 2017; Campos et al., 2021). Currently, the decrease of fish diversity in coastal marine ecosystems has been related to intense fishing activities that remove larger predators (Godoy et al., 2016; Riquelme-Pérez et al., 2019) and also by the low densities and slow recovery of *L. trabeculata* following harvesting by fishers (Bularz et al., 2022; Pérez-Matus et al., 2025). *L. trabeculata* has been shown to exhibit faster growth and recovery after harvest in sites at northern (27°S) and north-central Chile (29°S) when compared with central Chile (32°S), regardless of management regimes (Ruz et al., 2026). It also showed lower recovery rates in OA areas than TURF areas after three years from kelp harvesting. The kelp–depleted conditions generally promote the dominance of herbivores such as the sea urchin *A. nigra* and the snail *T. luctuosa*, which graze on recruits, juveniles, and adults of *L. trabeculata* increasing kelp mortality (Perreault et al., 2014; Pérez-Matus et al., 2025). In this way, strong ecological feedback alone can maintain the contrast between TURF and OA areas. Nevertheless, because harvesting intensity, management history, enforcement, and habitat characteristics were not quantified in our study, the lower diversity observed at warm (northern) sites cannot be attributed to fishing pressure or temperature alone and likely reflects the interaction of multiple environmental and management-related processes.

Our study suggests that distinct temperature regimes can influence the richness and composition of marine communities managed under two regimes (i.e., TURF and OA areas). Ecological differences between OA and TURF areas were associated with management practices, yet our cold vs. warm temperature regimes imply differential exposure to recently upwelled waters and within-group multivariate dispersion was evident among temperature regimes for all species groups. Hence, we cannot attribute the interactive pattern detected by our surveys to an interaction of management and temperature alone. In this context, the persistence and recovery of foundation species such as kelp *L. trabeculata* and *Macrocystis pyrifera* –heavily exploited by small-scale fishers– seems to have completely failed in warm OA areas, as observed in Guanaqueros. The stark ecological contrast likely results from the interaction between ecological processes and environmental conditions, beyond temperature, that do not promote kelp recolonization, such as limited propagule dispersal (Parada et al., 2026). The protracted recovery of kelp stands is of particular concern, both for the rest of the food web and for maintenance of ecosystem services that provide income for small-scale fisheries (Bularz et al., 2022; Gonzalez-Aragon et al., 2024; Pérez-Matus et al., 2025). This result illustrates the pitfalls of establishing management regimes independent of environmental context (Chevallier et al., 2021). Our results suggest that the interaction between management and

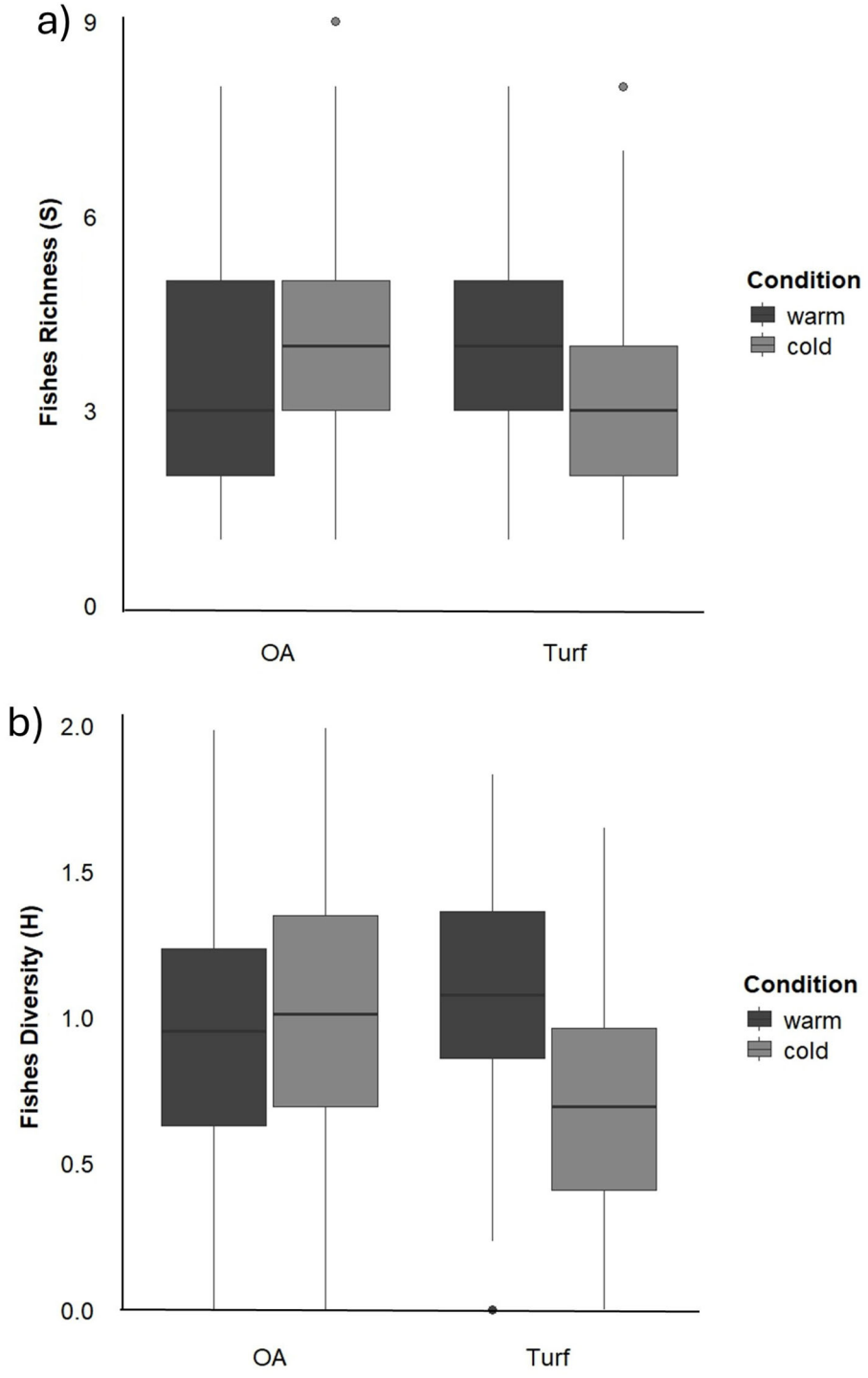


FIGURE 4
(a) Richness (*S*) and **(b)** diversity (*H'*) of fish communities recorded at four sites in northern-central Chile according to their management regimes (i.e., TURF and OA areas) and temperature regimes (i.e., warm and cold). A GLM analysis presented in Table 4 indicated significant differences in *S* for the interaction between management and temperature regime.

temperature regimes, a proxy for other environmental processes in upwelling regions, should be integrated into ecosystem-based management approaches to directly support the sustainability of small-scale fisheries (Hamilton et al., 2022; Ruz et al., 2026). In this context, we propose that persistent temperature regimes, together with established fisheries management, could serve as a novel tool to enhance the conservation and sustainability of coastal marine ecosystems.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

JV-D: Visualization, Formal analysis, Writing – review & editing, Investigation, Writing – original draft. DG-A: Methodology, Formal analysis, Writing – review & editing, Writing – original draft. MN: Resources, Investigation, Writing – original draft, Writing – review & editing. RE: Writing – review & editing, Supervision, Writing – original draft, Funding acquisition, Resources, Validation. BB: Resources, Data curation, Investigation, Visualization, Conceptualization, Validation, Funding acquisition, Supervision, Writing – review & editing, Project administration, Software, Methodology, Writing – original draft, Formal analysis.

Funding

The author(s) declared that financial support was received for this work and/or its publication. This work was funded by Agencia Nacional de Desarrollo Científico y Tecnológico (ANID) through the project FONDECYT 1221699 awarded to BRB and project FONDECYT 1221534 awarded to RAE. Additional funding was provided by the Instituto Milenio en Socio-Ecología Costera, (SECOS) ANID ICN2019_015. RAE acknowledges support from ANID-Concurso de Fortalecimiento al Desarrollo Científico de Centros Regionales 2020–R20F0008–CEAZA.

Acknowledgments

The authors acknowledge the extensive and committed support by Jorge "Flaco" Guerra during long drives and cold dives, together with the fishers of Puerto Oscuro, Punta de Talca, Guanaqueros and Chungungo for providing access to their TURFs and guidance while in the field for site selection.

Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2026.1947989/full#supplementary-material

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