


RESEARCH ARTICLE

A sedimentary DNA record of the Atacama Trench reveals biodiversity changes in the most productive marine ecosystem

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Abstract

The hadopelagic environment remains highly understudied due to the inherent difficulties in sampling at these depths. The use of sediment environmental DNA (eDNA) can overcome some of these restrictions as settled and preserved DNA represent an archive of the biological communities. We use sediment eDNA to assess changes in the community within one of the world's most productive open-ocean ecosystems: the Atacama Trench. The ecosystems around the Atacama Trench have been intensively fished and are affected by climate oscillations, but the understanding of potential impacts on the marine community is limited. We sampled five sites using sediment cores at water depths from 2400 to ~8000m. The chronologies of the sedimentary record were determined using $^{210}\text{Pb}_{\text{ex}}$. Environmental DNA was extracted from core slices and metabarcoding was used to identify the eukaryote community using two separate primer pairs for different sections of the 18S rRNA gene (V9 and V7) effectively targeting pelagic taxa. The reconstructed communities were similar among markers and mainly composed of chordates and members of the Chromista kingdom. Alpha diversity was estimated for all sites in intervals of 15 years (from 1842 to 2018), showing a severe drop in biodiversity from 1970 to 1985 that aligns with one of the strongest known El Niño events and extensive fishing efforts during the time. We find a direct impact of sea surface temperature on the community composition over time. Fish and cnidarian read abundance was examined separately to determine whether fishing had a direct impact, but no direct relation was found. These results demonstrate that sediment eDNA can be a valuable emerging tool providing insight in historical perspectives on ecosystem developments. This study constitutes an important step toward an improved understanding of the importance of environmental and anthropogenic drivers in affecting open and deep ocean communities.

KEYWORDS

ancient DNA, Atacama Trench, community, deep sea, hadal, sedDNA, time-series

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1 | INTRODUCTION

Anthropogenic pressures have degraded ocean ecosystems, depleting them of marine life, with most of the ocean experiencing enhanced cumulative human related impacts over the last century, with an increase in resource use per capita (Duarte, 2014; Duarte et al., 2020; Halpern et al., 2019). For example, industrial fisheries, initiated with the development of combustion engines and refrigeration with the Industrial Revolution, are believed to have been a major driver of change (Duarte et al., 2020), depleting targeted and untargeted fish stocks (Gislason, 2003; Pope et al., 2000) and triggering a cascade of change in ocean food webs (Daskalov, 2002). Furthermore, fisheries have also impacted habitats directly through methods such as trawling, which reduces habitat complexity, alters the compaction of the sediment, changes the trophic structure of communities, imposes damage to biota, and potentially reduces benthic production and diversity (Kaiser et al., 2006; Løkkeborg, 2005).

Unfortunately, the extent of these and other anthropogenic impacts often remains uncertain due to lack of the necessary baselines on pre-disturbance ocean states. Indeed, unknown baselines challenge our capacity to develop appropriate management targets and metrics for recovery.

One of the most intensely fished ecosystems of the world is the Humboldt upwelling and current system, flowing along the coasts of Ecuador, Peru, and Chile, which supports the most productive fishery of the world, a main source of income in Ecuador, Peru, and Chile (Montecino & Lange, 2009). Landings from Chilean fisheries rank among the highest of the world (OECD, 2020) and reached an all-time high in 1988, when the overexploitation resulted in the dramatic decline of fish stocks and led to the total closure (bans) of the fishery for multiple species, particularly the native snail *Concholepas concholepas* and the lobster *Cervimunida johni* (Bernal et al., 1999; Yanez et al., 2017). Further regulations from 1989 to 1991 focused on the regulation of fishing activity, focusing mainly on tuna, bonito, and sardines (Bernal et al., 1999). However, as of 2019, 70% of targeted species were considered to be harvested at non-sustainable levels according to the Environment Status Report released by the Chilean government (<https://sinia.mma.gob.cl/iema-2020/>). The decline in Chilean fish stocks with industrial fishing can cascade through the food web to have profound consequences on the ecosystem and its communities (Petit et al., 2018).

Changes in biodiversity are influenced by overexploitation and climatic oscillations that are one of the main drivers of ocean productivity. These include the El Niño-Southern Oscillation (ENSO), involving changes in circulation affecting sea surface temperature (SST) conditions that affect upwelling and productivity patterns in the tropical Pacific (Cai et al., 2020). In addition, the Pacific Decadal Oscillation (PDO), affects SSTs being a sum of several processes with different origins over a larger timescale (Cerdeira et al., 2019). A particularly intense ENSO year in 1997 negatively impacted on industrial pelagic fisheries all over Chile, with a particular decline of the anchoveta (Comite Oceanografico Nacional-Chile, 2004). Other notable moderate to strong ENSO events occurred in 1930, 1940,

1983, 1987, and 1991 (Vargas et al., 2006). Climatic oscillations in the Chilean upwelling zone may mask or amplify anthropogenic effects on pelagic biodiversity patterns, which can only be resolved with confidence through use of baseline data, pre-dating industrial fisheries, which, as for most marine ecosystems, is unfortunately not available.

Biodiversity records retrieved using environmental DNA (eDNA) within sediments coupled with radioisotope-derived sediment chronologies offer a method to reconstruct ecosystem trajectories over time (Siano et al., 2021; Thorpe et al., 2022; Tsugeki et al., 2022; Wesselmann et al., 2022). eDNA is based on the detection of short DNA fragments that organisms release in the environment, including epithelial cells or extracellular DNA (exDNA; Díaz-Ferguson & Moyer, 2014), which are potentially deposited and preserved in the sediments. These deposited fragments are then extracted from the sediment and identified using high-throughput sequencing to then be matched with reference sequences of organisms through bioinformatic processing (Deiner et al., 2016). These sequences thus provide a proxy for biodiversity at the time the sediment layer was deposited, which can be resolved in parallel using geochronology methods.

The Chilean coast presents an exceptional potential for eDNA sediment chronologies, because of the presence of the Atacama Trench, the longest deep-sea trench in the world (Danovaro et al., 2002; Jamieson, 2015), which extends along the coast, focusing sediment inputs of different origin and exhibits low oxygen concentrations, fostering high organic carbon preservation rates (Oguri et al., 2022). High sedimentation rates also allow for the construction of high-resolution sediment chronologies, compared with millenary time scales which is the norm for low sedimentation rates of deep-sea sediments (Arias-Ortiz et al., 2018). The role of the Atacama Trench sediments as a depository for organic material (Glud et al., 2021; Oguri et al., 2022) underlying the world's most productive fishery could provide highly valuable information on biodiversity changes through recent time in the Chile upwelling ecosystem. Hadal trenches are, however, challenging to sample and few vessels within the global oceanographic fleet are equipped to access their sediments.

Here we build sedimentary DNA (hereafter referred to as sedDNA) chronologies of pelagic fauna community composition from sediment records retrieved from the Atacama Trench to examine how industrial fisheries and climatic oscillations affected the biodiversity of pelagic organisms in the overlying ecosystem. We focus particularly on the period between the 70s and the 90s, in which these waters suffered from overfishing and extreme climatic events. Furthermore, we monitor the changes in the number of reads of two taxonomic groups: fish and jellyfish. Fish are of great importance to the ecosystem and economy of the region, and are likely taxa to be heavily affected by both overfishing and ENSO events, and the occurrence and abundance of jellyfish in upwelling regions has been heavily linked to fishing intensity (Richardson et al., 2009), giving us a good opportunity to explore the relation between these two taxa and how they change by fishing pressure.

2 | METHODS

2.1 | Study area

The Atacama Trench is one of the deepest sections of the Peru–Chile Trench (Figure 1), reaching a maximum depth of more than 8000 m, a length of 5900 km and a mean width of 100 km, making it the world's largest trench (Danovaro et al., 2002; Jamieson, 2015). Additionally, it is the closest trench to a continent, being only about 160 kilometers away from the coast of Peru and Chile (Lemenkova, 2019), and, therefore, may reflect records of biodiversity from both coastal and open-ocean ecosystems. Most importantly, it underlies the productive upwelling zone associated with the Humboldt current that flows south along the coast from Peru to Chile, creating an upwelling plume that extends from near the coast to about 1000 km offshore, enhancing ocean productivity (Blanchette et al., 2009; Daneri et al., 2000). This ecosystem is subject to the effects of annual, inter-annual (El Niño and La Niña) and multidecadal (El Viejo and La Vieja) climate oscillations that cause high variability in the

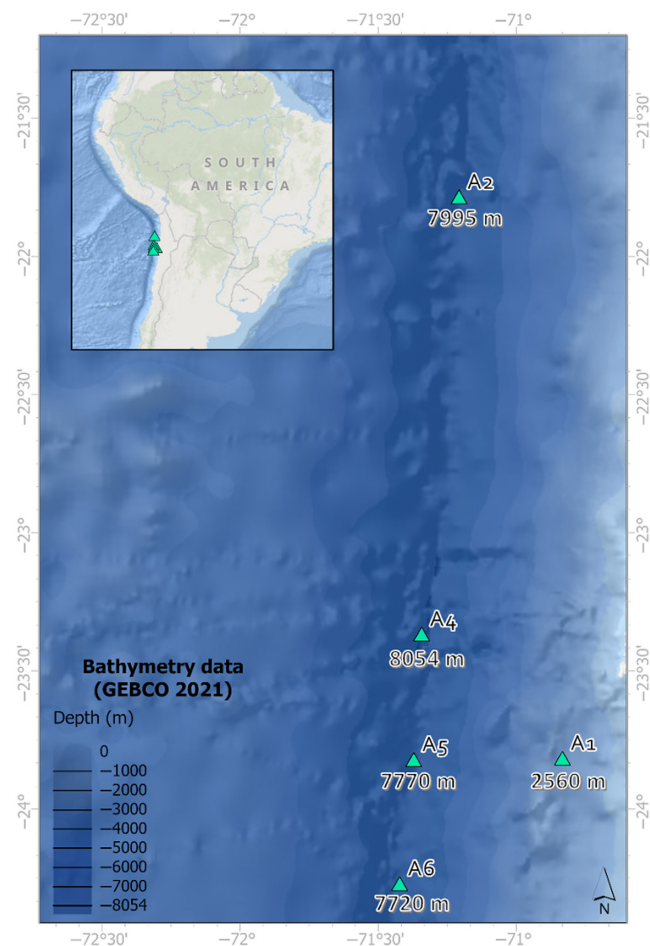


FIGURE 1 Study area and sampling locations where sediment cores were taken in the Atacama Trench near the Antofagasta region in Chile along with the depths at which samples were taken. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

ocean ecosystem (Comite Oceanografico Nacional-Chile, 2004). The trench supports enough sedimentation to allow relatively high-resolution benthic chronologies (Oguri et al., 2022). As the trench was formed by the active Nazca plate, the region where the Atacama Trench is located is exposed to earthquakes, tsunamis, and volcanic activity (Lemenkova, 2019) that affect the sediment deposition in the hadal trench (Oguri et al., 2013). Hence, sediment slumping may massively occur during earthquakes, affecting the regularity of sedimentary deposition, generating so-called mass wasting events that may in turn affect the chronology of the sediment (Oguri et al., 2022).

2.2 | Sediment sampling and sample processing

Sediment cores were collected in March 2018 from RV Sonne (BMBF, Germany, SO261) using a multiple core sampler. Cores were obtained from five different sites, with water depths ranging between 2560 and 8050 m (Figure 1). The cores retrieved were sliced on board to have multiple layers at an interval of 1 cm for the upper 10 cm sediments, 2.5 cm for 10–20 cm depth sediments, and 5 cm for >20 cm sediments. In order to minimize contamination, latex gloves were used at all times, and the ceramic knife used for slicing was washed with bleach, ethanol and Milli-Q water in between each layer collection (Xu et al., 2021). The sediment layers retrieved were freeze-dried until DNA extraction.

Sediment cores collected in parallel were used for assessing the vertical chronology with procedures and results as presented in Oguri et al. (2022). An assessment for the approximate dates were based on excess ^{210}Pb ($^{210}\text{Pb}_{\text{ex}}$; half-life of 22.3 years) dating during the past ~150 years. As the particle reactive $^{210}\text{Pb}_{\text{ex}}$ is produced from decay from elements in the atmosphere and in the water column, and accumulates on sediment surface, $^{210}\text{Pb}_{\text{ex}}$ profile makes it possible to identify layers deposited during mass wasting events as they have constant $^{210}\text{Pb}_{\text{ex}}$ concentrations (Koide et al., 1972). Total ^{210}Pb concentration was analyzed and quantified by gamma-ray spectroscopy at the Japan Agency for Marine–Earth Science Technology (JAMSTEC) and by alpha spectroscopy to measure ^{210}Po produced from total ^{210}Pb after establishing secular equilibrium in the samples at Edith Cowan University (ECU), respectively. At both institutions, ^{214}Pb concentrations that can be regarded as the secular equilibrium fraction of ^{210}Pb supported by ^{226}Ra in the sediments were measured with gamma-ray spectroscopy. The $^{210}\text{Pb}_{\text{ex}}$ concentration was determined by subtracting the ^{214}Pb concentration from the total ^{210}Pb concentration (Oguri et al., 2022).

The rate of sedimentation and the age of deposition younger than seven half-lives of ^{210}Pb (~150 years; Oguri et al., 2022) were then estimated by the decline curve from the profile of $^{210}\text{Pb}_{\text{ex}}$ concentration (Figure S1). In order to more accurately determine the age of each sediment layer, year estimation results from both institutions were averaged together.

The samples collected from mass wasting event layers (5.5–11.25 cm depth in core A2, 7.5–9.5 in core A4 and 11.25 to 13.75

in core A5) were removed from further analyses, as they may carry sediment from upper parts of the trench slope, making these layers unlikely to be chronological, and susceptible to bias our results. Similarly, a surface sediment mixing layer was found in core A5 at 0–3 cm from the $^{210}\text{Pb}_{\text{ex}}$ profile, and thus only the top 0–1 cm was utilized for analyses. Bioturbation has been recognized to produce constant $^{210}\text{Pb}_{\text{ex}}$ concentrations. In order to identify whether this played a role in our chronological dating, photographs of the split cores were compared and are available in Oguri et al. (2022). The authors argue that in the case of these sediments, the effect of bioturbation is negligible due to the anoxic conditions of the sediment, leading to a visible absence of burrows and large infauna over the ~100 cores sampled along the expedition.

2.3 | sedDNA analyses: Extraction, amplification, and sequencing

DNA was extracted from the sediment samples utilizing the DNA extraction protocol from Lever et al. (2015), which specifically targets exDNA using the extraction method with a carbonate removal treatment (Geraldi et al., 2020). An extraction blank of nuclease-free water was included for every batch extracted (set of 12 samples). exDNA was extracted due to its abundance in sediments, being estimated that >80% of total DNA in marine sediment is extracellular and >95% of this DNA is then adsorbed to the sediment matrix (Dell'Anno & Danovaro, 2005). Furthermore, although it depends on the environmental factors in each site, exDNA generally possesses a longer preservation time by its binding onto organic or mineral colloids in the sediment (Nagler et al., 2022), and its reliability and cost-efficiency when compared to total DNA for biodiversity studies over space and time (Pansu et al., 2021).

We used two different primer pairs targeting eukaryotes (Table S1) and amplifying sections in the 18S rDNA gene (Ficetola et al., 2021), one of the V7 region, Euka02 (Guardiola et al., 2016) and one of the V9 region, 18S Mini (Amaral-Zettler et al., 2009). Two primers were utilized for this project as the species recovery rate has been shown to amplify when using more than one genetic marker, also allowing to reduce amplification bias (Zhang et al., 2018). Furthermore, as primers have been shown to yield notable differences in results in taxonomic ranges, richness and community composition despite coming from the same sample (Min et al., 2023), we utilize both a v7 and v9 region primer to accurately confirm changes over time.

An Illumina adapter was included with each primer and PCR reactions utilized a final volume of 10 μL , which consisted of 5 μL of Qiagen multiplex PCR master mix (QIAGEN, Valencia, CA), 0.3 μL of 10 mM of primers (forward and reverse), 3.4 μL of PCR grade water, and 1 μL of extracted DNA. Five replicate PCR assays were run independently and pooled afterward to reduce the risk of PCR bias. For each PCR run, two extraction blanks and two positive blanks (DNA from organisms targeted by primers) were added to confirm there was no contamination. After optimization to increase the amplified

DNA yield, the thermal conditions for amplification in each PCR for the v7 primer were 15 mins at 95°C, followed by 35 cycles of 30 s at 94°C, 45 s at 53°C and 90 s at 72°C with a final extension at 72°C for 10 mins and indefinite hold at 4°C. For the v9 primer, thermal conditions were 10 mins at 95°C, followed by 40 cycles of 30 s at 94°C, 45 s at 58°C, and 90 s at 72°C with a final extension at 72°C for 10 mins and indefinite hold at 4°C.

PCR products were visualized with gel electrophoresis (1.5%) to ensure proper amplification. Products were then cleaned using AMPure XP magnetic bead-based purification (Beckman Coulter, Brea, CA, USA) following the MiSeq library preparation guide. For the creation of the pooled library, an equimolar amount of each sample was added, with a maximum of 50 μL of sample added to minimize dilution.

DNA was sequenced on Illumina MiSeq platform at King Abdullah University of Science and Technology (KAUST), Saudi Arabia. For the analysis of sequences, CUTADAPT (Martin, 2011) was first used to remove the primers. Further analyses were conducted in R version 3.5.1 following the DADA2 workflow (Callahan et al., 2016) to correct the data by the filtering of forward and reverse reads, the modelling of errors, the de-replication of amplicons and the removal of chimeras using the filterandtrim, learn-errors, derepfastq, and removeBimeraDenovo functions respectively. Afterward, unique reads named Amplicon Sequence Variants (ASVs) were determined using DADA2 and identical pair reads were merged with the mergePairs function.

Taxonomy was then assigned to the ASVs utilizing the RDP classifier (Lan et al., 2012). The reference libraries were created from the SILVA database (version 132 SSU Nr99) for the 18S primer pairs (script for pipeline and reference library creation available at <https://github.com/ngeraldi>). Further filtering of the data obtained was then performed using the *decontam* package and the PCR and extraction blanks to remove sequences possibly resulting from contamination with a threshold of 0.5 (v1.10.0; Davis et al., 2018). For a more accurate depiction of marine pelagic diversity across time, all sequences that were not assigned to at least the taxonomic level of Order were excluded from further analyses.

Furthermore, as the objective of the study was to focus exclusively on the pelagic species inhabiting the area, a literature review of each of the previously filtered ASVs was performed to determine the main habitat type of the identified taxonomic groups at the adult life stage and classify taxa as benthic or pelagic. Only ASVs corresponding to pelagic organisms were included in the analyses.

2.4 | Environmental data

Climatic data were obtained for each of the different sample sites at the respective time periods indicated by the dating of the cores. SST data were obtained from the ICOADS gridded dataset, available by NOAA (<https://psl.noaa.gov/data/gridded/tables/sst.html>), spanning a period from 1800 to the present worldwide. To better understand the important effect of oscillations in the area, ENSO

data were obtained from two different sources. The Oceanic Niño Index (ONI) (https://origin.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ONI_v5.php) provided by NOAA tracks the SSTs over a 3-month period in the east-central tropical Pacific and indicates the tendency toward warmer or cooler conditions than average, starting from 1950. The Niño SST Index (Niño 1+2 region) specifically tracks the smallest and eastern-most region of SST Indices and corresponds with coastal South America, providing an average monthly SST with an extended dataset from 1870.

Similarly, data for the Interdecadal Pacific Oscillation (IPO) index was obtained from NOAA (<https://psl.noaa.gov/data/timeseries/IPOTPI/>), spanning from 1854 to the present with monthly information. It is based on "the difference between the sea surface temperature anomaly (SSTA) averaged over the central equatorial Pacific and the average of the SSTA in the Northwest and Southwest Pacific" (Henley et al., 2015). The oscillation indexes were averaged to have the measure of temperature change in 1 year.

The chlorophyll-*a* concentration was obtained from NASA's SeaWiFS public global dataset spanning from 1997 to 2010 and from NASA Earth Observations having data from 2002 to the present, as well as the database compiled by Boyce et al. (2012), which combined the most recent observations and those made from the 1880s with more basic tools. It is important to note the lack of chlorophyll measurements in the area until recent years, which limits the information that can be extracted from this analysis. Catches in the Exclusive Economic Zone of Chile in the region and Aquaculture production by year from 1950 to present were obtained from FishStatJ, the software provided by the UN (FAO, 2011), which provides the total amount of tons harvested per year for each country, and were used as a proxy for the impact of extractive human activities in the region. The time series of these variables were modelled using LOESS (locally estimated scatterplot smoothing) and linear regression to best understand how they have changed through time.

2.5 | Data analysis

All the analyses were repeated separately for the v7 and v9 sedDNA findings. Each layer from each core was treated as a separate sample containing its own community at a specific point in time.

Prior to analysis, data were rarefied and transformed to convert ASV counts into presence/absence, as the total number of reads does not necessarily represent an accurate depiction of the abundance of taxa in the environment (Skelton et al., 2022). In order to group the years into time periods to increase the robustness of the reconstructed biodiversity in an unbiased manner with a similar number of samples in each group, we calculated the number of groups and class intervals for each group, resulting in 11 different time periods spanning 15 years each from 1842 to 2018.

We used the phyloseq R package (McMurdie & Holmes, 2013), to plot the relative abundance of the most abundant phyla found over the estimated years across all cores. As some samples had equal estimated years, the merge_samples function was utilized to

group said samples into one. Furthermore, this relative abundance plot was done for each core individually to understand the differences between cores. Similarly, in order to determine the change in the community for the most abundant groups of animals due to their ecological and cultural importance, we first plotted the relative abundance of the Animalia Kingdom for the v7 primer due to its higher abundance, finding that the Chordata and Cnidaria phyla comprise over 70% of the abundance (Figure S2). With this, we then plotted the relative abundance of the Orders pertaining to Chordata and Cnidaria.

Alpha diversity (Richness of taxa) was then calculated and plotted utilizing the total number of unique pelagic ASVs and the Chao index for the time period, combining all cores to resolve how diversity has changed in the overall area of the Atacama Trench. Additionally, in order to determine the difference in abundances for the phylum Cnidaria and the Actinopteri class, we utilized the number of reads rather than presence/absence data using only the v7 primer, which presented the highest number of reads for both taxa. Kruskal–Wallis tests were run to determine the effect of the abundance of cnidarians over fish and viceversa, as well as the effect of fishing over the abundance of both taxa.

Differences between richness of taxa between the different time periods were tested using Kruskal–Wallis tests to better illustrate changes in diversity and when they occur. Beta diversity, the dissimilarity between samples based on the presence and absence of ASVs, was calculated through the Jaccard distance method. This dissimilarity between each core was then utilized for the plotting of ordination analyses using non-metric multidimensional scaling (NMDS) to showcase how different the communities in the Atacama Trench are from each other. The DeSeq2 package (Love et al., 2014) was utilized for identifying differentially abundant ASVs over time to understand which ASVs were driving community changes over the years.

Finally, with the use of the manyglm function of the mvabund package (Wang et al., 2012), a generalized linear model utilizing a negative binomial distribution was fitted to a response variable with our chosen predictor variables in order to test how these variables affect the community over time. For this study, the response variable was a presence/absence matrix of taxa found in each sample. With the glm applied, we then ran Wald chi-squared tests to check for the effect of the predictor variables individually and in interaction with one another. This allowed us to test how these variables are affecting the changes in presence or absence of each unique ASV in each sample. These generalized linear models were also run for the subset of presence/absence tables of fish and cnidarians, so as to evaluate the effect of climate effects and anthropogenic disturbances in these taxa specifically.

Our predictor variables to test for the effects of the climate oscillations, ocean state variables and anthropogenic disturbance were subjected to a correlation matrix to avoid multicollinearity prior to the use of generalized linear models. The correlation threshold considered here was the combination of variables with a value $\geq .8$ or $\leq -.8$. The predictor variables chosen for further multivariate

analyses were, for each 15-year time period of each sample: the SST, the chlorophyll-a concentration, the El Niño SST Index 1+2, the ONI, the IPO index averaged for the 15-year period and the reported catch and aquaculture production average for the 15-year periods based on data available for the region.

While the ONI and IPO index proved to have a correlation with each other (.94), we opted to include both for the analyses as we believe they offer distinct enough information, with the Niño 1+2 Index providing the average temperature in the area, while the IPO and ONI Index provide the change in temperature in degrees Celsius from the average.

3 | RESULTS

Fish catches in the area of the Atacama Trench increased from 1960, continuing to rise exponentially until its highest point in 1995 with 7,837,699 tons of fish caught and slowly declining thereafter following a capture limit put in place by the Chilean government in 2001 (Figure 2a). Aquaculture production remained low until 1987 and increased greatly thereafter coinciding with the global expansion of industrial aquaculture (Figure 2b). The chlorophyll-a concentration increased linearly over time (Figure 2c), along with the SST, with temperature warming at an average rate of 0.11°C per decade since 1850 (Figure 2d). An oscillation pattern can be observed in both ENSO and PDO, with seawater temperatures decreasing toward 1930 and then increasing in 1950, with a maximum seawater temperature observed in 1997 (25.9°C), coinciding with an El Niño event between 1997 and 1998 that caused a fishing crisis in Chile before decreasing again until 2018 (Figure 2e,f).

After removing possible contaminated sequences, quality control, and filtering the data to retain only pelagic taxa, a total of 509,948 reads from 1479 different taxa were generated for the v7 primer, while 514,727 reads from 2115 different taxa were generated for the v9 primer from 48 unique sediment layers in five sediment cores collected in different locations (Table 1). The metabarcoding data of both primers assigned a total of 24 phyla, 46 classes, 126 orders, 187 families, 252 genera, and 282 species to these reads (Table 1). One in every 10 ASVs could be identified to species level, pointing at limited barcoding library resources for this important ocean ecosystem, as well as a possible DNA degradation toward the oldest layers identified in the lesser number of reads, which make the sequences unable to be identified. Fishes and cnidarians in the v7 primer had a total of 9205 and 63,585 reads respectively.

3.1 | Community composition of the Atacama trench

The most predominant taxa found both in v7 and v9 primers in all cores and across time were from the Animalia and Chromista Kingdoms. Within these, chordates and cnidarians for Animalia and

radiolarians, ciliates, and ochrophytes for Chromista represent the most abundant phyla (Figures 3 and 4). Plants, however, present only a small fraction of the sedDNA found in the sites, and all correspond to the Chlorophyta phylum. This pattern is consistent across sites, except for Site 6, where the abundance of cnidarians was much higher, a higher dominance of radiolarians and ciliates occurred across time, and no chordates were detected with the v9 primer at this site. A total of 14 phyla were shared among the two primers and both present similar patterns of taxa across time (Figures 3 and 4). Both primers presented unique taxa, with nine phyla only being found in the v7 primer (Bacillariophyta, Dinophyceae, Gnathostomulida, Haplosporida, Hemichordata, Kinorhyncha, Sarcomastigophora, Xenacoelomorpha, and Zoopagomycota), and three phyla only being found in the v9 primer (Euglenozoa, Foraminifera and Planctomycetes). The Euglenozoa phylum in particular, unique to the v9 primer, comprised a large part of the relative abundance.

In both primers, the relative abundance of individuals across time in the Atacama Trench fluctuates continuously, yet some groups maintain a high presence throughout, mainly the Chordata, Cnidaria, Radiozoa, Myxozoa, and Ochrophyta phyla. (Figures 3 and 4). While the v7 primer shows a relatively stable community with similar relative abundances across time, the v9 primer shows a higher fluctuation, with the Euglenozoa, Radiozoa, and Ochrophyta phyla driving the changes.

When examining the composition of chordates and cnidarians across time, a total of 17 different orders were identified. There is a consistent community with most Orders appearing throughout all years, with salps, siphonophores, and anthoatechates having the largest relative abundance (Figure 5).

Looking at cores separately, core A1, the closest to the coast, presents a larger amount of nematode reads, particularly of the Enoplida order. In cores A2 and A5, the order Chattonellales, a group of green algae dominate the reads. Lastly, for cores A4 and A6, jellyfish present the most abundant taxa, with the Rhizostomae order being related the most to these cores (Figures S3 and S4).

3.2 | Diversity changes over time

sedDNA taxonomic richness, defined here as the number of unique ASVs that were confirmed as pelagic and passed previous filters, did not differ significantly across sites sampled, with the v7 primer ranging from an average (\pm SE) of 299 ± 37 unique ASVs at Core 1, the sample obtained at the shallowest depth (2560m) and closest to shore (31.84km) to 338 ± 42 at Core 2 (Table 1). For the v9 primer, richness followed a similar pattern, varying from 267 ± 51 at Core 1 to 359 ± 67 at Core 2 (Table 1).

The temporal changes in species richness were also consistent for both primers, with species diversity increasing from the earliest year considered, just before the Industrial Revolution (1842), to peak between 1954 and 1969. Detected diversity then experienced a decrease toward the end of the 20th Century followed by a further increase since 1986 to then remain uniform or decline afterward,

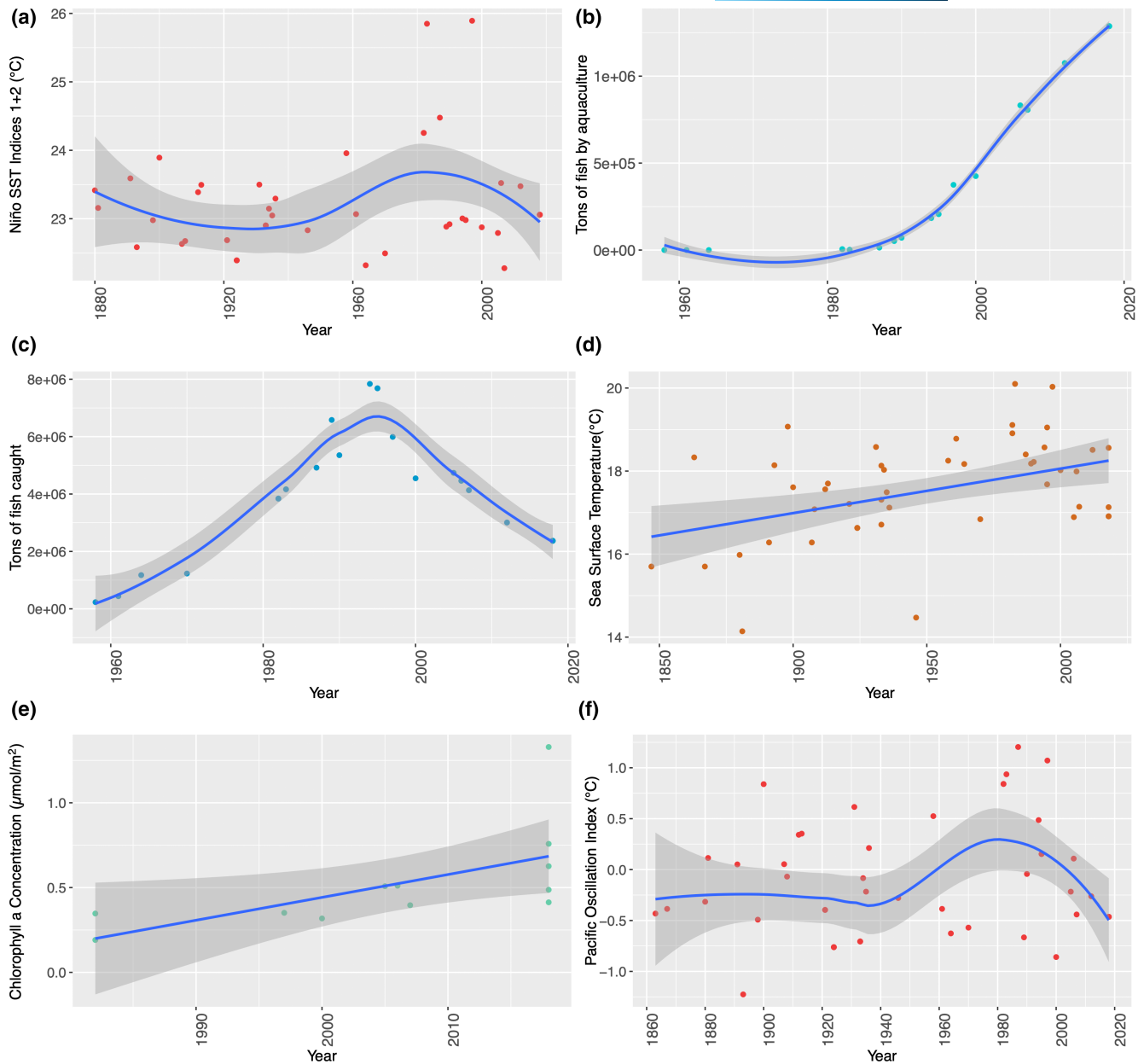


FIGURE 2 Time series of climate and ocean state and human activity in Chile: (a) tons of fish caught in Chile, (b) tons of fish produced by aquaculture in Chile, (c) chlorophyll-a concentration, (d) average sea surface temperature (SST), (e) El Niño SST Index 1 + 2, f) Interdecadal Pacific Oscillation Index. Blue lines represent the linear (panels a, d, e) and LOESS (panels b, c, f) regressions, while the gray bands represent the 95% confidence lines of each regression.

depending on the site (Figure 6). In spite of this apparent shift in abundance, no statistically significant differences were found in the richness among all the different time periods using the v7 primer (Kruskal-Wallis $\chi^2 = 10.483$, $df = 10$, $p = .3991$), nor the for v9 primer (Kruskal-Wallis $\chi^2 = 5.383$, $df = 10$, $p = .8641$).

Beta diversity for both primers demonstrated that although the alpha diversity of sites may differ, the ASVs present do not seem to represent different communities when analyzing the spatial differences across all sites. An overlap of communities shown through the NMDS analysis evidenced with both markers indicates that community composition was not significantly different across sites, with the exception of Core A6 for the v9 primer. (Figure 7).

In the time period when pelagic diversity declined the most according to our data (1970–1985), a total of eight ASVs were identified as having the most influence in the decline in the abundance of reads (false discovery rate- or FDR-corrected p -value > .05). From these eight ASVs, six pertained to the Chromista kingdom identified up to different taxonomic levels: ASVs from the ciliate orders of Stichotrichida, Euplotida, and Philasterida, as well as orders from the Pleurosigmataceae, Bacillariaceae, and Collospheeridae families were the groups that changed the most during this period. The two-remaining influential ASVs pertain to the Animalia kingdom and are identified to the species level as *Tetraplatia volitans* (a hydrozoan) and *Pyrosomella verticillata* (a tunicate).

Core	Sediment layer	Rate/JAMSTEC	Rate/ECU	Approximate year	ASVs v7	ASVs v9
A1	0–1 cm	2018	2018	2018	302	175
	1–2 cm	2005	1999	2002	286	257
	2–3 cm	1991	1981	1986	399	420
	3–4 cm	1978	1962	1970	477	561
	4–5 cm	1964	1943	1953	351	2
	5–6 cm	1951	1924	1937	400	387
	6–7 cm	1937	1905	1921	303	318
	7–8 cm	1924	1886	1905	84	151
	8–9 cm	1910	1867	1889	193	229
9–10 cm	1897	1848	1873	197	170	
A2	0–1 cm	2018	2018	2018	146	66
	1–2 cm	1984	1996	1990	371	324
	2–3 cm	1949	1974	1962	393	497
	3–4 cm	1915	1952	1933	443	523
	4–5 cm	1880	1929	1905	357	412
	5–6 cm	Undetermined ^a	Undetermined ^a	1887	-	-
	6–7 cm	Undetermined ^a	Undetermined ^a	1887	-	-
	7–8 cm	Undetermined ^a	Undetermined ^a	1887	-	-
	8–9 cm	Undetermined ^a	Undetermined ^a	1887	-	-
	9–10 cm	Undetermined ^a	Undetermined ^a	1887	-	-
	10–12.5	Undetermined ^a	Undetermined ^a	1887	-	-
12.5–15		1874	1874	317	334	
A4	0–1 cm	2018	2018	2018	357	403
	1–2 cm	2000	2003	2002	126	254
	2–3 cm	1983	1988	1985	300	369
	3–4 cm	1965	1973	1969	266	276
	4–5 cm	1947	1959	1953	88	152
	5–6 cm	1929	1944	1936	194	285
	6–7 cm	1911	1929	1920	165	228
A5	0–1 cm	2018	2018	1993 ^b	286	209
	1–2 cm	1993	1999	1993 ^b	-	-
	2–3 cm	1967	1979	1993 ^b	-	-
	3–4 cm	1941	1959	1950	280	192
	4–5 cm	1916	1940	1928	245	201
	5–6 cm	1890	1920	1905	234	151
	6–7 cm	1864	1901	1883	224	217
	7–8 cm	1839	1881	1860	400	635
	8–9 cm	-	1861	1861	380	413
9–10 cm	-	1842	1842	346	311	
A6	0–1 cm	2018	2018	2018	361	448
	1–2 cm	1995	2003	1999	353	150
	2–3 cm	1972	1987	1980	142	419
	3–4 cm	1948	1972	1960	332	436
	4–5 cm	1925	1957	1941	340	428
	5–6 cm	1902	1941	1922	221	309
	6–7 cm	1879	1926	1902	116	148
7–8 cm	1855	1911	1883	176	213	

TABLE 1 Summary of the calculated years of the deposited sediment in each of the layers according to analyses in Japan Agency for Marine–Earth Science and Technology (JAMSTEC) and Edith Cowan University (ECU) as well as the estimated approximate year averaged from both sources in all sample sites and the amount of unique Amplicon Sequence Variants (ASVs) found in both primers.

^aLayer where a mass wasting event occurred.

^bLayer where surface mixing occurred.

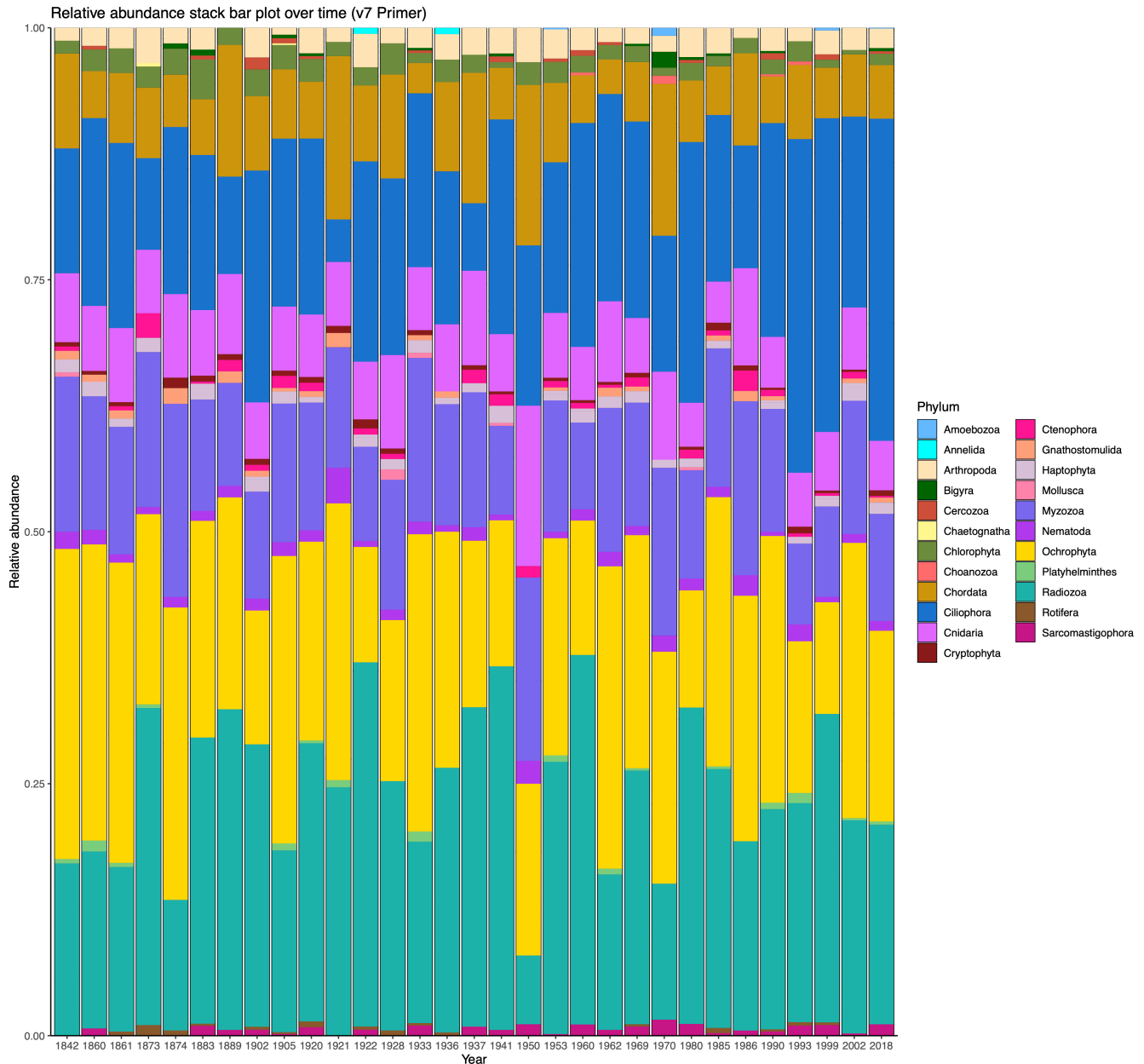


FIGURE 3 Bar plot of the relative abundance for the community composition of pelagic phyla found in each core for the v7 primer. Each bar represents a total community at a given year calculated by the sediment chronology, and each color represents the percentage of reads by a specific phylum in the total abundance of reads of that community.

3.3 | Effects of natural and anthropogenic influence over diversity

The predictor variables that showed a consistent relationship with the changes in community composition based on the presence/absence of each unique ASV were those related to changes in SST. For both primers, the SST (°C) and the ONI (°C) proved to be most closely associated with the changes in the presence and absence of ASVs (Table 2). While the tons of fish landings and aquaculture production proved to not be significant individually, both the Niño 1+2 Index (°C) and its interaction with the tons of fish landings were determined to be statistically significant. The strong ENSO events

recorded in 1983 and the exponential rise of fishing during the 80s (Figure 2) align with the period of time when diversity reached a minimum according to our data (1970–1985).

In the Actinopteri and Cnidaria groups, a similar pattern was found in read abundance across the time periods for the two of them. Cnidarians present a sharp increase in reads between 1922 and 1937 (Figure 8), while fish present an increase in reads between 1938 and 1953, both followed by a decrease in reads. The generalized linear models revealed a significant relationship only for the effect of the tons of fish landings over Cnidarian abundance ($p = .023$), while no other predictor variable proved significant for either group's abundance over time (Table S2).



FIGURE 4 Bar plot of the relative abundance for the community composition of pelagic phyla found in each core for the v9 primer. Each bar represents a total community at a given year calculated by the sediment chronology, and each color represents the percentage of reads by a specific phylum in the total abundance of reads of that community.

4 | DISCUSSION

Our sedDNA-based dataset of pelagic organisms revealed a highly diverse, species-rich community, composed mainly of animals and chromistas in the Chilean Humboldt upwelling and current system overlying the Atacama Trench. The latter demonstrates the prevalence of unicellular algae in the ecosystem, as expected with the high primary production in the surface waters. For Chromista, the reads in the Atacama Trench consist primarily of skeleton-forming unicellular organisms: Bacillariophyceae and Polycystinea. Indeed, diatoms are known as the main primary producers in upwelling regions (Irwin

et al., 2012), and Polycystinea are the largest and most common groups of radiolarians that can be found throughout the water column (Krabberød et al., 2011).

For animals, there was a dominance of chordates and cnidarians across all years and in all the sampled sites with the two primer pairs, with salps and different cnidarian orders presenting the highest relative abundance (Figure S2; Figure 5). Within these, the Scyphozoa and Thaliacea classes presented the most reads, showing this ecosystem to be rich in gelatinous organisms. Thaliacea are tunicates widespread in tropical waters and are able through rapid asexual reproduction to form extensive swarms in a short span of

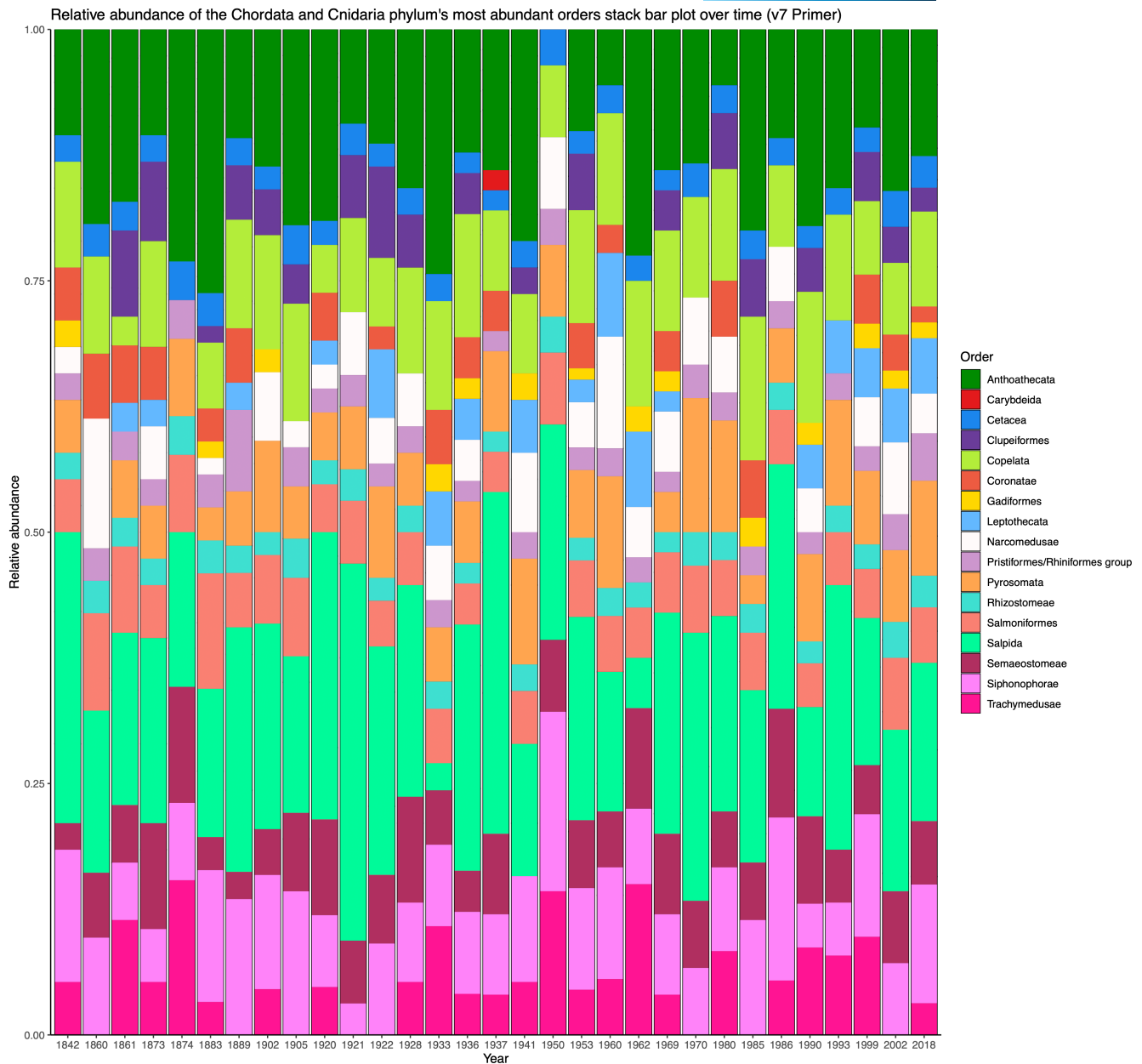


FIGURE 5 Bar plot of the relative abundance for the community composition of Orders within the Chordata and Cnidaria phylums for the v7 primer. Each bar represents the total abundance of these two groups at a given year calculated by sediment chronology. Each color represents the percentage of reads by each specific Order in the abundance of reads of that community.

time (Weikert & Godeaux, 2008). However, in similar studies in the deep sea off Crete and the United States (Paffenhöfer et al., 1995; Weikert & Godeaux, 2008), Thaliacea did not represent a significant part of the zooplankton community as inferred by sampling with traditional net sampling. Indeed, gelatinous organisms show a bloom and burst behavior, creating large patches of organisms followed by a sharp decrease in abundance (Deibel & Paffenhöfer, 2009) that is challenging to detect in conventional surveys, but delivers large depositional events to the deep sea, where they play a major role in supporting carbon sequestration (Luo et al., 2020). Hence, our results suggest that sediment records may provide reliable assessments of the time series of organisms that have bloom and burst cycles

such as diatoms and gelatinous zooplankton. Sediment DNA records may prove a valuable sampling tool to capture long-term patterns in these groups, which are difficult to capture in traditional time-series sampling.

4.1 | Changes in diversity over time and proposed explanations

When analyzing taxa richness over time, our results indicate a decline between the 1970 and 1985 period. In these 15 years, pelagic diversity reached its lowest point in the pelagic ecosystem of the

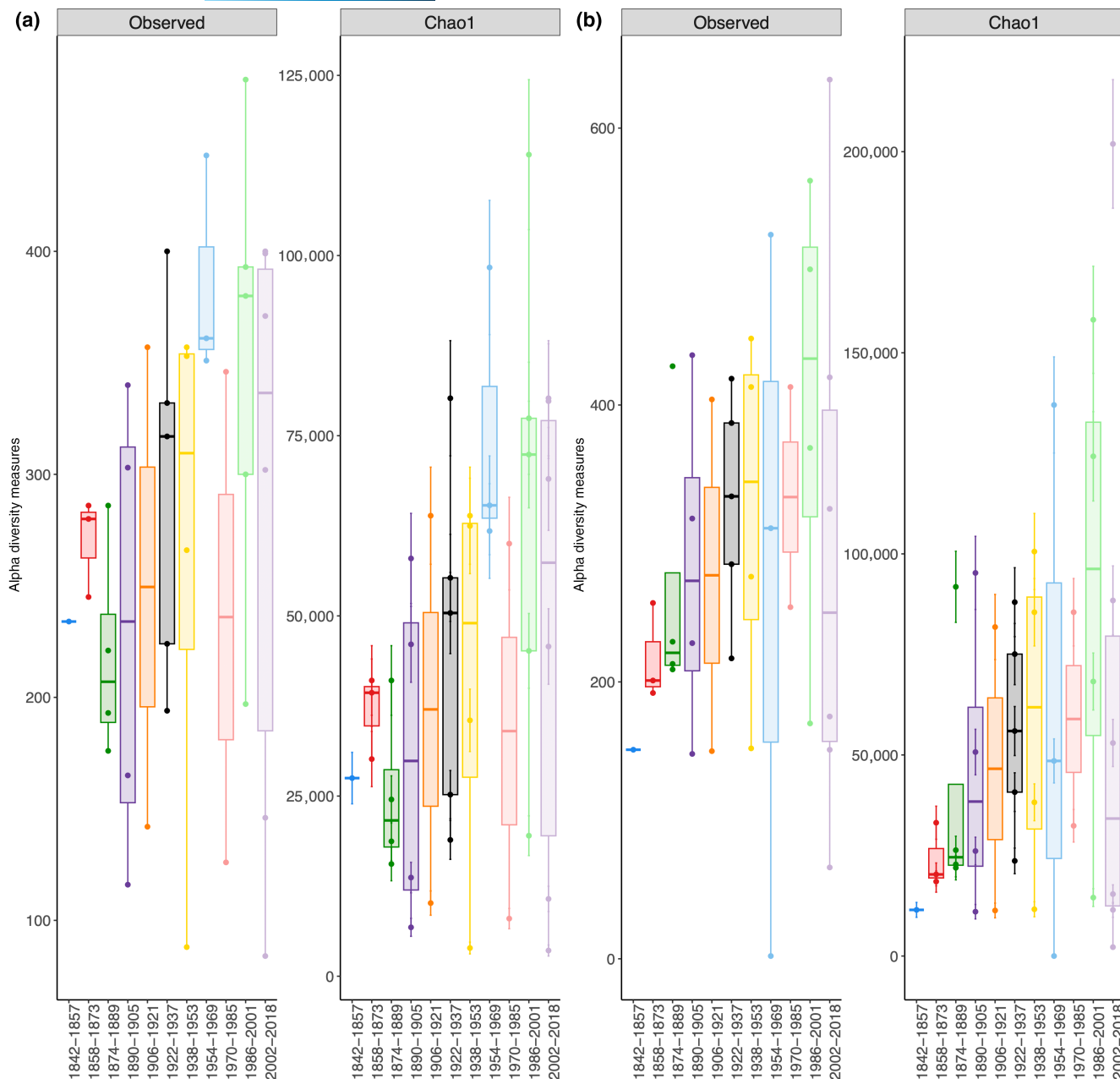


FIGURE 6 Observed diversity (number of unique Amplicon Sequence Variants) and Chao index alpha diversity measures of the Atacama Trench with diversity from all cores pooled through the different time periods for (a) The v7 primer and (b) The v9 primer. Each point represents a different sample, and the boxes represent the interquartile range between the first and third quartiles. The horizontal lines in the middle of the boxes represent the median across all samples in that time period, while the whiskers are the lowest and highest values within 1.5 times the interquartile range from the first and third quartiles.

Atacama Trench. This trend was found at all sampling sites and for both primer pairs across the two diversity indexes tested (Figure 6). An analysis of the taxa in this decline through differentially abundant tests reveals that it was attributable mainly to the Chromista kingdom which declined the most and drove this pattern. While this may be a result of the overall abundance of algae, diatom, dinoflagellate, oomycete, and protozoan DNA over other groups, this decrease in diversity suggests that these small eukaryotes are affected by the environmental and anthropogenic pressures just as much as the ones larger in size such as chordates. Indeed, Díaz-Ochoa et al. (2011)

analyzed the productivity of the last two centuries utilizing sediment cores with geochronologies in the same area of this study. In their paper, they report a shift from higher oxygenation conditions in the water to a less oxygenated state since the early 1960s, and suggest a shift from the phytoplankton community in turn. Our study did not directly compare the paleoproductivity and its impact on the diversity of the Atacama Trench. However, we did find a perceived change in the patterns of abundance in members of the Chromista kingdom after the 1960s, particularly in the case of Euglenozoa's increase in relative abundance and Radiozoan's decrease in the v9 primer

FIGURE 7 Graphic representation of the ordination analysis of non-metric multidimensional scaling (NMDS) showcasing the relatedness of communities between the different cores based on beta diversity for (a) The v7 primer and (b) The v9 primer. Each point represents a community in each sample, while the position of each point on the graphic represents the dissimilarity based on a distance matrix between the different samples. The colored ellipses surrounding the points connect each of the points within the same core, thus showcasing how similar they are to each other and to other cores.

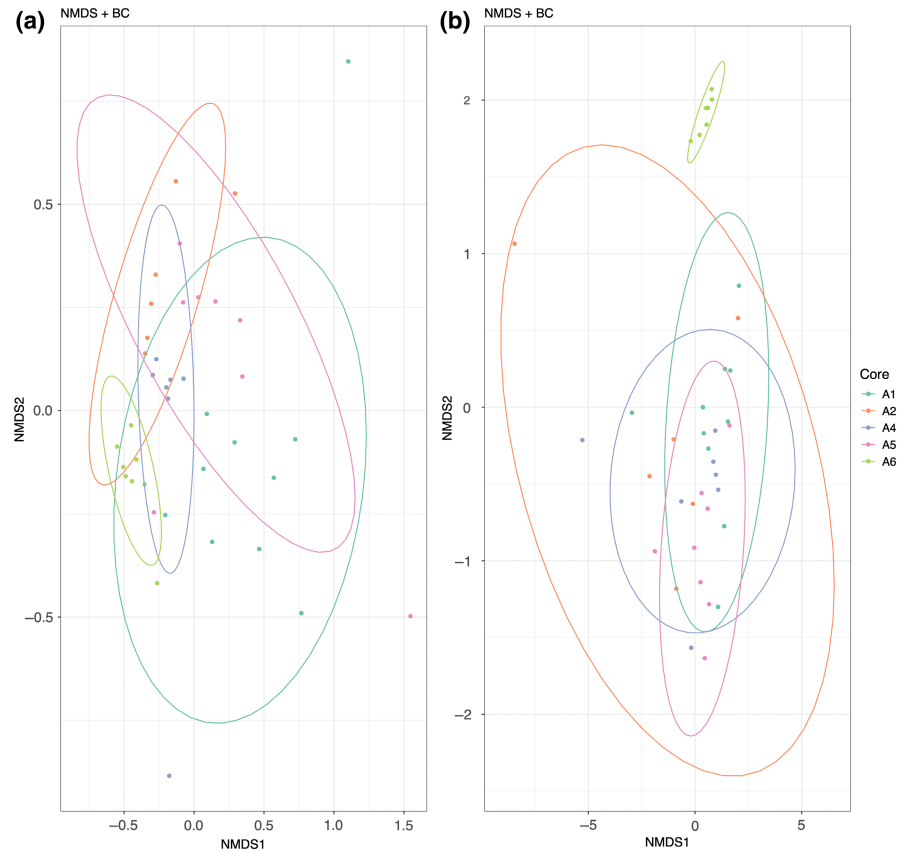


TABLE 2 Significance values based on the Wald chi-squared test applied on the generalized linear models to determine whether explanatory predictors affect the community composition, here taken as the presence/absence of every unique Amplicon Sequence Variant (ASV) in each unique sample.

Predictor	v7 primer		v9 primer	
	Wald value	Pr(>wald)	Wald value	Pr(>wald)
Time period	35.42	0.724	35.94	0.259
Sea surface temperature ^a	32.83	0.027 ^a	45.49	0.001 ^a
Interdecadal Pacific Oscillation	26.61	0.700	32.68	0.563
Index				
Niño 1+2 Index	19.67	0.515	30.25	0.005 ^a
Oceanic Niño Index	27.67	0.039 ^a	32.81	0.026 ^a
Niño 1+2+Tons of fish by fishing ^a	24.24	0.096	30.39	0.005 ^a
Chlorophyll-a concentration	21.63	0.229	19.85	0.610
Tons of fish by fishing	21.97	0.568	27.67	0.087
Tons of fish by aquaculture	21.45	0.215	24.73	0.184

^aStatistically significant predictor.

(Figure 4), thus providing possible evidence of this likely change in the phytoplankton community due to oxygen conditions in the area. The Euglenozoa found in this study pertain to the Diplonemida and Kinetoplastida Orders, species-rich groups that have widely diverse lifestyles, ranging from heterotrophy and photosynthesis to parasitism and symbiosis (Kostygov et al., 2021). Flegontova et al. (2020) demonstrated that these groups have been shown to change in response to environmental conditions, showing a higher abundance in nutrient-rich conditions while avoiding high oxygen concentration, high density of algae and high salinity, providing a possible explanation to the increase in Euglenozoa in our data as Chromista relative abundance decreases.

The decrease in alpha diversity coincides with the strongest known period of ENSO effects worldwide. The second highest known Niño SST values for the region were registered in 1983 (25.85°C) and the ONI also registered an anomaly of +1.116°C average temperature increase throughout this year (Figure 2). The effect of these abnormal climate conditions is reinforced by our results showing a correspondence from the two ENSO indexes over the community data as reconstructed with both primer pairs.

The SST and ONI thus emerge as robust predictors of the presence/absence of different ASVs found in the Atacama Trench for both primers ($p < .05$ and $p \leq .005$ for V7 and V9, respectively; Table 2). The Niño 1+2 Index, along with its interaction with fishery catches, also proved significant only in the case of the v9 Primer ($p = .005$; Table 2). It is widely known that climate change has increased SSTs (Collins et al., 2010), as well as the variability and

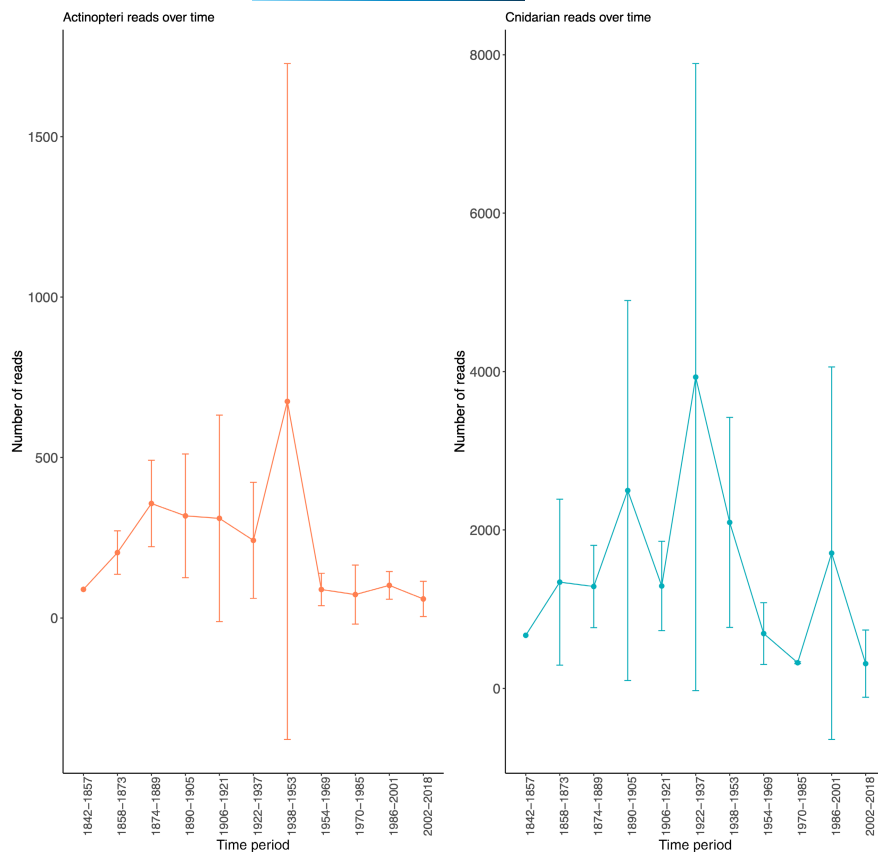


FIGURE 8 Total abundance measured by a number of reads of the groups of interests of fish (Actinopteri) and cnidarians over the 15-year time periods. The vertical bars in each point represent the standard error for the number of reads.

incidence of extreme ENSO events (Cai et al., 2021). During the El Niño event of 1983, coinciding with the alpha diversity decrease in pelagic eukaryotes in our records, harsh conditions were reported around the world, with the decimation of entire populations of different marine animals (Edgar et al., 2010), a large loss of corals due to bleaching (Glynn, 1991) and a large wave of migration of multiple tropical fauna toward the colder waters of South Chile (Riascos et al., 2017). Indeed, ocean warming influences productivity regimes, amplifying the effects of ENSO, and induces changes in the resource availability, horizontal and vertical distribution of species and their movement patterns, altering species dynamics and community composition (Talukder et al., 2022).

While for our data the temperature-related predictors provide the best explanation for diversity change, we agree that there are a number of different effects and complex interactions influencing the change in pelagic communities over time and the community change cannot be explained through these predictors alone. For example, one of the main explanations for the high mortality in Chilean waters in different species during intense ENSO periods is food deficiency, as upwelling activity decreases, and nutrients are not supplied to the surface in the Humboldt Current Upwelling (Diaz & Markgraf, 2000). Levin et al. (2002) studied several sediment stations on the Humboldt Current system during the strong ENSO event of 1997, finding that for the abundance of specific taxa such as nematodes, the oxygen concentration and food availability and quality play a crucial role. Similarly, Salvattecchi et al. (2018) used fish scales deposited in sediment layers to reconstruct the biomass fluctuations of

two important fishing targets: anchovy and sardine and how they are affected by temperature change and upwelling. With their findings, they challenge the idea of anchovy and sardine regimes dictated only by multidecadal temperature fluctuations, and show that paleo data independent from fisheries is needed to fully understand the pelagic communities, incorporating regional dynamics, food quality for fish, among others.

Fisheries are known to have effects at different levels over marine communities, but their impact over open-ocean communities is less studied. At the species level, target species of fisheries are generally more prone to depletion and extinction due to the effects in population dynamics and structure as the demand for food keeps rising (McCauley et al., 2015). Furthermore, fishing pressures have been noted to likely influence the age and size at maturation of the exploited stocks and cause behavioral changes that can propagate to other species in the community (Ortuño Crespo & Dunn, 2017). ENSO events in Chile can influence the feeding grounds and migratory pathways of certain species, causing juvenile age groups to become more vulnerable to fishing and further decrease the breeding population (Arcos et al., 2001). Hence, the significant interactions of ENSO and fish catches in affecting diversity in the Chilean Humboldt Current Upwelling.

The lowest values of alpha diversity also coincide with the increase in fishing pressure in Chilean waters (Figure 2a). Starting from 1977, fishing catches in Chile rose exponentially hitting its highest point in 1994 (7,837,699 tons per year), and then rapidly decreased to one third of the maximum (Figure 2c). Despite the known effects

of overfishing in the area, our results do not show any indices of a direct effect of fishing in Chile on overall taxa richness. This could be attributed to the generality of the catch data, as this information is only available for the country as a whole, and it is impossible to obtain fishing data specific to the region sampled until the 2000s. Similarly, due to the nature of our samples, it is possible that sedDNA here does not detect the change occurring in the taxa directly targeted by fishing, as most of the fisheries are concentrated in the coastal part of the Chilean waters.

The Fishing and Aquaculture General Act (FAGA) was introduced in Chile in the 1990s for the establishment of differential access regimes for industrial and artisanal fishing (Bernal et al., 1999). Regulation was further strengthened following overexploitation and the occurrence of an El Niño event during 1997 and 1998, which caused the largest fishing crisis of the decade. A maximum capture limit was firmly established in 2001 to avoid further depletion of fisheries resources, leading to a great decrease in the harvest of jurel and anchovies (Soto & Paredes, 2018). These regulations to limit overfishing in Chile reduced the anthropogenic pressures on the ecosystem (Boehlert, 1996; Smith, 1994). Indeed, it is these efforts that may suggest that the richness of taxa should increase. However, the v9 primer specifically indicates a drop in richness in the latest time period (2002–2018) (Figure 6), suggesting that the benefits of these regulations may have been offset by the effect of recent higher ocean temperatures on pelagic biodiversity over the Atacama Trench (Figure 2). Indeed, ocean warming is considered a threat to marine biodiversity, responsible for the decline of about 14% of marine species threatened by extinction (Luybaert et al., 2020).

While this study revealed a decrease in alpha diversity at a certain period of time, the community composition of the core pelagic community of the Atacama Trench examined through beta diversity over the 175 years covered by this study seems to have remained mostly stable. Indeed, dissimilarity analyses revealed a low variance of beta diversity, signaling a low change in the diversity of species from one time period to another, and from one core to another (Figure 7). The resilience of community composition of the pelagic community overlaying the Atacama trench may be rooted in the specific environmental characteristics of this biogeochemical province. The pelagic ecosystem overlaying the Atacama Trench is characterized by important upwelling events that lead to characteristically high primary production (Fossing et al., 1995). This provides an abundant supply of resources throughout the food web that can support a diverse community despite temporal variability. Bakun et al. (2015) have described Eastern Boundary Upwelling Systems (EBUS) as being highly variable across different time scales, which in turn has made these systems resilient to natural climate variability. Able to have a fast recovery from disturbances and keep a high productivity and ecosystem function, these systems are largely able to maintain their core communities. Indeed, our results align with the expected resilience of the Atacama Trench as an EBUS following the adverse 1970–1985 years characterized by a large ENSO event and an overfishing period yet being able to keep its community

composition. However, under the current influence of anthropogenic climate change and overexploitation, it is difficult to predict future trends, as these changes may exceed previous natural variability in the system.

4.2 | Fish and jellyfish dynamics

Both the Actinopteri and Cnidaria groups presented a pattern of read abundance across time, particularly with cnidarians presenting over 10 times the abundance of fish (Figure 8). Although being an important component in highly productive regions, it is believed that their abundance has risen in recent blooms to the detriment of other organisms with overfishing as the main factor (Richardson et al., 2009). Indeed, our results seem to support the change in abundance of cnidarians caused by an increase in the amount of fishing done in the region ($p=.023$, Table S2). Previous studies in the similar upwelling region of the Benguela Current have shown that overfishing depleted the abundance of small pelagic fish, leading to a dramatic increase in jellyfish abundance (Roux et al., 2013). This is mainly explained by the lack of competition for resources as the diets between these fish and jellyfish overlap significantly (Brodeur et al., 2008; Shoji et al., 2009), and the structuring role that small pelagic fishes play in the food webs as trophic controls (Cury & Shannon, 2004). In the case of fish abundance, we did not find any relationship between fishery catches and the abundance of Actinopteri reads ($p=.145$, Table S2), possibly reflecting the targeted nature of the fishery in the region, focused on anchoveta, sardines, and hake (Gozzer-Wuest et al., 2023). However, these targeted fisheries could also support the hypothesis of an increase in jellyfish abundance due to the depletion of small pelagic fish. Indeed, climate change scenarios experiments have already predicted a reduction in the recruitment of small pelagic fishes in the Humboldt Current system (Brochier et al., 2013), which, combined with our results, may give us insight into the future of this system, should the current trend continue.

An alternative explanation to this phenomenon has been suggested by Condon et al. (2013), who demonstrated that this increase in abundance is not due to deteriorating conditions in the global oceans, but rather, to worldwide oscillations characterized by about 20 years' periodicity, with a particularly noticeable rising phase during the 1990s. Indeed, while a cyclic pattern is shown through our results (Figure 8), the coarse time resolution of our data set does not allow to test for a 20-years cycle, although it shows an oscillation of 40 years in the Atacama Trench region.

4.3 | Sedimentary DNA challenges

Our assessment is affected by challenges associated with environmental DNA, such as the lack of good taxonomic resolution in reads. Originally, a total of 11,558 and 19,101 unique ASVs were identified for the v7 and v9 primers respectively. However, about 15% of taxa

were identified as benthic (1,714 and 3,023 ASVs for v7 and v9 respectively) and removed from analysis, and only about 10% of the remaining ASVs could be used in the analyses due to not having the minimum required taxonomic level of Order.

Both v7 and v9 primers have their own limitations and target certain organisms better than others. The v7 primer used here (Euka02) shows a high universality, being able to capture a wide array of eukaryotes but has limited taxonomic resolution (Ficetola et al., 2021; Meyer et al., 2021). In contrast, while the v9 marker can amplify all eukaryotes, it is known to be more useful in the amplification of protists and microbial organisms in general (Choi & Park, 2020; Stoeck et al., 2010), and is shown in our findings of large readings of Euglenozoa not found in the v7 primer. These limitations, inherent to the primers used, are further aggravated by the dependence on reference sequences for species present in the area, as many abundant taxa present in the DNA reads did not seem to be represented in reference libraries. This signals the need to increase our effort in barcoding marine species, particularly in the Humboldt Upwelling region and across the ocean, to improve the capacity to assign taxa to reads in sedDNA studies and enhance the power of sedDNA studies to resolve present and past biodiversity in the ocean.

In addition, the patterns of change in abundance should be considered as relatively coarse when comparing taxa, as PCR biases may over-amplify some sequences compared with others (Nichols et al., 2018). The use of more than one primer in this study limits PCR bias to a certain degree by overcoming the effects of overamplification of certain groups, primer bias, artifacts, and contamination by obtaining multiple detection hits (Stat et al., 2017) that showcase a similar community and patterns of diversity over time according to both primers.

Another set of limitations that must be overcome to grasp the full potential of sedDNA to reconstruct past biota, are the inherent limitations of ancient DNA. Being highly fragmented and degraded as time passes, fragments tend to be short (~69 bp; Armbrrecht et al., 2020). As only trace amounts of DNA are preserved, they are prone to be contaminated by modern eDNA, and as we do not yet completely understand how aDNA is degraded over time and maintained in the sediment layers, it is impossible to extrapolate the abundance of reads found to determine a proxy for the abundance of taxa in these environments.

Overall, strong ENSO events and the warming of waters due to climate change all likely contributed to the important biodiversity decline between 1970 and 1985. These effects will continue to be a significant influence in the region's marine biodiversity as evidenced by a tendency toward a biodiversity decline with recent ocean warming in the region studied. The results presented demonstrate the power of sedDNA coupled with sediment chronologies to retrieve past biodiversity dynamics in marine ecosystems where baselines are lacking. Indeed, we were able to demonstrate long-term patterns of biodiversity change related to ENSO and fishery catches and show that there is a significant relation between the amount of fish caught and gelatinous organisms such as cnidarians increasing in abundance, yet not finding such a relation with Actinopteri

in general, highlighting the specificity of Chilean fisheries toward smaller pelagic fish, finally giving a prospect toward the future based on these findings of the past.

Hence, despite the limitations of sedDNA studies, which are continuously improved, they provide an emerging and robust option to retrieve baselines and biodiversity trajectories of ecosystems for which historic records are lacking, which unfortunately, affect most ocean ecosystems.

AUTHOR CONTRIBUTIONS

Diego Elihu Rivera Rosas: Data curation; formal analysis; methodology; software; validation; visualization; writing – original draft; writing – review and editing. **Nathan R. Gerald:** Conceptualization; data curation; investigation; methodology; supervision; writing – review and editing. **Ronnie N. Glud:** Funding acquisition; investigation; writing – review and editing. **Kazumasa Oguri:** Funding acquisition; investigation; writing – review and editing. **Sophie A. Haond:** Investigation; writing – review and editing. **Carlos M. Duarte:** Conceptualization; funding acquisition; methodology; project administration; resources; supervision; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT


The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Sequence Read Archive (SRA) in NCBI with SubmissionID: SUB13728710, BioProject ID: PRJNA1001897. Taxonomic data derived from these sequences and metadata for every sample for each of the two primers is publicly available in Dryad, <https://doi.org/10.5061/dryad.66t1g1k92>. Sediment core description is available in Oguri et al.'s (2022) supporting information <https://agupubs.onlinelibrary.wiley.com/doi/full/10.1029/2022JG006814>. 210Pbex profiles of the Atacama Trench are available from Pangaea, <https://doi.pangaea.de/10.1594/PANGAEA.947927>. Sea Surface Temperature (SST) data was obtained from the ICOADS gridded dataset, available by NOAA (<https://psl.noaa.gov/data/gridded/tables/sst.html>). The Oceanic Niño Index, Niño SST Index (Niño 1+2 region) and Interdecadal Pacific Oscillation Index data was obtained from NOAA (https://origin.cpc.ncep.noaa.gov/products/analysis_monit

oring/ensostuff/ONI_v5.php; <https://psl.noaa.gov/data/timeseries/IPOTPI/>). Chlorophyll-a concentration data was obtained from the SeaWiFS's Project (<https://oceancolor.gsfc.nasa.gov/SeaWiFS/>). Lastly, aquaculture production and fish landings for Chile were retrieved from UN's FishSatJ software (<https://www.fao.org/fishery/en/statistics/software/fishstatj>).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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