Marine Ecology

WILEY

marine ecology

RESEARCH ARTICLE OPEN ACCESS

Long-Term Dynamics of the Northern Humboldt Current System Pelagic Fish Community: A Look Into Community Shifts

Paola Galloso[1,2] | Pierre Legendre[1,2] | Giancarlo M. Correa[3] | Miquel De Cáceres[4]

[1]Département de Sciences Biologiques, Université de Montréal, Montréal, Québec, Canada | [2]Québec Centre for Biodiversity Science, McGill University, Montréal, Québec, Canada | [3]AZTI Marine Research, Basque Research and Technology Alliance (BRTA), Sukarrieta, Bizkaia, Spain | [4]CREAF, Campus de Bellaterra, University Autònoma de Barcelona, Barcelona, Spain

Correspondence: Paola Galloso (gallosopl@gmail.com)

Received: 3 September 2024 | **Revised:** 11 May 2025 | **Accepted:** 20 August 2025

Funding: This research was supported by the Natural Sciences and Engineering Research Council of Canada (NSERC) research (Grant no. 7738) to P.L.

Keywords: ecological dynamic regime | ecological trajectories | long-term changes | northern Humboldt Current System | pelagic fish community

ABSTRACT

The northern Humboldt Current System (nHCS) has high environmental variability that impacts key demographic and community-scale processes. Understanding the role and ecological implications of these interannual or long-term events is crucial in describing the dynamics of the nHCS community. Using catch data from pelagic assessment surveys from 1983 to 2019 and the community trajectory analysis framework, we tested and characterised the patterns and compositional dynamics of the nHCS pelagic fish community over space and time. Spatially, changes were evaluated for ecological regions with similar community composition. We found that the community has experienced constant interannual variability consistent with the long-term warm and cold periods previously identified in the system. Two shifts in 1990 and 2001 were identified and associated with a change in the average oceanographic conditions in the system. Coastal fish species dominated the community after 2001, while oceanic and tropical species were more abundant before 1990. We found lower and higher interannual variability for the coastal and oceanic areas, respectively. Moreover, the coastal area reported a higher change in the community structure from 1983 to 2019. Temperature and oxygen were two oceanographic variables significantly associated with the main changes in the community, finding that warmer and less oxygenated years lead to higher diversity. This study helps to understand the magnitude, direction, and mechanisms involved in the long-term changes of the nHCS pelagic fish community.

1 | Introduction

Biological communities are dynamic and constantly evolving, responding to temporary or long-lasting events of biological or anthropogenic origin (Dornelas 2010). These changes can significantly impact system states, community structure and spatial arrangements (Andersen et al. 2009), which can be defined as ecological dynamic regimes (Sánchez-Pinillos et al. 2023, 2024). Most of the large-scale variations in marine communities have been mainly attributed to regime-scale fluctuations of the oceanic conditions (Alheit and Ñiquen 2004; Collie et al. 2008; Mollmann et al. 2015; Beaugrand et al. 2015) or the internal dynamics of the system (Toumi et al. 2023). Fish populations vary on a range of temporal scales from interannual to decadal to millennial (Finney et al. 2010; Salvatteci et al. 2018). This variability can also be accompanied by changes at different scales in the spatial distribution patterns of fish abundance (e.g., Fredston-Hermann et al. (2020); Hastings et al. (2020)).

Moreover, changes in spatial patterns can lead to new environmental forces and interactions among species, influencing the community dynamics (Frank et al. 2007).

In marine communities, ecological dynamic regimes in zooplankton (Hare and Mantua 2000; Beaugrand 2003; Ayón et al. 2011; Aronés et al. 2019), fish (Mantua et al. 1997; Mantua and Hare 2002; Chavez et al. 2003; Kuwae 2017; Salvatteci et al. 2018; Litzow et al. 2020; Siple et al. 2020) and seabirds (Passuni et al. 2018) communities have been primarily associated with climate variability (DeYoung et al. 2004, 2008; Lees et al. 2006), but also with overfishing (Lees et al. 2006; Jiao 2009). One of the most studied shifts in pelagic ecosystems is the overlap fluctuations of sardine (*Sardinops* spp.) and anchovy (*Engraulis* spp.) catches during the last decades, suggesting a fluctuation in the dominance of those species in some coastal areas (Alheit and Ñiquen 2004; Takasuka et al. 2007; Alheit and Bakun 2010; Salvatteci et al. 2018; Siple et al. 2020). Initially, it was hypothesised that the cyclic fluctuations between anchovies and sardines in the Pacific Ocean could happen on a longer time scale (Chavez et al. 2003). However, paleoceanographic studies have argued that there is limited data to support an abundance fluctuation between these species or replacement as key forage species in the Northeast Atlantic and Humboldt ecosystems (Salvatteci et al. 2018; Siple et al. 2020).

Coastal upwelling is a major process that refers to an upper vertical movement of water from deep to shallow areas (Kämpf and Chapman 2016), which produces a high nutrient supply to the surface (Messié and Chavez 2015). Four major upwelling systems are known as Eastern Boundary Upwelling Systems (EBUS): the California and Humboldt systems in the eastern Pacific, and Canary and Benguela in the eastern Atlantic Ocean. For these major upwelling systems, long-lasting patterns of oceanographic variability and their impacts on the ecosystem have been described. For example, the Pacific Decadal Oscillation (PDO) and its relation to Pacific salmon catches in the northeastern Pacific (Mantua et al. 1997; Litzow et al. 2020). In the Benguela System, dynamic regimes have also been identified and associated with top-down and bottom-up processes (Cury and Shannon 2004). In the Humboldt system, Espino (2013) also related changes in jack mackerel (*Trachurus murphyi*) biomass to the PDO, where high and low abundance periods have been associated with the warm and cold phases, respectively.

The Humboldt Current System (HCS) is a dynamic and highly productive upwelling system (Bakun and Broad 2003; Chavez et al. 2003, 2008; Alheit and Ñiquen 2004), which is attributed to the low-latitude location of the HCS and the given susceptibility to interact with extreme interannual ecosystem disturbances (Bakun and Weeks 2008). The HCS also has high fish productivity, supported principally by one species: the Peruvian anchovy (*Engraulis ringens*) (Chavez et al. 2008), which is the target species of the largest monospecific fishery worldwide (FAO 2020). El Niño Southern Oscillation (ENSO) and its warm phase, El Niño (EN), are the leading modes of variability in the HCS (Gutiérrez et al. 2016; Bonino et al. 2019). The EN is an irregular climatic event comprising the Pacific Ocean sea surface temperature anomalies and atmospheric pressure, resulting in changes in the thermocline depth, circulation of ocean currents, and biological productivity (Chavez et al. 2008). On the other hand, La Niña (LN) is the cold phase of the ENSO, increasing the upwelling in the HCS and favouring the habitat of the Peruvian anchovy and other coastal fishes.

Historically, in the HCS, EN events and overfishing have been associated with a dramatic reduction in Peruvian anchovy biomass and, before 1999, an increase in sardine biomass (Muck 1989; Bakun and Broad 2003; Alheit and Ñiquen 2004). Using data from the 1950s to the early 2000s, Chavez et al. (2003) identified dominance shifts between Peruvian anchovy and sardine in 1975 and the late 1990s and named 'El Viejo' to the warm periods when the sardine was dominant and 'La Vieja' to the cold periods when Peruvian anchovy became more important. Large-scale changes in sea surface temperature, food availability, prey size spectra (Chavez et al. 2003; Alheit and Ñiquen 2004) and near-surface oxygen concentrations (Bertrand et al. 2011) have been associated with the fluctuating anchovy and sardine-dominated periods. Aronés et al. (2019) and Ayón et al. (2011) observed two regimes in zooplankton biomass, with higher biomass before 1973 and after 1992, and lower values between 1973 and 1992. Likewise, Alegre et al. (2015) also observed a shift in the diet composition of jack mackerel in the early 1990s, from Engraulidae to mostly euphausiids, zoea larvae and red squat lobster (*Pleuroncodes monodon*).

The northern part of the HCS (nHCS) is an area where climate change and environmental variability are most evident, which may trigger changes in key demographic and community-scale processes. In the nHCS, most long-term studies have focused on fish species with economic value (Ayón et al. 2011; Alegre et al. 2015; Salvatteci et al. 2018; Aronés et al. 2019), but little is known about the compositional dynamics of the pelagic fish community and the processes that trigger their changes in diversity, spatial structure, and species association. In this study, we used a long-term dataset (1983–2019) and community trajectory analysis (CTA) (de Cáceres et al. 2019; Sturbois, de Cáceres, et al. 2021) to investigate the long-term dynamics of the pelagic fish community in the nHCS. We examined the variations of three diversity metrics (alpha, beta and gamma) and the species composition and how they were associated with oceanographic conditions. Due to evidence previously listed of large changes in oceanographic conditions and population dynamics of commercially important pelagic fishes in the nHCS during the 1990s, we expect to find substantial changes in the pelagic community dynamics around the same period, mainly associated with changes in the environment. This study brings new insights into the shifts in the fish community during the last decades and may support fisheries planning and ecosystem-based management, particularly to assess future community shifts under increasing warming, deoxygenation, and acidification due to climate change in upwelling ecosystems.

2 | Materials and Methods

2.1 | Survey Data

We used taxonomic data from the pelagic assessment scientific surveys carried out by the Marine Institute of Peru (IMARPE) from 1983 to 2019. These surveys are usually conducted twice a year during the austral summer and spring, covering the entire area of the Peruvian coast from 3° S to 18° S and up to approximately 100 nautical miles (NM) from the coast (Castillo et al. 2009). The surveys follow a systematic sampling design consisting of parallel and equidistant cross-shore transects of ~100 NM and ~10 to 15 NM inter-transect spacing (Figure S1). The primary objective of these surveys is to collect information on the geographic distribution, abundance, and biological samples of the Peruvian anchovy and other commercial pelagic species to provide management advice to stakeholders (Castillo et al. 2009; IMARPE 2020). To obtain biological information, scientists perform pelagic mid-water trawl samplings (~150 to 200 trawls per survey, Figure S1) at depths between 10 and 100 m approximately, using a fine mesh with a diagonal mesh size of 43 mm. Although the trawl locations cover the entire survey area, they are unevenly distributed, with more trawls typically conducted in coastal areas. Acoustic scientists determine the trawl locations based on data about fish abundance collected by scientific echo sounders. This approach increases the likelihood of effectively representing the species that inhabit the ecosystem. Finally, fishery biologists conduct the taxonomic identification of all species caught in a trawl, recording their weight (kg), body size, and biological information (more information on the survey sampling protocol in Castillo et al. 2009). Throughout the study period, there were years influenced by different phases of the ENSO, including EN and LN events of varying magnitudes, as well as neutral years.

2.2 | Preliminary Processing of Survey Data

For this study, we excluded surveys conducted during spring and only considered the summer surveys (January to April, Table S1) to minimise the bias on the data's seasonal variability. In addition, spring surveys were not conducted for some years and produced many data gaps. The second data filter accounted for variations in survey area coverage by retaining trawl data obtained between 5° S and 16° S and within 0 to 80 NM from the coastline. Figure S2 shows all the trawl samples performed by year during the studied period. Finally, we considered only surveys with evenly distributed sampling trawls across the study area. A total of 32 years met this criterion (Table S1). While mid-water trawls catch various marine species, our study focused only on fish taxa. In addition, we standardised the taxonomic information to ensure that it was homogeneous and comparable for the whole study period (see Appendix S1). This standardisation was necessary because the capability of surveyors to identify organisms up to the species level fluctuated over the years, which might have a significant impact on our results. After standardisation, we were left with 66 different fish taxa (Table S2), which we used for our analyses. We divided the catch per species by a measure of fishing effort (trawling time in minutes) to produce a catch per unit effort (CPUE) per species, which was used as an index of abundance.

2.3 | Identifying Ecological Regions

We investigated temporal community changes in areas with similar ecological dynamics. To do so, we examined the spatial structure of the nHCS pelagic fish community through a space-constrained hierarchical clustering (Guénard and Legendre 2022). This clustering approach considers the (i) information of the dissimilarity matrix computed among sites based on the fish community composition data, and (ii) the constraint through the spatial contiguity among sites (Legendre and Legendre 2012). The spatial contiguity matrix of the sites is represented by a list of link edges constructed through Delaunay triangulation that describes the spatial connections among sites (Guénard and Legendre 2022). This matrix generated the list of link edges used by the clustering function as a constraint during the clustering process. We computed the clustering for all data sets using the *constr.hclust* function from the R package adespatial (Dray et al. 2022). The clustering approach employed was Ward's agglomerative method with the constraint of spatial contiguity. With this approach, we identified 'ecological regions' with similar species composition, which we used for our analyses described further on.

2.4 | Identifying Temporal Patterns

We calculated three types of species diversity: (i) alpha diversity: average number of taxa (i.e., richness) per trawl, (ii) gamma diversity: total number of taxa, and (iii) beta diversity: representing the overall community variability over space (Legendre and de Cáceres 2013). To calculate the beta diversity, we used the beta.div function of the R package *adespatial* (Dray et al. 2022). The three diversity values were calculated annually for the entire study area and by ecological region. We first used Hellinger to transform the species composition data matrix for the beta diversity. Pelagic surveys usually perform more trawls in coastal areas due to a higher presence of the Peruvian anchovy (Moron et al. 2019) (Figure 1). In addition, more trawls per survey were performed after 1995. This uneven sampling effort might affect the interannual comparison of diversity values. To address this issue, we calculated the diversity values following a bootstrap methodology. We randomly selected 54 trawls with replacement and calculated the three diversity indices and then repeated this procedure 500 times. In addition, we performed this procedure by ecological region (a stratified sampling using ecological regions as strata).

A hierarchical cluster analysis was performed to investigate the changes in taxa composition at the annual scale for the entire study area. We used the Hellinger dissimilarity and Ward's Minimum Variance as the clustering method (Legendre and Legendre 2012; Borcard et al. 2018). The Hellinger coefficient avoids giving excessive weight to rare species and emphasises the differences in species composition between years. We applied species fidelity analysis (Borcard et al. 2018) to determine the optimal number of groups (i.e., clusters).

2.5 | Identifying Trajectory Patterns

Community trajectory analysis (CTA) addresses the study of community dynamics through the geometric analysis and comparison of community trajectories in a space defined by the dissimilarity among pairs of community observations (de Cáceres et al. 2019). For this method, it is essential to carefully choose

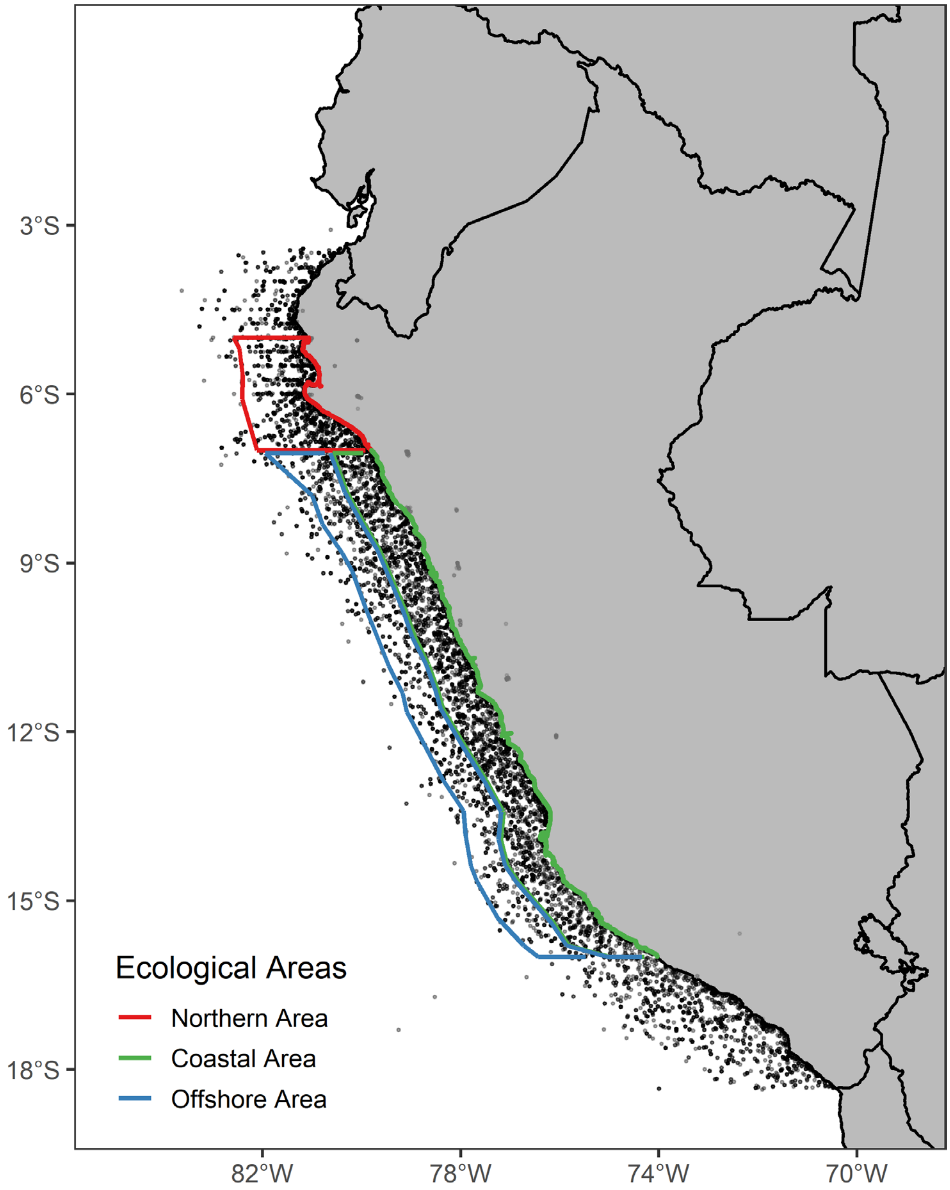

FIGURE 1 | Survey trawl points (black dots) sampled from 1983 to 2019 in the nHCS. Coloured polygons show the three ecological regions: Northern (red), Coastal (green), and Offshore (blue). Only points localised inside the regions were considered in the trajectory analyses.

the dissimilarity coefficient to distinguish gradual from abrupt changes in the compositional dynamics of the community. Using the Hellinger distance coefficient on species abundance, we defined the multivariate space of resemblance between the nHCS pelagic fish community observations. This approach also has the advantage of satisfying the metric and Euclidean properties of the dissimilarity matrix (Legendre and Legendre 2012; Legendre and de Cáceres 2013), which are recommended for this method.

Community trajectories are usually displayed visually using two to three axes of a multivariate ordination (Matthews et al. 2013; Lamothe et al. 2019). We represented the trajectories of fish communities using the first two axes of the ordination of the principal coordinates analysis (PCoA) for the two given scenarios: (i) by year for the entire area, and (ii) by year for each ecological region. Using the entire multivariate space, we applied the CTA framework to describe the overall fish compositional dynamics of the community from 1983 to 2019 and to determine whether the different ecological regions go in similar directions in compositional dynamics.

In particular, we estimated the following CTA metrics: trajectory segment length (distance of the trajectory between two consecutive years); the distance to initial state (DIS—trajectory distance from 1983 to 2019); the total trajectory length (the sum of all the trajectory lengths); and the angle between two consecutive segments (see de Cáceres et al. (2019) and Sturbois, de Cáceres, et al. (2021) for detail statistical information). All these metrics allow describing the resistance and resilience of communities, which can be interpreted as changes in the structure of the community due to the interannual and long-term variability of the nHCS. We additionally computed the overall directionality of the trajectory, which gave us information on the degree to which the community dynamics consistently follow a particular direction in the multivariate space. The directionality (DIR) metric takes values between 0 and 1, where the maximum value means that all trajectory segments follow an entirely directional pathway (de Cáceres et al. 2019). All CTA analyses were performed using the R package *ecotraj* (de Cáceres et al. 2019; Sturbois, Cormy, et al. 2021).

To identify potential abrupt transitions that may suggest community dynamic regimes, we used a breakpoint analysis using the dominant mode of variability of the CTA, characterised by the first axis of the ordination of the PCoA. We used the R package *strucchange* (Zeileis et al. 2024), which implements a sequential algorithm described by Bai and Perron (2003) and is designed to detect the simultaneous estimation of multiple breakpoints in a time series. We used the Bayesian Information Criterion (BIC) to select the optimal number of breakpoints.

2.6 | Environmental Data

Oceanographic information is also collected during scientific pelagic surveys. For our study, we used information on dissolved oxygen (DO, mL/L) and chlorophyll-a concentration (μg/L) from Niskin bottles taken at standard depths (0, 10, 25, 50, 100 m). However, we only consider values from a fixed depth of 0 m (i.e., surface) since some sampling sites did not have information for all depths, which could introduce bias in our analyses. DO is determined on board with the modified Winkler method. For chlorophyll-a, samples are filtered on board and then preserved in a cooler to be analysed in the laboratory. We only considered surveys with oceanographic information representative of the study area (Figure S3). We calculated the median value over sampling sites per survey to obtain a single variable representative of the study area. In addition, we used the El Niño Coastal Index (ICEN) (Takahashi et al. 2014) as a proxy of temperature in the nHCS. The ICEN is calculated from the anomaly of the temperature of the region El Niño 1 + 2 (90° W-80° W, 10° S-0°), acting as a proxy of the sea surface temperature off Peru. The ICEN was available every month during the study period, so we calculated the average monthly values covering each survey (Table S1).

In addition, we identified water masses over space following the classification by Bertrand et al. (2004), which is based on temperature and salinity ranges (Table S3). Since we could not have access to field sea surface temperature (SST) and salinity (SSS) data, we used potential SST and SSS data from the Copernicus—Global Ocean Physics Reanalysis based on the currently available real-time global forecasting CMEMS system, having a 0.083°×0.083° spatial resolution and monthly temporal resolution (from January to April) from 1993. We averaged the monthly SST and SSS values per year and location. Five water masses were identified: (i) Cold coastal water (CCW), (ii) Superficial subtropical water (SSW), (iii) Superficial equatorial water (SEW), (iv) Superficial tropical water (STW), and (v) Uncategorised, which did not fit into the SST and SSS ranges proposed by Bertrand et al. (2004), and probably characterised by a mix of CCW and SSW.

2.7 | Environmental Effects

We used Generalised Additive Models (GAMs) to explore the relationship between the interannual compositional dynamics of the nHCS pelagic fish community and environmental variables (DO, chlorophyll-a, and ICEN).

The first ordination axis of the CTA (PCoA 1) and the diversity values (alpha, beta and gamma diversity) were used as dependent variables for each GAM model, while each environmental variable was treated as an independent variable with a smooth term:

$$g\left[E\left(I_{\mathrm{y}}\right)\right] = \alpha + s\left(V_{\mathrm{y}}\right) + \epsilon_{\mathrm{y}}$$

where g is the identity link function, I_{y} is the community dynamics index in year y and follows a normal distribution. V represents the oceanographic variable, and ϵ is the error term. s is the smooth function (thin plate regression spline) that uses 10 as the dimension of the basis to represent the smooth term. We performed this GAM model for the entire study area and by ecological region. All models were performed using the *mgcv* R package (Wood 2023).

3 | Results

3.1 | Ecological Regions

The space-constrained hierarchical clustering results showed three spatial clusters (ecological regions hereafter). In Figure S4, we observed two principal groups located close to the coast and offshore areas. In addition, a small region in the north is detected. These results agree with the characteristics of the main marine currents in the nHCS (Zuta and Guillén 1970). Based on these identified spatial patterns, we standardised these detected areas by defining the following ecological regions (Figure 1): (i) Northern: from 5° S to 8° S of latitude and 0 to 80 NM distance from the shoreline; (ii) Coastal: covering an area from 8° S to 16° S and within the first 40 NM from the shoreline; and (iii) Offshore: parallel to the coastal region from 40 NM to 80 NM of distance to the coast.

3.2 | Temporal Changes

The time series of bootstrapped mean alpha, gamma and total beta diversity values for the total study area slowly increased from the early 1990s to the 1997–1998 extreme EN event, decreasing after 1999 (Figure 2). From 1983 to 2019, we observed a persistent interannual variability of mean alpha diversity values in most regions, increasing during the extreme and strong EN events and decreasing afterwards. Conversely, we observed lower diversity values during LN events (LN 2010–2011). By ecological region, we observed that the northern area had the largest alpha diversity values. The total beta diversity values for the coastal area were the lowest, meaning a lower variability of taxa among trawls from 1999, but increased after 2014 (Figure 2). For gamma diversity, the temporal series showed a tendency to increase during the first years of the 1990s, fluctuating from an average of 10 taxa to a period with 25 taxa after 1995. This tendency is observed for

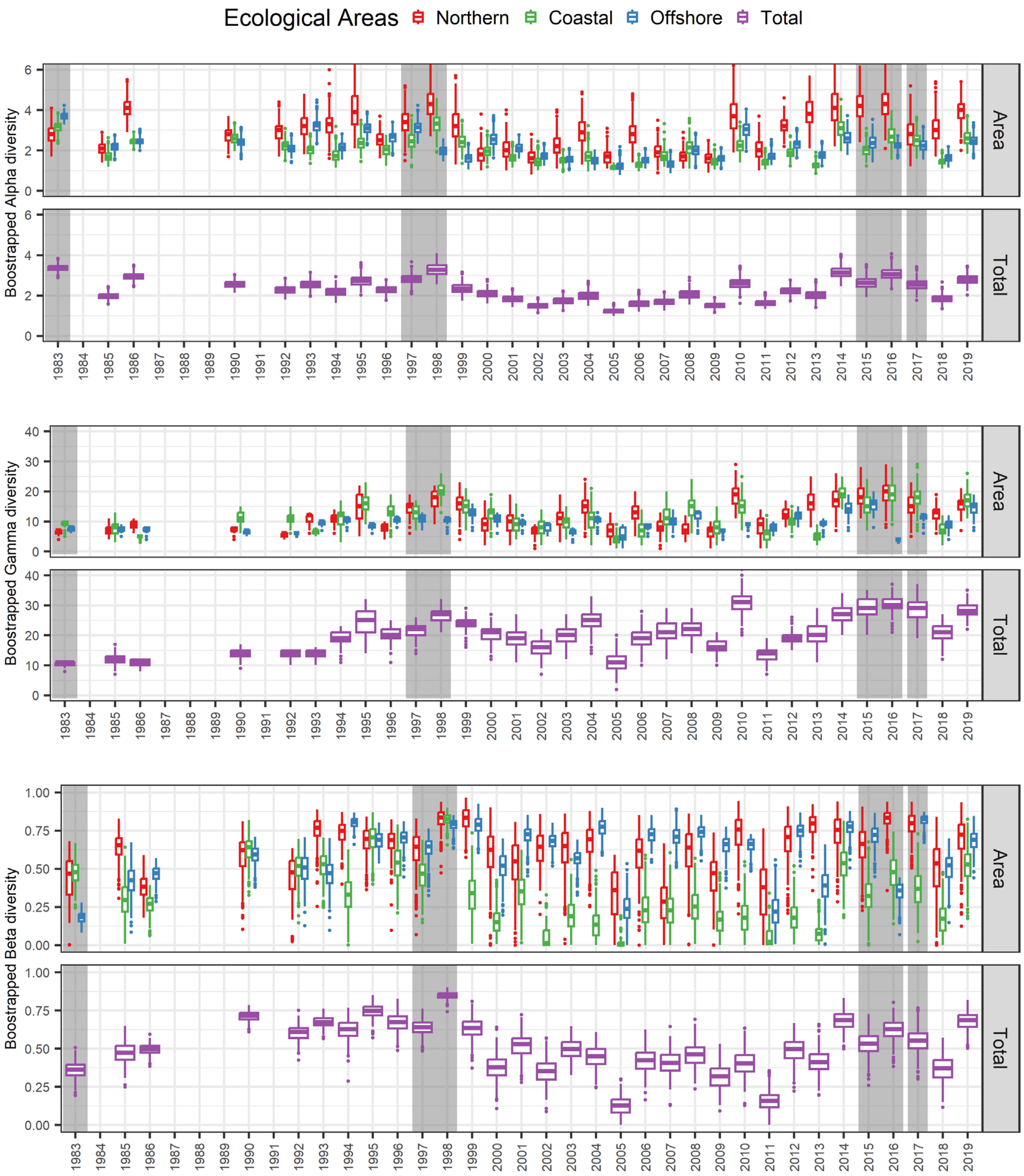

FIGURE 2 | Bootstrapped alpha (top), gamma (centre) and beta (bottom) diversity values for the three ecological regions (top) and the total study area (bottom) from 1983 to 2019. The colours of the ecological regions are based on Figure 1. Grey bars represent the El Niño (EN) events: EN extreme 1983, EN extreme 1997 to 1998, EN strong 2015 to 2016, and Coastal EN 2017.

the whole area and by ecological region, where the northern and coastal regions had the largest values.

The hierarchical cluster analysis identified two main groups (Figures S5 and S6). We observed that the clusters aggregated contiguous years, with high similarity from 1983 to 1986 and 1990 to 2019, where the second period was also divided into two clusters (1990–1998 and 1999–2019). Figure 3 shows the change in taxa abundance between the cluster periods. Species such as the Pacific sardine (*S. sagax*), jack mackerel (*T. murphyi*), Peruvian hake (*M. gayi peruanus*), chub mackerel (*S. japonicus*) and large-tooth flounders (Paralichthyidae) dominated before 1992. In contrast, after 1997, the nHCS was mainly dominated by many coastal species. The Peruvian anchovy (*E. ringens*) was

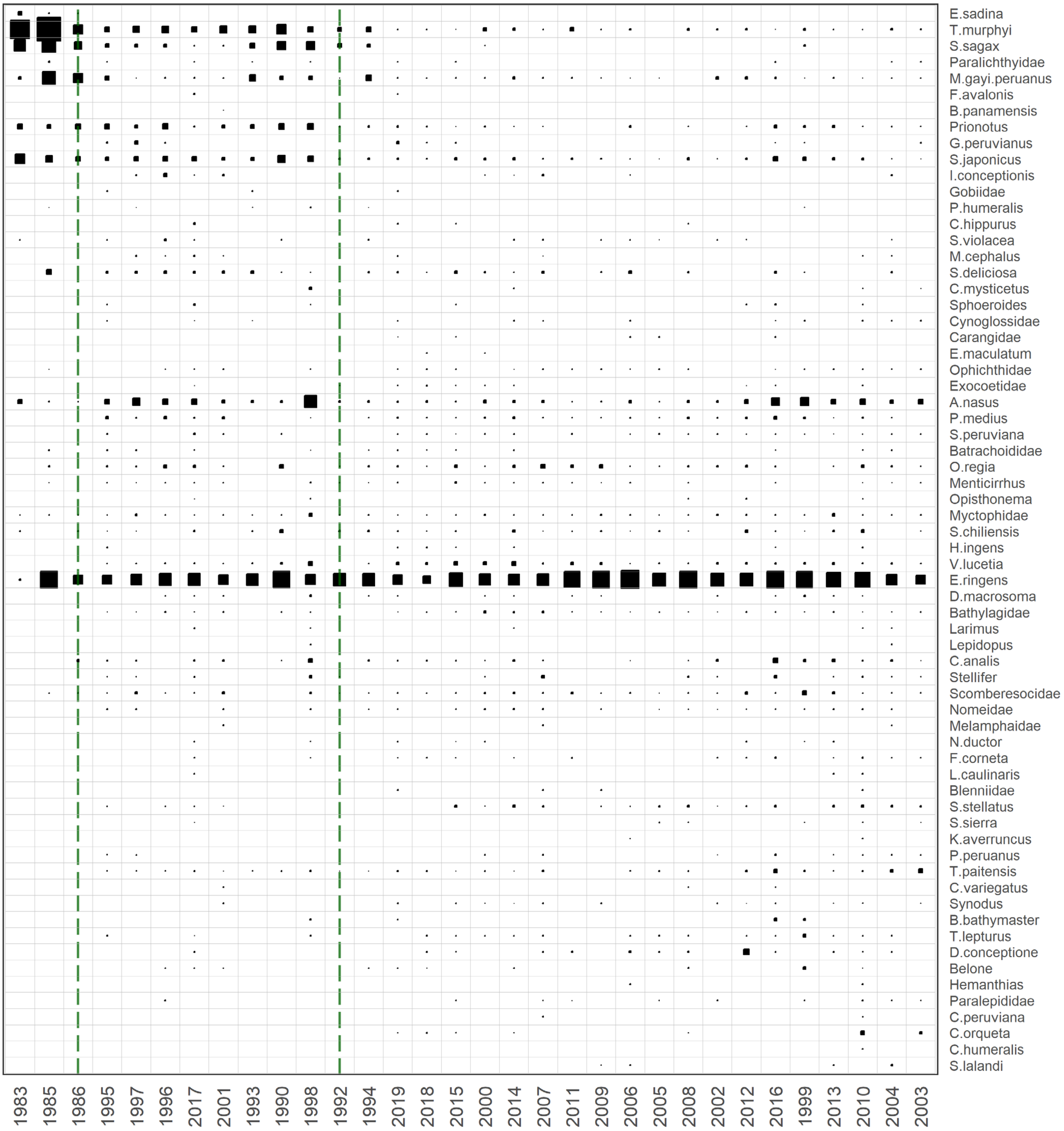

FIGURE 3 | Mean abundance of fish species by year. Fish species and years are ordered after their grouping through hierarchical clustering (Figure S4) which expresses a temporal gradient in the species abundance. The two dashed green lines discriminate the clusters.

present during both periods, but was more abundant during the second cluster period and after 1992.

3.3 | Community Trajectory Patterns

3.3.1 | By Total Area

The PCoA in Figure 4 displays the annual trajectory of the nHCS pelagic fish community, representing 83% of the total variance on the first two axes. The lengths of trajectory segments ranged from 0.05 to 0.79 (distances between adjacent dates in the PCoA plot) and were relatively stable over time ($L = 0.296$, $\mathrm{SE} = 0.032$; total trajectory length = 9.18). The longest segment, depicting a significant change in community composition, is the transition from 1986 to 1990 (considering the time interval of 4 years). From 1997 to 1999, we observed a saltatory and directional movement of the community through the multivariate species-space. These years are associated with quite variable oceanographic conditions in the HCS (Table S1): weak EN in 1994, moderate LN in 1996, and extreme EN in 1997–1998.

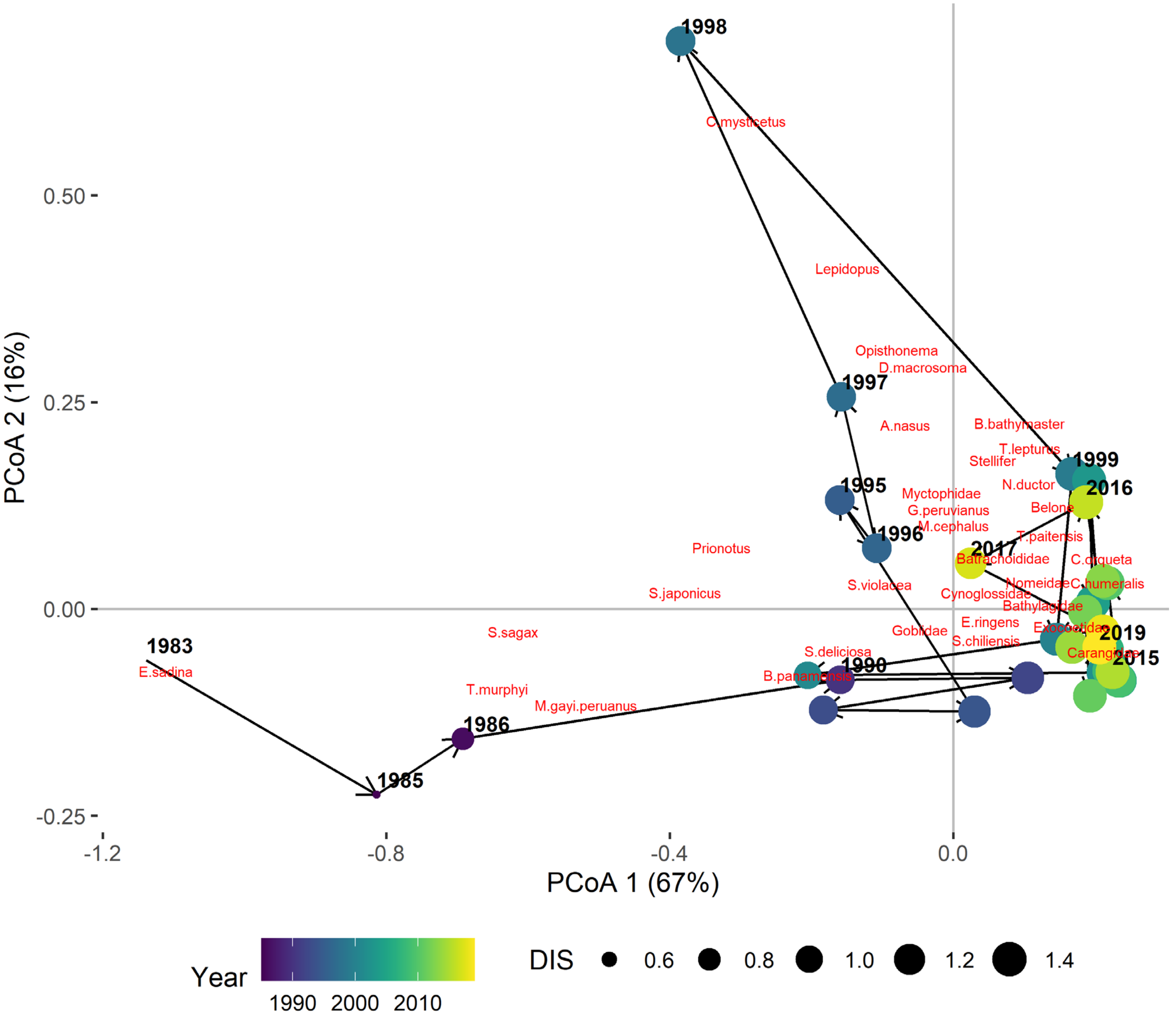

FIGURE 4 | PCoA ordination of the pelagic fish community states of nHCS compositional trajectory along the 33 summer survey years from 1983 to 2019. Point sizes refer to the trajectory distance to the initial state (DIS, distance from a year to the 1983 community composition). Species (names in red) are projected onto the PCoA ordination.

TABLE 1 | Trajectory values. *L* = mean trajectory segment length; angle = mean trajectory angle; DIS = trajectory distance to initial state (1983 to 2019); NCR = mean net change ratio; Traj = total trajectory distance from 1983 to 2019; and DIR = directionality by ecological regions and the whole study area. SE = standard error.

Ecological Area	*L* + SE	Angle + SE	DIS + SE	NCR + SE	Traj	DIR
Northern	0.472 + 0.06	123.824 + 4.81	1.277 + 0.05	0.231 + 0.04	14.637	0.422
Coastal	0.267+ 0.05	117.078 + 5.30	1.328 + 0.02	0.289 + 0.16	8.286	0.387
Offshore	0.769 + 0.08	125.255 + 4.68	1.182 + 0.06	0.142 + 0.03	23.853	0.41
Total	0.296 + 0.03	112.198 + 5.66	1.262 + 0.04	0.306 + 0.04	9.184	0.383

From 1999, the community entered a period of gradual and non-directional variability. Besides, 2001 (LN weak) and 2017 (coastal EN) are years where trajectories move towards the initial state in 1983 (recovering trajectory), both followed by a subsequent year of departure to a different state (departing trajectory). At the end of the trajectory, the distance to the initial state (trajectory length from 1983 to 2019, DIS = 1.385) was higher than the mean value of net change (0.306, SE = 0.04). In addition, the overall directionality value of 0.383 (Table 1 and angle values higher than 90°, Table 1 and Figure S8) showed that

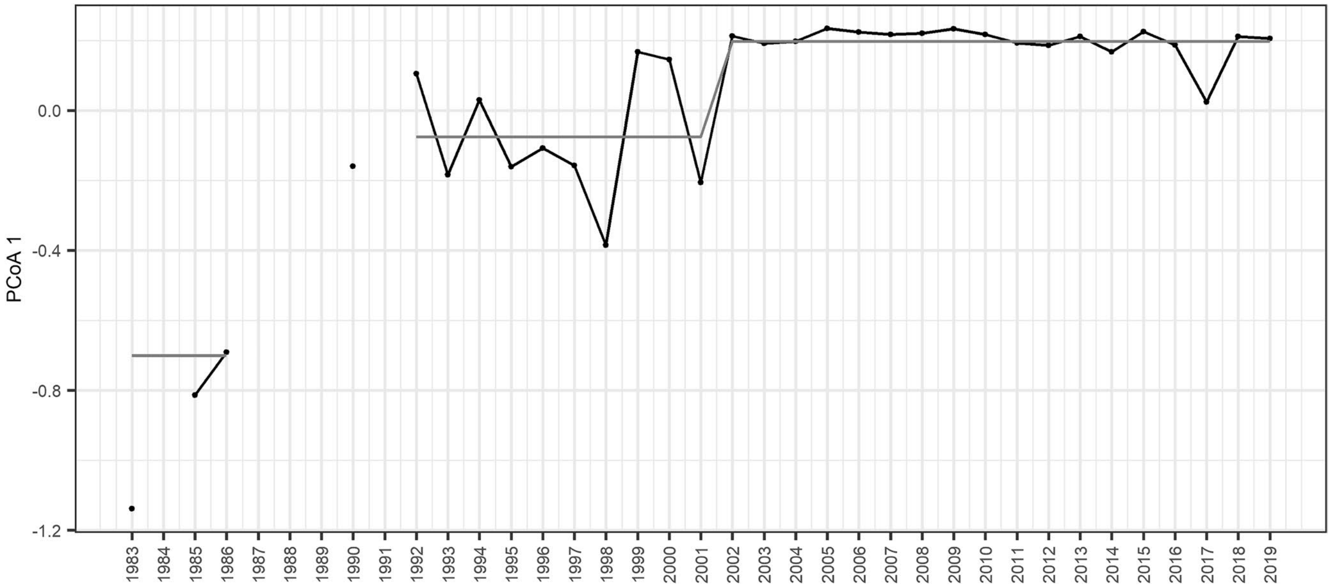

FIGURE 5 | Values by year of the first axis of ordination of the PCoA. Grey lines indicate significant breakpoints detected: the first period from 1983 to 1990, the second from 1992 to 2001, and the third from 2002 to 2019.

the annual trajectories of the total study area rotated on themselves or oscillated around a point of non-directionality.

Considering the first axis of the PCoA (PCoA 1), two significant breakpoints were obtained, corresponding to 1990 and 2001 (Figure 5, Table S4). These results suggest three periods of community change that we define as community dynamic regimes. The first period was from 1983 to 1990, the second from 1992 to 2001, which could be interpreted as a transition period, and the third period was from 2002 to 2019.

3.3.2 | By Ecological Region

Figure 6 and Figure S7 showed the ordination of the compositional states of the three different ecological regions, where the first two axes of the PCoA represented 69% of the total variance. All regions' trajectories occupied similar positions on the ordination, describing a change from 1995 to another community state of close and constant variability.

The mean trajectory segment length and total trajectory length in the coastal region (Table 1) were shorter than the other two ecological regions, meaning that the community fish composition in the coastal region was more similar and less variable from year to year (also observed with the alpha and total beta diversity values (Figure 2)). The offshore region had the highest total trajectory length (23.853) but the lowest mean net change (0.142, SE = 0.03) and the lowest distance to the initial state (DIS = 1.182, SE = 0.06). For the offshore region, the community dynamics generated longer interannual trajectory distances (length values), principally from 2007 to 2010 and 2016 to 2019 (Figure 7). The angles of the community trajectories by region had values higher than 90° (Figure S8), with mean values: (i) northern: 123.83° (SE = 4.81); (ii) coastal: 117.08° (SE = 5.31); and (iii) offshore: 125.26° (SE = 4.68) (Table 1). Directionality was very similar between regions, with values of 0.42, 0.39 and 0.41 for the northern, coastal and offshore regions, respectively (Table 1).

3.4 | Environmental Effect

When exploring the relationship between community features (i.e., PCoA 1, alpha, gamma and beta diversity values) and environmental variables for the total area, the GAM model suggests that dissolved oxygen (DO) had a positive relationship with PCoA 1 (Figure 8, first row), although highly influenced by EN events in 1983 and 1998. In addition, DO also had a negative relationship with alpha and beta diversity. On the other hand, we did not find a clear relationship between chlorophyll-a and any community variable; however, there is some indication of a weak negative relationship with gamma diversity (Figure 8, second row). We only found a significant positive relationship between ICEN and alpha diversity (Figure 8, third row).

For the northern ecological region, the GAM models showed a significant positive relationship between DO and PCoA 1, and a dome-shaped relationship between ICEN and PCoA 1 (Figure S9, first column), although highly influenced by EN 1983. Like the northern region, the relationship between PCoA 1 and DO was also positive in the coastal region, and the relationship between PCoA 1 and ICEN was dome-shaped and highly influenced by EN 1983 (Figure S10, first column). In addition, the ICEN had a significant positive relationship with the three diversity indices in the coastal region (Figure S10, last row). Finally, for the offshore area, PCoA 1 had a positive and negative relationship with DO and ICEN, respectively (Figure S11).

The spatial distribution of the water mass categories showed that the SSW (surface subtropical waters) dominated the system before 1999 (Figure S12). After 1999, we detected an extension of

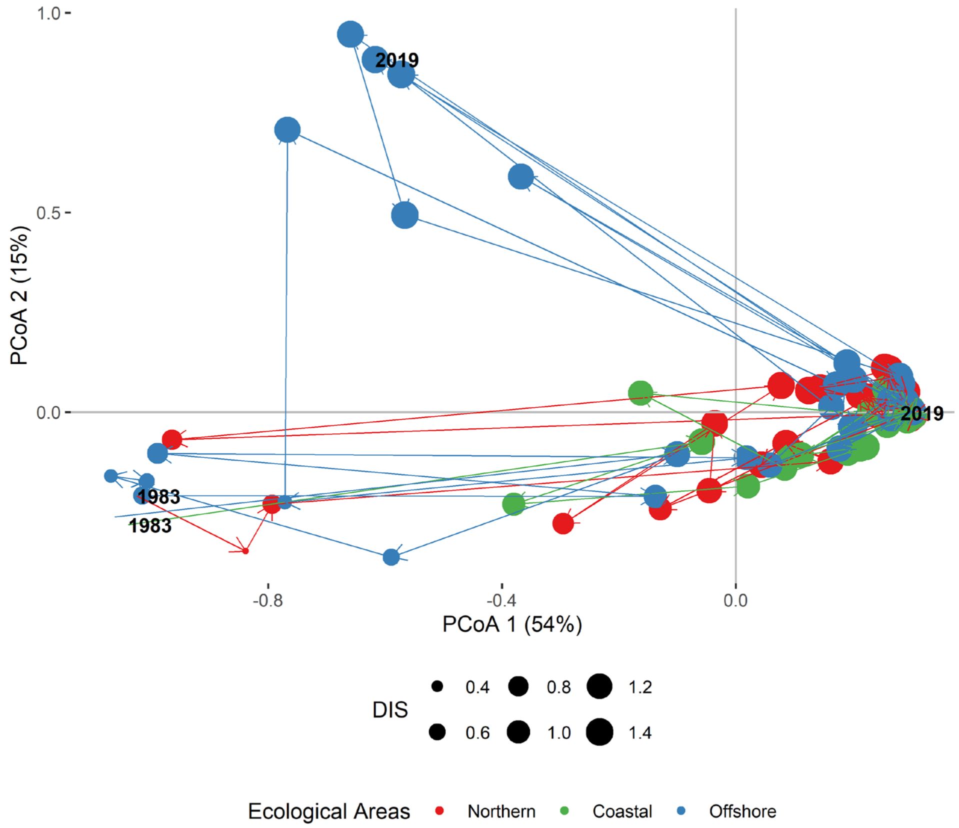

FIGURE 6 | PCoA ordination of the compositional states of the three ecological regions, with trajectories indicated by arrows. Each region is in a different color (following Figure 1): (a) Northern (red), (b) Coastal (green), and (c) Offshore (blue). Point sizes refer to the trajectory distance to the initial state (DIS, distance from a year to the 1983 community composition).

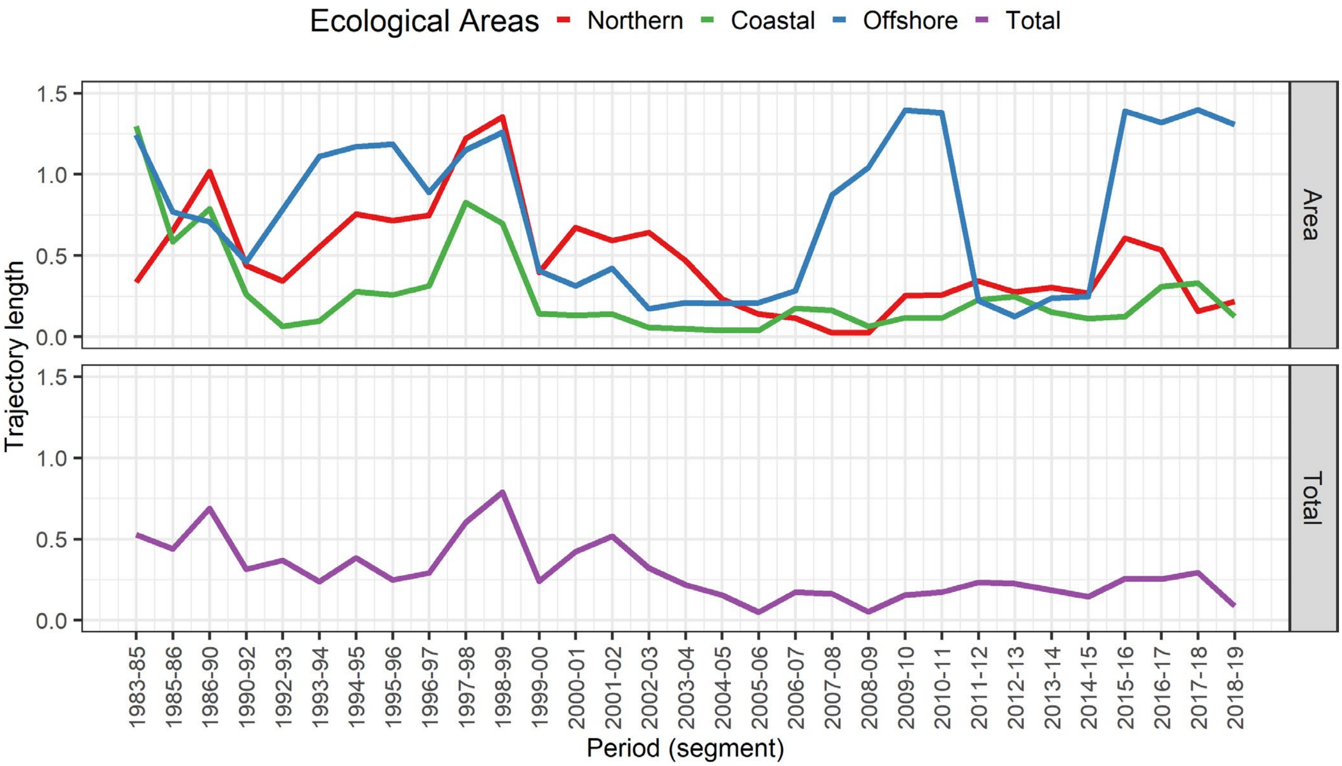

FIGURE 7 | Trajectory segment lengths of the nHCS pelagic fish community observed in the three ecological regions and total area from 1983 to 2019. Each region is in a different colour (following Figure 1).

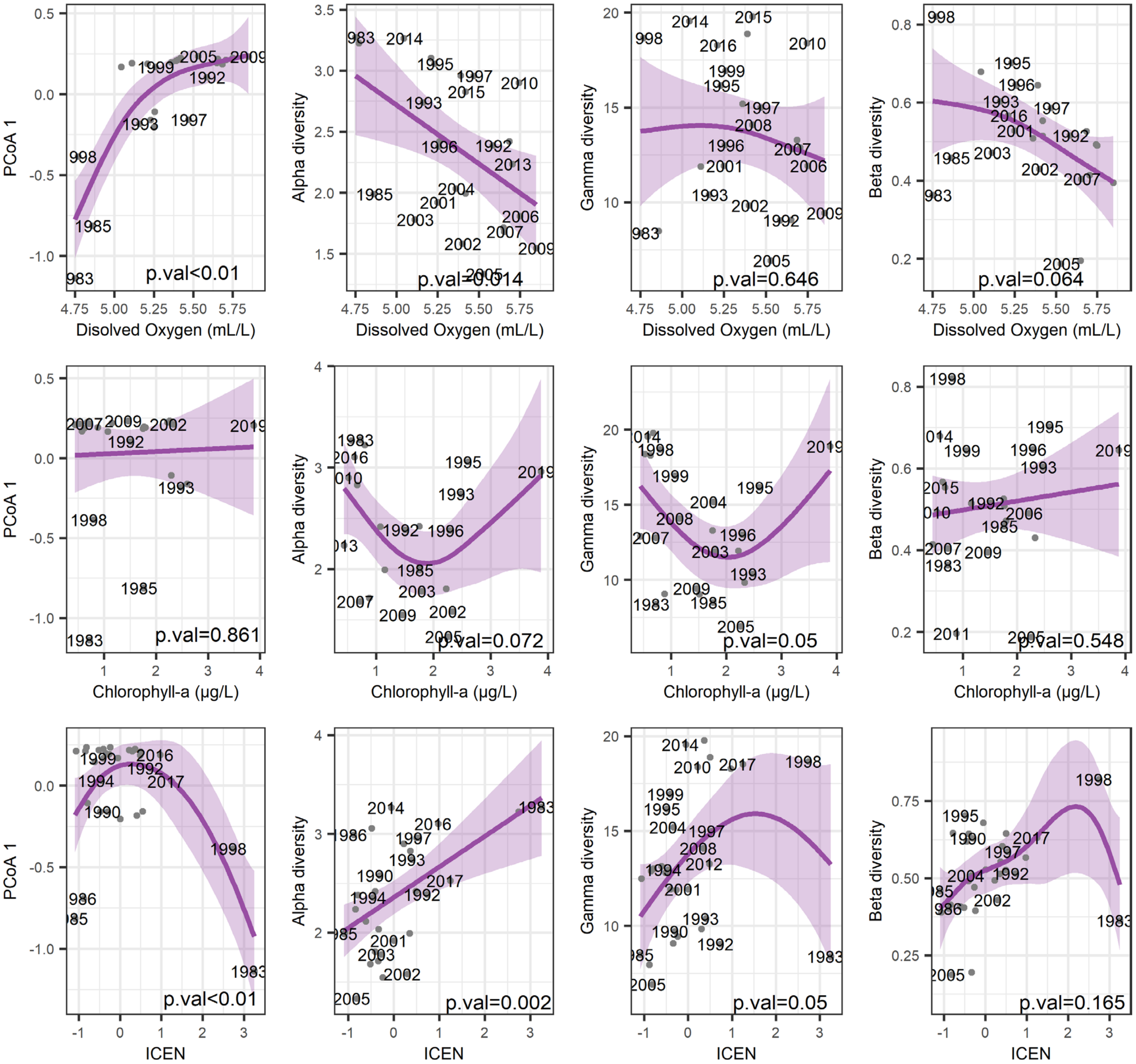

FIGURE 8 | GAM results for the effects of environmental covariates (dissolved oxygen, chlorophyll-a concentration, and ICEN as a proxy of temperature) on the analysed community features: PCoA1, alpha diversity, gamma diversity, and beta diversity.

SEW (superficial equatorial waters) in several years north of 8° S and compression to the south of SSW. In addition, in 1998 and 2017, we noticed a larger extension of the STW (superficial tropical waters) in northern areas. CCW (cold coastal waters) were restricted to small coastal zones in southern areas and became more frequent after 1998. Unclassified water masses were more predominant south of 8° S with a large extension and were characterised by SST ranges of 22°C to 24°C and SSS of 34.8 to 35.1 (Figures S13 and S14, Table S3).

4 | Discussion

In this study, we used a long-term dataset and CTA to investigate the ecological dynamics of the nHCS pelagic fish community. This analysis showed high interannual variability in the community, with increased alpha, gamma and beta diversity values from 1990 to 1998, a period with lower diversity values from 1999, and a slight increase from 2014. The cluster and breakpoints analyses suggest three principal periods with similar species composition: the first from 1983 to 1990, the second from 1992 to 2001, and the third from 2002 to 2019. Subtropical species such as Pacific sardine, jack mackerel and chub mackerel dominated the system from 1983 to 1990 and from 1992 to 1998. In contrast, after 2000, the nHCS was mainly dominated by coastal fishes. The CTA results by ecological region show habitat-dependent community dynamics; however, they follow a similar temporal sequence to the total area, highlighting the system's constant non-directional variability, principally from 2002 to 2019. Temperature and oxygen were related to some community features, suggesting an essential role in regulating the compositional dynamics of the pelagic fish community.

Water masses in the nHCS change spatially in location and extent over time (Swartzman et al. 2008), leading to changes in oceanographic conditions such as nutrient accumulation, primary production, prey availability (Aronés et al. 2019) and fish distribution (Bertrand et al. 2004; Gutiérrez et al. 2007). In our results, we found that the dominance and identity of fish taxa changed over the years, which can be related to the variation of the spatial extent of favourable habitats, also changing the spatial distribution of fishes (Bertrand et al. 2004), leading to migration to other areas during environmentally mediated alterations (Gutiérrez et al. 2007). For example, during EN events, oceanic species tend to move closer to the coast while tropical species move to the southern regions (Ñiquen and Bouchon 2004), producing an increase in the number of species inhabiting the nHCS and explaining the higher alpha and gamma diversity values observed during EN events in our results.

Before 2000, oceanic water (SSW) predominated in the nHCS and jack mackerel, and sardines were more abundant. During this period, the system was warmer, less productive and more oxygenated, favouring small phytoplankton and zooplankton, which supported species like sardine (Bertrand et al. 2011) and possibly both jack and chub mackerel (Alegre et al. 2015). A reorganisation of the system occurred after the EN extreme 1997–98, with an intrusion of tropical waters into the northern region and extension of mixed waters over the study area that coincided with the highest beta diversity value in 1998. In the following years, the extension of CCW and mixed water masses led to a gradual decrease in alpha and beta diversity values. After 1999, the oceanographic characteristics in the nHCS established that small pelagic and coastal fish species such as anchovy, longnose anchovy and Myctophidae became dominant species and distributed evenly along the nHCS. After 2014, we noted an increase in diversity values, which can be attributed to the high variability in the system caused by the increase in temperature (Figure S13) with the recurrent El Niño events from 2015 to 2018 (ENFEN 2024).

For the entire study area, our breakpoint analysis suggests three periods with contrasting fish composition that we define as community dynamic regimes: (i) 1983 to 1990, (ii) 1992 to 2001, and (iii) 2002 to 2019. The presence of breakpoints indicates sudden shifts in the community, yet it does not clarify the underlying drivers or the type of ecosystem response. However, these patterns of dynamic regimes coincide with the so-studied overlap fluctuations of anchovy and sardine populations (Chavez et al. 2003; Alheit and Ñiquen 2004), as well as other marked changes found in the nHCS, especially in oceanographic conditions and low trophic levels. These ecosystem shifts have been related to changes in the dominance of water masses, oxygen concentration, and phytoplankton and zooplankton composition (Alegre et al. 2015; Aronés et al. 2019). The results presented here provide new evidence of a community dynamic regime in the nHCS in the late 1990s for fishes.

Overfishing may also be a driver of the variability of some fish populations, which might impact the entire community structure. For sardines, the increase in fishing pressure in the late 1990s in the nHCS and the adverse environmental conditions have been associated with this species' drastic decline in abundance (Cárdenas-Quintana et al. 2015), suggesting an important effect of overfishing. For jack mackerel, the decrease in biomass coincided with the removal of larger individuals during a period of high fishing effort in the late 1990s (Gerlotto et al. 2012), which might also suggest an important effect of fishing (Hintzen et al. 2014). Regarding the Peruvian anchovy, there is no evidence of overfishing during the studied period and their fluctuations might be mostly attributed to changes in the environment (Swartzman et al. 2008). However, for other pelagic species with less commercial importance, there is no evidence that the fishery is a crucial driver of their biomass fluctuations. This suggests that factors such as environmental conditions, species interactions and food availability are the main drivers of fish community dynamics.

Without a clear dominance of straight departing or recovering trajectory, community trajectories constantly go to a different state yearly from 1983 to 2019. In fact, the low directionality value for the total area is perhaps due to the constant variability of the system: interannual, long-lasting or extreme environmental changes. It can also imply that changes can be induced by different species groups between periods, supporting our cluster results. From 2002 to 2019, the community indicates overall stability, showing lower and more stable trajectory lengths. However, we observed patterns from 2000 to 2001 and 2016 to 2017: the community had a recovery trajectory and went towards the transition period (1992 to 2001). A weak LN event characterised 2001, and a marine heatwave event (coastal EN) ocurred in 2017. The marine heatwave event was short-lasting (January to May, ENFEN (2024)) and of rapid development, characterised by a higher temperature anomaly but restricted to the coast of northern Peru (Gutiérrez and Bouchon 2021), where an intrusion of tropical water masses was observed. The fishery catches of tropical and oceanic species increased during this coastal EN, suggesting a higher presence, which may have produced a fish community more like the period before 2000.

We spatially divided the nHCS area into three ecological regions of similar fish species composition. The identified spatial structure of these regions is associated with the distribution of water masses in this ecosystem, where upwelled cold coastal waters dominate the 'coastal region', warm equatorial waters dominate the 'northern region', and subtropical oceanic warm masses dominate the 'offshore region'. The coastal region had the lowest CTA metrics (i.e., trajectory segment lengths and total trajectory), describing higher temporal stability from 1983 to 2019 than the other regions. Even though two community shifts were described in the study area, we observed that the offshore region had a different trajectory transition after the EN extreme event of 1997–1998. After 2000, Bertrand et al. (2011) describe a transition of the nHCS system to a period with colder temperatures and increased upwelling and nutrient supply and the development of large plankton and a shallow oxycline, which favoured small pelagic and coastal fishes in the nHCS. This may explain the dominance of coastal fishes after 2000 and the lower presence of tropical and oceanic species in coastal regions. Likewise, the community trajectory of the northern region was similar to the one found for the nHCS, probably due to the expansion of cold coastal waters after 2000 (Swartzman et al. 2008), which may retract tropical water masses to northern regions that are not included in our dataset.

We observed the lowest mean net change (NCR) values in the offshore region, but the mean trajectory length and total trajectory were higher. Low NCR values indicate significant changes in the direction of trajectories between years (correlated with angles > 90°), suggesting that different species groups cause these changes between years. Long trajectories returning to their initial ecological state over extended periods of abrupt changes may indicate resilience in this region. This characteristic was mainly observed from 2002 to 2019, with a significant change during the coastal EN 2017, when the community went towards the transition period (1990–2001). This community transition increased species changes among sites (i.e., beta diversity), followed by a rapid state change towards the cold period in 2018. In addition, these non-directional saltatory changes could occur when systems face multiple short-term and delineated disturbances (Lamothe et al. 2019), as in the nHCS.

The GAMs results show that the compositional dynamic of pelagic fishes (i.e., PCoA 1) is mainly positively correlated to DO in the entire study area and by ecological region. During the third period (2002–2019), the system was also characterised by low alpha diversity values (low number of species locally). During this time, the larger values of near-surface oxygen concentration concord with the dominance of coastal species. The Oxygen Minimum Zone (OMZ), a key parameter in the nHCS (Bertrand et al. 2011), forms vertical and horizontal boundaries for many organisms (Chavez et al. 2008) where significant trophic interactions can take place (Grados et al. 2012). Considering that the interannual variability in oceanographic conditions in the system (e.g., EN events) generates changes in the OMZ with implications for the pelagic system (Montecino and Lange 2009), our results showed that oxygen is one important component in regulating the long-term compositional dynamics of the nHCS pelagic fish community.

The shallow thermocline of the HCS is a key element in plankton development and fish's high productivity. The interannual and multidecadal events also regulate the depth of this thermocline, resulting in dramatic changes in the ecosystem states (Chaigneau et al. 2013). Therefore, temperature may play a key role in modulating the differences in the community compositional dynamics between the coastal and offshore regions observed in our study, supported by the significant relationships between the ICEN and the species composition and diversity indices. This positive relationship between the community features and temperature (ICEN) may be related to seasonal changes, and considering that our study relies on summer surveys, a period characterised by warmer waters and increased productivity due to reduced cloud cover (Echevin et al. 2008). In the total area, the bottom value in the curve of the chlorophyll-a covariate model was characterised by the first years of the 2000s decade, when the system was less diverse. Interannual temperature changes, described by the ICEN, showed higher values at EN extreme events (EN extreme 1983 and 1997–98), which had concordance with the characteristics of the system during these periods.

5 | Caveats

We used long-term taxonomic information collected by scientists from scientific surveys with consistent sampling methodology over several years. Survey data serve as the best source for investigating the dynamics of the fish community, offering temporal and spatial information about changes in this community in the nHCS. Although other long-term data sources could provide information on different aspects of community variations, they are influenced by external factors. Such is the case of catch information from fisheries, which is influenced by gear type, fishermen's behaviour, fishing season and fishing grounds. Data collected from acoustic surveys are also available and provide valuable insights into the spatio-temporal dynamics of certain species. However, available acoustic information is limited to a few specific taxa (Castillo et al. 2009) and lacks the necessary temporal resolution for the objectives showcased in this study.

The environmental variables used in this study are representative of the physical (e.g., temperature and oxygen) and some biological (e.g., phytoplankton) features of the ecosystem. However, zooplankton is another variable to consider in future analyses, since it is the main prey of several fish species analysed in our study. In addition, we only used environmental information representative of the ocean surface, which, in some cases, may not represent the processes occurring in the entire epipelagic zone. For our classification of water masses, we primarily observed areas labelled as uncategorised, which did not align with any definitions of water masses provided by Bertrand et al. (2004), possibly because these regions were characterised by mixed water masses (CCW combined with SSW due to their spatial extent). Additionally, our environmental data source (Copernicus) does not come from field samplings as in Bertrand et al. (2004), which may have caused a discrepancy with the proposed classification.

6 | Conclusions

Our study found that the pelagic fish communities of the nHCS are in constant interannual and long-term dynamics. We identified three principal community regimes: (i) 1983–1990, (ii) 1992–2001 and (iii) 2002–2019, consistent with the long-term warm and cold periods previously identified in this ecosystem. In addition, we observed that the community dynamics and their variability over the years differed by ecological regions. Specifically, we noted that the coastal area had a lower interannual variability in the community structure, whereas the oceanic area showed a higher variability. Furthermore, the coastal area experienced more significant change from 1983 to 2019 than the offshore and northern regions. Temperature and oxygen levels were two oceanographic variables significantly associated with the community's primary changes, indicating that warmer and less oxygenated years led to a higher diversity. Understanding the functioning of the nHCS diversity is essential to appropriately manage this highly productive system within an ecosystem-based management framework.

Author Contributions

All authors contributed to the study's conception and design. P.G. contributed to the data standardisation and formal analysis. P.G. wrote the first draft of the manuscript, and all authors commented on previous versions of it. All authors read and approved the final manuscript.

Acknowledgements

We kindly thank the Marine Institute of Peru (IMARPE) for providing the data for this study. We also thank Andrés Chipollini and Miguel Ñiquen, who guided us with the taxonomic standardisation of the community data. This research was supported by the Natural Sciences and Engineering Research Council of Canada (NSERC) research Grant no. 7738 to P. Legendre.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that supports the findings of this study are not openly available. The data are, however, available from the authors upon reasonable request and with the permission of the Marine Institute of Peru (Instituto del Mar del Peru—IMARPE) to Paola Galloso Sanchez.

References

Alegre, A., A. Bertrand, M. Espino, et al. 2015. "Diet Diversity of Jack and Chub Mackerels and Ecosystem Changes in the Northern Humboldt Current System: A Long-Term Study." *Progress in Oceanography* 137: 15. https://doi.org/10.1016/j.pocean.2015.07.010.

Alheit, J., and A. Bakun. 2010. "Population Synchronies Within and Between Ocean Basins: Apparent Teleconnections and Implications as to Physical–Biological Linkage Mechanisms." *Journal of Marine Systems* 79: 267–285. https://doi.org/10.1016/j.jmarsys.2008.11.029.

Alheit, J., and M. Ñiquen. 2004. "Regime Shifts in the Humboldt Current Ecosystem." *Progress in Oceanography* 60, no. 2: 201–222. https://doi.org/10.1016/j.pocean.2004.02.006.

Andersen, T., J. Carstensen, E. Hernández-García, and C. M. Duarte. 2009. "Ecological Thresholds and Regime Shifts: Approaches to Identification." *Trends in Ecology & Evolution* 24, no. 1: 49–57. https://doi.org/10.1016/j.tree.2008.07.014.

Aronés, K., D. Grados, P. Ayón, and A. Bertrand. 2019. "Spatio-Temporal Trends in Zooplankton Biomass in the Northern Humboldt Current System Off Peru From 1961-2012." *Deep Sea Research Part II: Topical Studies in Oceanography* 169: 104656. https://doi.org/10.1016/j.dsr2.2019.104656.

Ayón, P., G. Swartzman, P. Espinoza, and A. Bertrand. 2011. "Long-Term Changes in Zooplankton Size Distribution in the Peruvian Humboldt Current System: Conditions Favouring Sardine or Anchovy." *Marine Ecology Progress Series* 422: 211–222. https://doi.org/10.3354/meps08918.

Bai, J., and P. Perron. 2003. "Computation and Analysis of Multiple Structural Change Models." *Journal of Applied Econometrics* 18: 1–22. https://doi.org/10.1002/jae.659.

Bakun, A., and K. Broad. 2003. "Environmental 'Loopholes' and Fish Population Dynamics: Comparative Pattern Recognition With Focus on El Niño Effects in the Pacific." *Fisheries Oceanography* 12: 458–473.

Bakun, A., and S. J. Weeks. 2008. "The Marine Ecosystem Off Peru: What Are the Secrets of Its Fishery Productivity and What Might Its Future Hold?" *Progress in Oceanography* 79, no. 2: 290–299. https://doi.org/10.1016/j.pocean.2008.10.027.

Beaugrand, G. 2003. "Long-Term Changes in Copepod Abundance and Diversity in the North-East Atlantic in Relation to Fluctuations in the Hydroclimatic Environment." *Fisheries Oceanography* 14: 270–283.

Beaugrand, G., A. Conversi, S. Chiba, et al. 2015. "Synchronous Marine Pelagic Regime Shifts in the Northern Hemisphere." *Philosophical Transactions of the Royal Society, B: Biological Sciences* 370, no. 1659: 20130272. https://doi.org/10.1098/rstb.2013.0272.

Bertrand, A., A. Chaigneau, S. Peraltilla, J. Ledesma, M. Graco, and F. P. Chavez. 2011. "Oxygen: A Fundamental Property Regulating Pelagic Ecosystem Structure in the Coastal Southeastern Tropical Pacific." *PLoS One* 6, no. 12: 8.

Bertrand, A., M. Segura, M. Gutiérrez, and L. Vásquez. 2004. "From Small-Scale Habitat Loopholes to Decadal Cycles: A Habitat-Based Hypothesis Explaining Fluctuation in Pelagic Fish Populations Off Peru." *Fish and Fisheries* 5, no. 4: 296–316. https://doi.org/10.1111/j.1467-2679.2004.00165.x.

Bonino, G., E. Di Lorenzo, S. Masina, and D. Iovino. 2019. "Interannual to Decadal Variability Within and Across the Major Eastern Boundary Upwelling Systems." *Scientific Reports* 9, no. 1: 1–14. https://doi.org/10.1038/s41598-019-56514-8.

Borcard, D., F. Gillet, and P. Legendre. 2018. *Numerical Ecology With R*. 2nd ed. Springer International Publishing: Imprint: Springer.

Cárdenas-Quintana, G., M. Franco-Meléndez, J. Salcedo-Rodríguez, D. Ulloa-Espejo, and J. Pellón-Farfán. 2015. "The Peruvian Sardine, *Sardinops sagax*: Historical Analysis of the Fishery (1978-2005)." *Ciencias Marinas* 41, no. 3: 203–216. https://doi.org/10.7773/cm.v41i3.2466.

Castillo, P. R., S. Peraltilla, A. Aliaga, et al. 2009. "Protocolo Técnico Para la Evaluación Acústica de Las Áreas de Distribucióm y Abundancia de Recursos Pelágicos en el Mar Peruano. Versión 2009." *Instituto Del Mar Del Perú* 36, no. 1–2: 23.

Chaigneau, A., N. Dominguez, G. Eldin, et al. 2013. "Near-Coastal Circulation in the Northern Humboldt Current System From Shipboard ADCP Data." *Journal of Geophysical Research: Oceans* 118, no. 10: 5251–5266. https://doi.org/10.1002/jgrc.20328.

Chavez, F. P., A. Bertrand, R. Guevara-Carrasco, P. Soler, and J. Csirke. 2008. "The Northern Humboldt Current System: Brief History, Present Status and a View Towards the Future." *Progress in Oceanography* 79: 95–105. https://doi.org/10.1016/j.pocean.2008.10.012.

Chavez, F. P., J. Ryan, and S. E. Lluch-Cota. 2003. "From Anchovies to Sardines and Back: Multidecadal Change in the Pacific Ocean." *Science* 299: 2017–2021. https://doi.org/10.1126/science.1075880.

Collie, J. S., A. D. Wood, and H. P. Jeffries. 2008. "Long-Term Shifts in the Species Composition of a Coastal Fish Community." *Canadian Journal of Fisheries and Aquatic Sciences* 65: 1352–1365. https://doi.org/10.1139/F08-048.

Cury, P., and L. Shannon. 2004. "Regime Shifts in Upwelling Ecosystems: Observed Changes and Possible Mechanisms in the Northern and Southern Benguela." *Progress in Oceanography* 60: 223–243. https://doi.org/10.1016/j.pocean.2004.02.007.

de Cáceres, M., L. Coll, P. Legendre, et al. 2019. "Trajectory Analysis in Community Ecology." *Ecological Monographs* 89, no. 2: e01350. https://doi.org/10.1002/ecm.1350.

DeYoung, B., M. Barange, G. Beaugrand, et al. 2008. "Regime Shifts in Marine Ecosystems: Detection, Prediction and Management." *Trends in Ecology & Evolution* 23, no. 7: 402–409. https://doi.org/10.1016/j.tree.2008.03.008.

DeYoung, B., R. Harris, J. Alheit, G. Beaugrand, N. Mantua, and L. Shannon. 2004. "Detecting Regime Shifts in the Ocean: Data Considerations." *Progress in Oceanography* 60: 143–164. https://doi.org/10.1016/j.pocean.2004.02.017.

Dornelas, M. 2010. "Disturbance and Change in Biodiversity." *Philosophical Transactions of the Royal Society, B: Biological Sciences* 365: 3719–3727. https://doi.org/10.1098/rstb.2010.0295.

Dray, S., D. Bauman, G. Blanchet, D. Borcard, S. Clappe, and G. Guénard. 2022. "Package Adespatial." R Package Version: 3–19.

Echevin, V., O. Aumont, J. Ledesma, and G. Flores. 2008. "The Seasonal Cycle of Surface Chlorophyll in the Peruvian Upwelling System: A Modelling Study." *Progress in Oceanography* 79: 167–176. https://doi.org/10.1016/j.pocean.2008.10.026.

ENFEN. 2024. "Eventos El Niño y La Niña Costeros." http://met.igp.gob.pe/variabclim/indices.html.

Espino, M. 2013. "The Jack Mackerel Trachurus Murphyi and the Envvironmental Macro-Scale Variables." *Revista Peruana de Biología* 20, no. 1: 9–20.

FAO. 2020. "FAO Fisheries and Aquaculture - Fishery Statistical Collections - Global Capture Production." In FAO Fisheries and Aquaculture Division [Online]. Rome.

Finney, B. P., J. Alheit, K.-C. Emeis, D. B. Field, D. Gutiérrez, and U. Struck. 2010. "Paleoecological Studies on Variability in Marine Fish Populations: A Long-Term Perspective on the Impacts of Climatic Change on Marine Ecosystems." *Journal of Marine Systems* 79: 316–326. https://doi.org/10.1016/j.jmarsys.2008.12.010.

Frank, K. T., B. Petrie, and N. L. Shackell. 2007. "The Ups and Downs of Trophic Control in Continental Shelf Ecosystems." *Trends in Ecology & Evolution* 22, no. 5: 236–242. https://doi.org/10.1016/j.tree.2007.03.002.

Fredston-Hermann, A., R. Selden, M. Pinsky, S. D. Gaines, and B. S. Halpern. 2020. "Cold Range Edges of Marine Fishes Track Climate Change Better Than Warm Edges." *Global Change Biology* 26: 2908–2922.

Gerlotto, F., M. Gutiérrez, and B. Bertrand. 2012. "Insight on Population Structure of the Chilean Jack Mackerel (*Trachurus murphyi*)." *Aquatic Living Resources* 25: 341–355. https://doi.org/10.1051/alr/2012036.

Grados, D., R. Fablet, M. Ballón, et al. 2012. "Multiscale Characterization of Spatial Relationships Among Oxycline Depth, Macrozooplankton, and Forage Fish Off Peru Using Geostatistics, Principal Coordinates of Neighbour Matrices (PCNMs), and Wavelets." *Canadian Journal of Fisheries and Aquatic Sciences* 69: 740–754. https://doi.org/10.1139/F2012-017.

Guénard, G., and P. Legendre. 2022. "Hierarchical Clustering With Contiguity Constraint in R." *Journal of Statistical Software* 103, no. 7: 1–26. https://doi.org/10.18637/jss.v103.i07.

Gutiérrez, D., M. Akester, and L. Naranjo. 2016. "Productivity and Sustainable Management of the Humboldt Current Large Marine Ecosystem Under Climate Change." *Environmental Development* 17: 126–144. https://doi.org/10.1016/j.envdev.2015.11.004.

Gutiérrez, D., and M. Bouchon. 2021. "The 2017 Coastal El Niño and Its Impacts on the Marine Ecosystem." *Boletin Instituto del Mar del Perú* 36, no. 2: 313–328. https://doi.org/10.53554/boletin.v36i2.340.

Gutiérrez, M., G. Swartzman, A. Bertrand, and S. Bertrand. 2007. "Anchovy (*Engraulis ringens*) and Sardine (*Sardinops sagax*) Spatial Dynamics and Aggregation Patterns in the Humboldt Current Ecosystem, Peru, From 1983–2003." *Fisheries Oceanography* 16, no. 2: 155–168. https://doi.org/10.1111/j.1365-2419.2006.00422.x.

Hare, S. R., and N. J. Mantua. 2000. "Empirical Evidence for North Pacific Regime Shifts in 1977 and 1989." *Progress in Oceanography* 47: 103–145.

Hastings, R. A., L. A. Rutterfors, J. J. Freer, R. A. Collins, S. D. Simpson, and M. J. Genner. 2020. "Climate Change Drives Poleward Increases and Equatorward Declines in Marine Species." *Current Biology* 30: 1572–1577.

Hintzen, N. T., A. Corten, F. Gerlotto, et al. 2014. "Hydrography and Jack Mackerel Stock in the South Pacific – Final Report." IMARES.

IMARPE. 2020. "Elaboración de la Tabla de Decisión Para la Determinación del Límite Máximo de Captura Total Permisible por Temporada de Pesca en la Pesquería del Stock Norte-Centro de la Anchoveta Peruana."

Jiao, Y. 2009. "Regime Shift in Marine Ecosystems and Implications for Fisheries Management, a Review." *Reviews in Fish Biology and Fisheries* 19: 177–191. https://doi.org/10.1007/s11160-008-9096-8.

Kämpf, J., and P. Chapman. 2016. *Upwelling Systems of the World*. Springer Berlin Heidelberg.

Kuwae, M. 2017. "Multidecadal, Centennial, and Millennial Variability in Sardine and Anchovy Abundances in the Western North Pacific and Climate–Fish Linkages During the Late Holocene." *Progress in Oceanography* 159: 86–98.

Lamothe, K. A., K. M. Somers, and D. A. Jackson. 2019. "Linking the Ball-and-Cup Analogy and Ordination Trajectories to Describe Ecosystem Stability, Resistance, and Resilience." *Ecosphere* 10, no. 3: e02629. https://doi.org/10.1002/ecs2.2629.

Lees, K., S. Pitois, C. Scott, C. Frid, and S. Mackinson. 2006. "Characterizing Regime Shifts in the Marine Environment." *Fish and Fisheries* 7: 104–127.

Legendre, P., and M. de Cáceres. 2013. "Beta Diversity as the Variance of Community Data: Dissimilarity Coefficients and Partitioning." *Ecology Letters* 16: 13.

Legendre, P., and L. Legendre. 2012. *Numerical Ecology*. 3rd ed. Elsevier.

Litzow, M. A., M. J. Malick, N. A. Bond, C. J. Cunningham, J. L. Gosselin, and E. J. Ward. 2020. "Quantifying a Novel Climate Through Changes in PDO-Climate and PDO-Salmon Relationships." *Geophysical Research Letters* 47: 9. https://doi.org/10.1029/2020GL087972.

Mantua, N. J., and S. R. Hare. 2002. "The Pacific Decadal Oscillation." *Journal of Oceanography* 58: 35–44.

Mantua, N. J., S. R. Hare, Y. Zhang, J. M. Wallace, and R. C. Francis. 1997. "A Pacific Interdecadal Climate Oscillation With Impacts on Salmon Production." In *Bulletin of the American Meteorological Society*, vol. 78, 1069–1080. Bulletin of the American Meteorological Society.

Matthews, W. J., E. Marsh-Matthews, R. C. Cashner, and F. Gelwick. 2013. "Disturbance and Trajectory of Change in a Stream Fish Community Over Four Decades." *Oecologia* 173: 955–969. https://doi.org/10.1007/s00442-013-2646-3.

Messié, M., and F. P. Chavez. 2015. "Seasonal Regulation of Primary Production in Eastern Boundary Upwelling Systems." *Progress in Oceanography* 134: 1–18.

Mollmann, C., C. Folke, M. Edwards, and A. Conversi. 2015. "Marine Regime Shifts Around the Globe: Theory, Drivers and Impacts." *Philosophical Transactions of the Royal Society, B: Biological Sciences* 370: 20130260. https://doi.org/10.1098/rstb.2013.0260.

Montecino, V., and C. B. Lange. 2009. "The Humboldt Current System: Ecosystem Components and Processes, Fisheries, and Sediment Studies." *Progress in Oceanography* 83, no. 1: 65–79. https://doi.org/10.1016/j.pocean.2009.07.041.

Moron, G., P. Galloso, D. Gutiérrez, and J. Torrejon-Magallanes. 2019. "Temporal Changes in Mesoscale Aggregations and Spatial Distribution Scenarios of the Peruvian Anchovy (*Engraulis ringens*)." *Deep Sea Research Part II: Topical Studies in Oceanography* 159: 75–83.

Muck, P. 1989. "Major Trends in the Pelagic Ecosystem Off Peru and Their Implications for Management." In *The Peruvian Upwelling Ecosystem: Dynamics and Interactions*, edited by D. Pauly, P. Muck, J. Mendo, and I. Tsukayama, vol. 18, 438. ICLARM Conference Proceeding.

Ñiquen, M., and M. Bouchon. 2004. "Impact of El Niño Events on Pelagic Fisheries in Peruvian Waters." *Deep Sea Research Part II: Topical Studies in Oceanography* 51, no. 6: 563–574. https://doi.org/10.1016/j.dsr2.2004.03.001.

Passuni, G., C. Barbraud, A. Chaigneau, et al. 2018. "Long-Term Changes in the Breeding Seasonality of Peruvian Seabirds and Regime Shifts in the Northern Humboldt Current System." *Marine Ecology Progress Series* 597: 231–242.

Salvatteci, R., D. Field, D. Gutiérrez, et al. 2018. "Multifarious Anchovy and Sardine Regimes in the Humboldt Current System During the Last 150 Years." *Global Change Biology* 24: 1055–1068. https://doi.org/10.1111/gcb.13991.

Sánchez-Pinillos, M., V. Dakos, and S. Kéfi. 2024. "Ecological Dynamic Regimes: A Key Concept for Assessing Ecological Resilience." *Biological Conservation* 289: 110409. https://doi.org/10.1016/j.biocon.2023.110409.

Sánchez-Pinillos, M., S. Kéfi, M. De Cáceres, and V. Dakos. 2023. "Ecological Dynamic Regimes: Identification, Characterization, and Comparison." *Ecological Monographs* 93: e1589. https://doi.org/10.1002/ecm.1589.

Siple, M. C., T. E. Essington, L. A. K. Barnett, and M. D. Scheuerell. 2020. "Limited Evidence for Sardine and Anchovy Asynchrony: Re-Examining an Old Story." *Proceedings of the Royal Society B: Biological Sciences* 287: 20192781. https://doi.org/10.1098/rspb.2019.2781.

Sturbois, A., G. Cormy, G. Schaal, et al. 2021. "Characterizing Spatio-Temporal Changes in Benthic Communities: Taxonomic and Functional Trajectories of Intertidal Assemblages in the Bay of Saint-Brieuc (English Channel)." *Estuarine, Coastal and Shelf Science* 262: 107603. https://doi.org/10.1016/j.ecss.2021.107603.

Sturbois, A., M. de Cáceres, M. Sánchez-Pinillos, et al. 2021. "Extending Community Trajectory Analysis: New Metrics and Representation." *Ecological Modelling* 440: 109400. https://doi.org/10.1016/j.ecolmodel.2020.109400.

Swartzman, G., A. Bertrand, M. Gutiérrez, S. Bertrand, and L. Vasquez. 2008. "The Relationship of Anchovy and Sardine to Water Masses in the Peruvian Humboldt Current System From 1983 to 2005." *Progress in Oceanography* 79, no. 2: 228–237. https://doi.org/10.1016/j.pocean.2008.10.021.

Takahashi, K., K. Mosquera, and J. Reupo. 2014. "El Índice Costero El Niño (ICEN): Historia y Actualización. Boletín Técnico: Generación de Modelos Climáticos Para el Pronóstico de la Ocurrencia del Fenómeno El Niño." *Instituto Geofísico del Perú* 1, no. 2: 8–9.

Takasuka, A., Y. Oozeki, and I. Aoki. 2007. "Optimal Growth Temperature Hypothesis: Why Do Anchovy Flourish and Sardine Collapse or Vice Versa Under the Same Ocean Regime?" *Canadian Journal of Fisheries and Aquatic Sciences* 64: 768–776. https://doi.org/10.1139/F07-052.

Toumi, C., M. D. Cáceres, J. Grall, et al. 2023. "Long-Term Coastal Macrobenthic Community Trajectory Analysis Reveals Habitat-Dependent Stability Patterns." *Ecography* 2023: e06489. https://doi.org/10.1111/ecog.06489.

Wood, S. 2023. "Mgcv: Mixed GAM Computation Vehicle With Automatic Smoothness Estimation."

Zeileis, A., F. Leisch, K. Hornik, and C. Kleiber. 2024. "Strucchange: Testing, Monitoring, and Dating Structural Changes."

Zuta, S., and O. Guillén. 1970. "Oceanografía de Las Aguas Costeras del Perú." *Boletin Instituto Del Mar Del Peru* 2, no. 5: 157–324.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix S1:** maec70048-sup-0001-AppendixS1.docx.