



## RESEARCH ARTICLE OPEN ACCESS

# Composition and Functional Diversity of Juvenile Groundfish Assemblages in the California Current

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## ABSTRACT

**Aim:** Long-term monitoring data at the biogeographic scale are essential for developing baselines of biodiversity patterns and tools to diagnose natural cycles, trends, and anomalous events to assess threats from climate change. However, studies using these data often limit their analyses to relatively few metrics that may not adequately capture the breadth of biodiversity. Here, we calculate a suite of compositional and functional biodiversity metrics—collectively comprising ecoscapes—to better resolve assemblage-level responses to environmental variability and test the spatiotemporal lability of faunal biogeographic provinces.

**Location:** California Current Large Marine Ecosystem (CCLME).

**Taxon:** Young-of-the-year juvenile groundfish assemblages ( $n = 45$  taxa).

**Methods:** Species composition and abundance data from two long-term fisheries-independent surveys were collated with a functional trait database for pelagic taxa. Distinct assemblages were identified through cluster analysis. Compositional and functional alpha- and beta-level biodiversity metrics were then calculated to characterise assemblage-level biodiversity and to identify patterns of regional community composition and turnover in space and time.

**Results:** Ecoscapes revealed the assemblage structure, functional diversity, and turnover of juvenile groundfish from 1990 to 2023. Canonical CCLME biogeographic provinces were mostly supported, but with notable spatiotemporal variation and differences across compositional and functional diversity metrics. Highly productive (unproductive) years were associated with the widespread extent of assemblages characterised by high (low) biodiversity and abundance.

**Main Conclusions:** The differences between patterns of functional and compositional diversity of assemblages highlight the potential of ecoscapes to better resolve biogeographic patterns with promising applications for future studies. Ecoscapes may provide explicit links between biodiversity and ecosystem functioning and services, and additional insights into assemblage responses and resilience to environmental variability that can aid biodiversity monitoring and rapidly disseminate management-relevant information in a changing climate.

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## 1 | Introduction

The productivity and composition of marine ecosystems are undergoing modulation from climate change (Doney et al. 2012). Other persistent anthropogenic impacts on fisheries resources (e.g., overfishing, bycatch, and pollution) can further alter biodiversity patterns and cause unforeseen changes in the resilience and sensitivity of marine ecosystems to climate perturbations (Daskalov et al. 2007; Tittensor et al. 2021). To assess the potential for climate impacts to alter ecosystem states, it is important to disentangle natural variability and human-caused climate change. Attempts to address this challenge can benefit from biodiversity measurements across a broad spectrum of indices with monitoring and predictive tools accounting for their varying dynamics (Villamor and Becerro 2012). Wide-ranging ecosystem-level reference points are critical in light of global change (Morrison et al. 2024) and can be enhanced by incorporating complementary biodiversity metrics that together define ‘ecoscapes’ (i.e., statistically-derived snapshots of compositional and functional diversity) reflecting the processes shaping the structure of ecological assemblages. This is particularly important for species with similar population trends and shared responses to ecosystem and oceanographic variability (Dorn and Zador 2020; Ward et al. 2024). However, to recognise the likelihood for biogeographic shifts in assemblages arising from both natural variability and climate change, biodiversity assessments should extend across spatiotemporal gradients of oceanographic conditions and faunal prevalence (Monaco et al. 2021). This highlights the necessity of long-term monitoring data at the biogeographic scale of large marine ecosystems for developing baselines of biodiversity patterns and tools to diagnose natural cycles, trends, and anomalous events (Lindenmayer et al. 2012; Santora et al. 2017).

The California Current Large Marine Ecosystem (CCLME) is an eastern boundary upwelling system with distinctive oceanographic conditions and faunal assemblages occurring within biogeographic provinces, offering a natural case study to explore biodiversity patterns.

There are three generalizable biogeographic provinces (North, Central and South), each pertaining to seasonal upwelling patterns, and representing a latitudinal gradient of ocean processes arising from sub-Arctic, temperate and sub-tropical influences and interactions (Hickey 1979; Allen et al. 2006; Checkley and Barth 2009; Thompson et al. 2019). The boundaries of these provinces include coastal promontories, which are associated with distinct faunal breaks of marine fish and invertebrate assemblages (Gottsch 2016). In addition, the extent of the continental shelf varies, with extensive shelf habitat north of the Mendocino escarpment (i.e., North region), a generally more narrow but variable shelf in the Central region, and complex bathymetry and circulation patterns pertaining to deep basins south of Point Conception (i.e., South region; Santora et al. 2018). Although seasonal upwelling patterns also vary as a function of latitude, ocean conditions are generally more stable and homogenous in the North (which also has a downwelling winter phase), with the highest seasonal upwelling in the Central region, and near-persistent, lower intensity upwelling in the South (Parrish et al. 1981; Checkley and Barth 2009; Bograd et al. 2009).

Groundfish represent a diverse group of fish taxa with complex life histories that play a critical role in the ecology of benthic and pelagic food webs in the CCLME, and support some of most important commercial fisheries in North America (Miller et al. 2014). This includes Pacific hake (*Merluccius productus*), which is the most abundant groundfish and largest (by volume) fishery in this ecosystem, the highly speciose rockfishes (*Sebastodes* spp.; Love et al. 2002, Hyde and Vetter 2007), and numerous flatfish species whose distributions are associated with regional oceanographic patterns (Keller et al. 2015). While adult groundfish populations generally have strong bathymetric and habitat-type associations (Vetter and Lynn 1997; Allen et al. 2006; Howard et al. 2021), their pelagic juvenile stages are associated with the coupled oceanographic and biological dynamics within the epipelagic layer (i.e., upper 100 m) during a narrow temporal window when annual production of young typically occurs. This window is the focus of this biodiversity assessment.

The abundance of pelagic juvenile (Young-of-the-Year, YOY) groundfish typically peaks in late spring, coinciding with oceanographic conditions favourable to transport and retention, as well as higher levels of primary and secondary productivity (Parrish et al. 1981; Moser and Boehlert 1991). As such, this represents an ideal temporal window for monitoring biodiversity and species recruitment dynamics in the epipelagic realm of the CCLME (Santora, Schroeder, et al. 2021). In addition to representing the potential recruitment, and thus productivity, of groundfish populations, the pulse of YOY abundance represents a critically important contribution to the marine food web, supporting salmonids and other piscivorous fishes, resident and migratory seabirds, and marine mammals. The timing and availability of YOY groundfish is critical to ecosystem phenology and productivity of predator populations (Ainley et al. 1993; Warzybok et al. 2018; Gleiber, Hardy, Roote, et al. 2024), but only for a few months before they settle out within benthic and nearshore habitat such as kelp forests. The cyclical and event-scale variability of groundfish recruitment is associated with large scale transport patterns in the California Current, and the relative contributions of sub-Arctic and sub-tropical source waters (Ralston et al. 2013; Santora et al. 2017; Schroeder et al. 2019). Spatially, observations of YOY groundfish species fall into a few general categories: pelagic YOY rockfish tend to be spatially ubiquitous (Field et al. 2021), though they may concentrate on upwelling fronts and bathymetric features (Ralston et al. 2013). YOY flatfish distribution is variable by species across the shelf and slope (Pearcy et al. 1977; Santora et al. 2017). Other species (e.g., YOY Pacific hake) typically dwell deeper and thus concentrate along the continental slope and within submarine canyons (Sakuma and Ralston 1997; Santora et al. 2012). However, beyond these generalisations, little has been done to describe the species assemblage patterns of pelagic YOY groundfish, attributes of their functional diversity, or whether these complementary biodiversity facets can be leveraged for insights into the potential ecological effects and drivers of biodiversity that go beyond traditional taxonomic diversity metrics (e.g., species richness).

The use of functional traits—broadly defined as any characteristic of an organism affecting its fitness—is one promising avenue to link biodiversity to ecosystem functions (Violle

et al. 2007). Functional trait diversity correlates with ecosystem functionality more than species richness in many systems (Gagic et al. 2015; Lefcheck et al. 2015), and trait-based metrics can be compared across regions and taxa more readily than those based off taxonomy (Violle et al. 2014). Communities expressing diverse functional trait values also tend to display increased productivity and ecological redundancies which can buffer assemblages against environmental changes or other disturbance (Duffy et al. 2016). Traits can also illustrate community-level responses to external drivers through an array of complementary functional diversity metrics that suggest community responses to changes are often distinct from compositional biodiversity metrics (McLean et al. 2019), and are thus becoming more prominent in climate vulnerability assessments and as ecosystem indicators (Beauchard et al. 2017; English et al. 2022).

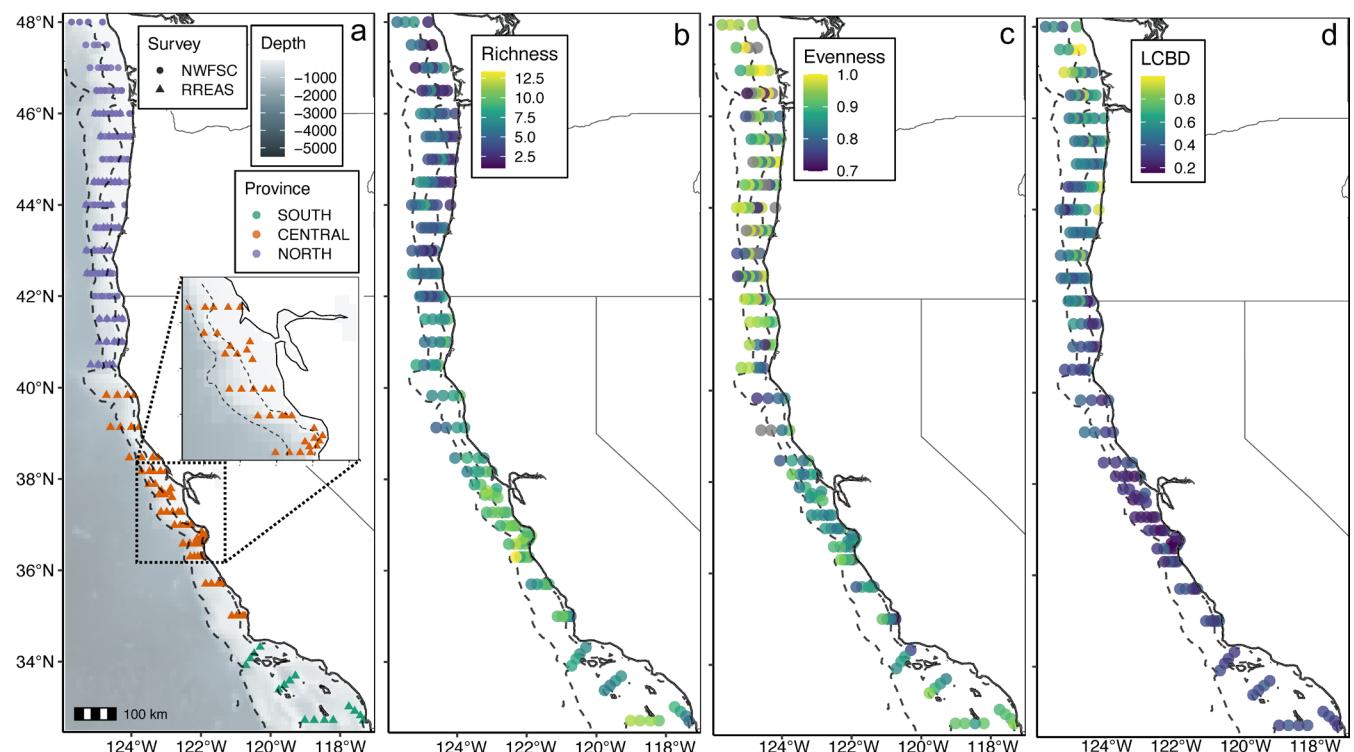
Here, we synthesise YOY groundfish species composition and abundance data from long-term (1990–2023) fisheries-independent surveys covering the entire CCLME and collate them with a newly developed functional trait database for pelagic species (Gleiber, Hardy, Morganson, et al. 2024). This provides the foundation to identify biogeographic patterns of regional community composition and turnover, and to define distinct species assemblages and characterise their ecological significance with a suite of compositional and functional biodiversity metrics. Annual snapshots integrating these metrics comprise ecoscapes that provide the broadest representation to-date of juvenile groundfish biogeography in the CCLME, and quantify assemblage shifts through space and time in accordance with strong pulses of reproductive output.

Specifically, we address three interrelated questions: (1) Do biodiversity metrics of pelagic juvenile groundfish reflect static biogeographic provinces or are they labile due to assemblage variability? (2) Do compositional and functional biodiversity metrics display similar trends and/or cycles through time within biogeographic provinces? (3) How do functional biodiversity metrics and assemblages reflect ecosystem conditions? We then assess our results in the context of climate variability and change, and discuss the potential use of ecoscapes for the identification of biodiversity markers and species assemblages that can be used to facilitate ecosystem monitoring and potentially improve recruitment estimation and ecological forecasting.

## 2 | Methods

### 2.1 | Mid-Water Trawl and Ecosystem Assessment Surveys

We compiled trawl data from two fisheries-independent NOAA surveys that monitor pelagic juvenile or YOY groundfish and other epipelagic microneuston: the Southwest Fisheries Science Center's Rockfish Recruitment and Ecosystem Assessment Survey (RREAS) conducted in California waters, and the Pre-recruit survey conducted by the Northwest Fisheries Science Center off of the coastal waters of Oregon and Washington (Sakuma et al. 2016; Brodeur et al. 2019; Field et al. 2021). The RREAS began in 1983 and has sampled coastal waters annually, with sampling conducted primarily in a 'Core' area of central California between 1983 and 2003 (Figure 1),



**FIGURE 1** | (a) Study area map with survey stations overlain on regional bathymetry. Dashed lines show 200 and 2000 m isobaths. (inset) RREAS core stations sampled in each year from 1990 to 2023. Canonical California Current biogeographic provinces are shown with symbol colour while ecosystem surveys are shown by symbol shape. (b-d) Station climatologies of richness, evenness, and Local Contributions to Beta Diversity (LCBD).

and expanded coverage to most or all California coastal waters from 2004 onward (albeit with some data gaps, and with sparse sampling in 2020, see Field et al. 2021 and Santora, Rogers, et al. 2021). Enumeration of non-rockfish taxa in the RREAS began in 1990 and thus marks the beginning of our study period. The Pre-recruit survey began in 2011, using identical sampling gear and protocols, although this survey experienced data gaps in 2012 and 2020. Both surveys used the same gear, a modified Cobb midwater trawl with a 26-m headrope and fine-mesh liner, fished at 30 m headrope depth using standardised methods, and fished only during hours of darkness due to the ability of YOY rockfish to avoid the net during daylight hours (Ralston et al. 2013; Sakuma et al. 2016; Field et al. 2021). Both survey designs were based on a fixed-station sampling grid that has been modified over time to optimise sampling efficiency. Surveys were conducted in late Spring (late April through mid- to late June) each year. Data from these surveys have been used extensively to inform stock assessments with indices of age-0 abundance (recruitment) and support investigations into fisheries oceanography and recruitment processes, early life history, forage species diversity, and a suite of additional ecosystem studies (Ralston and Howard 1995; Ralston et al. 2015; Santora et al. 2017; Santora, Schroeder, et al. 2021; Field et al. 2021).

Each station sampled within a given year comprised our sampling units (Figure 1); hauls at stations sampled more than once in a given year were averaged in accordance with previous studies using these survey data (Santora et al. 2012, 2017). Raw abundance data were  $\log(\text{CPUE} + 1)$  transformed prior to analyses. We divided the study area into three regions (i.e., South, Central and North; Figure 1) based on previous biogeographic work in the CCLME (e.g., Horn and Allen 1978) to test the spatiotemporal lability of these biogeographic boundaries for YOY groundfish. While these surveys catch a wide range of taxa including coastal pelagic fish and invertebrates (Santora, Schroeder, et al. 2021), our analyses focused on YOY groundfishes, including rockfishes (*Sebastodes* spp.) flatfishes, sculpins, and other groundfishes (e.g., Pacific hake, sablefish; Table S1). Only groundfish taxa present in greater than 1% of samples were retained for community analyses ( $n = 45$ ; Table S1). Most of these taxa were identified to the species level (37 of 45), although some groupings could only be identified to the subgenus or genus level due to challenges associated with species level identification. As previous studies have found that the relative abundance of some pelagic YOY taxa, particularly rockfish, can vary throughout the period in late spring in which the survey data are collected (Ralston et al. 2013), it is possible that temporal shifts in abundance and in sampling times could have a modest impact on some of these results. However, a rigorous evaluation of interannual variability in both assemblage structure and possible shifts in diversity metrics was beyond the scope of this study. Our suite of taxa represents over 77% of total commercial groundfish landings (based on a 2004–2023 baseline), despite covering just 40% (34 of 84) of the actively managed species in the Pacific Fisheries Management Council's Groundfish Fishery Management Plan. If landings of Pacific hake are included—the largest West Coast fishery by volume (but now managed by international treaty rather than the PFMC)—this fraction increases to over 98% of groundfish landings.

## 2.2 | Compositional Biodiversity Metrics

We calculated a suite of biodiversity metrics to summarise the composition of these juvenile groundfish at the assemblage level (Figure S1). These included alpha-diversity metrics: species richness, diversity (Shannon–Weaver Index), and evenness (Pielou's J). As diversity and species richness in these surveys has previously shown to be tightly coupled to CPUE (Santora et al. 2017; Santora, Rogers, et al. 2021), we also calculated a rarefied species richness metric, ES(50), to assess diversity differences between samples while attempting to control for CPUE. ES(50) is an estimation of the mean expected species richness of each haul after sampling 50 individuals in 100 bootstrap replicates. Because this metric requires raw count data, ES(50) was estimated for each haul on raw abundance data and then averaged to the level of our sampling units where stations had been sampled more than once in a year. For hauls with less than 50 individuals caught, this metric is based on extrapolation from a rarefaction curve; to minimise potential errors caused by this, ES(50) was only estimated for hauls with greater than 10 individuals, providing values for ~73% of our samples ( $n = 1437$ ).

Beta diversity indices were also developed to assess spatiotemporal turnover in assemblages. First, Bray–Curtis dissimilarity of species abundances between samples was calculated and subsequently visualised via Non-Metric Multidimensional Scaling (NMDS). The optimal NMDS solution was chosen from 99 iterations. We began with two-dimensional solutions, but increased to three dimensions if stress values were greater than 0.2. Then, we calculated climatological centroids in NMDS space for each province. These centroids represent the average position of all samples in a given region across the study period on each of the NMDS axes. Euclidean distances in NMDS space of each sample from their respective regional climatological centroid were calculated to represent region-specific ecological uniqueness of each sample. Annual centroids were also calculated and their distance to their respective regional climatological centroids were calculated to assess temporal changes within each region. In addition, Bray–Curtis dissimilarity was decomposed into local (LCBD) and species (SCBD) contributions to beta diversity. LCBD represents atypical assemblage composition or ecological uniqueness of each sample, while SCBD represents the degree an individual taxon contributes to assemblage differentiation throughout the study domain (Legendre and Cáceres 2013). Raw LCBD and SCBD scores were rescaled to a 0–1 range to aid interpretability.

Following, we defined compositionally distinct assemblages in our samples and assessed their spatiotemporal variability with hierarchical cluster analysis. Clusters were calculated based on Bray–Curtis dissimilarity using the 'Ward's D' method of agglomeration that minimises variance within clusters (Maechler et al. 2023). The optimal number of clusters within the data was calculated using the *nbclust()* R function, which finds the optimal number of clusters via consensus among 30 indices when varying the number of clusters between 1 and 10 (Charrad et al. 2014). Differences in biodiversity metrics by cluster and region were tested with Analysis of Variance (ANOVA) and Tukey's post hoc tests.

## 2.3 | Functional Diversity Metrics

We collated our data with the Pelagic Species Traits Database (Gleiber, Hardy, Morganson, et al. 2024) to assess the functional diversity of juvenile groundfish assemblages. We extracted species-level, life-stage specific (where available; see Table S2) trait values in four modules: habitat/behaviour, morphology, nutrition, and population status. Taxa that could not be identified to species level were not included in functional trait analyses (Table S1). We chose relevant traits from each module that reflect the contributions of each taxon to the ecosystem: maximum depth, vertical and horizontal habitat use, body shape, maximum total length, known temperature minima and maxima, gregariousness, energy density, and fished status (Table 1). Traits related to vertical and horizontal habitat use were fuzzy coded (*sensu* Chevenet et al. 1994) to reflect the diversity of habitats each taxon inhabits. Rather than coding these traits as categorical and selecting one mean trait value for each taxon, fuzzy coding incorporates intraspecific variation in functional traits by allowing for each taxon to display multiple values for habitat traits if they are found across habitats. Although trait values were extracted for the juvenile life stage only, the Pelagic Species Traits Database incorporates adult trait values for habitat and behaviour traits in cases where published values were unavailable or measurements could not be made on juveniles (see Table S2 and Gleiber, Hardy, Morganson, et al. (2024) for additional trait metadata). Thus, the majority of values for these traits likely represent the adult ontogenetic stage, as habitat limits and behavioural traits are not well-constrained for most juvenile groundfish in the CCLME. However, we consider the data appropriate given that we used these traits to describe the trait diversity of groundfish, rather than using them to explain or predict species- or assemblage-level spatiotemporal variation throughout the CCLME (i.e., response traits *sensu* Suding et al. 2008). In addition, these juvenile taxa eventuate into adults expressing these trait values, fulfilling the functions defined by the trait values presented herein. We did not perform imputation of missing trait data, as all traits except for energy density had >90% representation within our study taxa (Table S2); this trait was only available for ~43% of the focal taxa, but was included in assemblage analyses because values were present for most of the abundant taxa driving community structure in the system (Table S1).

Due to the high dimensionality of our dataset (45 taxa  $\times$  8 traits), we reduced species-level trait values (Table S1) to four dimensions with Principal Coordinates analysis (PCoA). The framework of Maire et al. (2015) was used to select the number of dimensions used in the PCoA based on the deviation between trait-based and functional-space-based distances (Figure S2). For each  $n$ -dimensional solution ( $n =$  to the number of PCoA dimensions), at least  $n+1$  taxa were required in each sample to calculate convex-hull based metrics (i.e., FRic, FEve and FDiv). To assess the sensitivity of selecting the number of axes, we calculated the Mean Absolute Deviation of trait-based versus species based dissimilarities in PCoA solutions ranging from 2 to 6 axes. Sample retention, error minimization, and parsimony were considered when choosing a solution (Magneville et al. 2022). After selecting the number of axes we calculated the loadings of each trait onto PCoA axes using linear regressions (continuous traits) or Kruskal-Wallis tests (categorical traits).

We then calculated species' dissimilarity based on the PCoA 'trait space', using the Gower dissimilarity metric due to the diverse nature of our trait dataset that included continuous, categorical, fuzzy-coded, and binary traits (Table 1). Dissimilarities were used to calculate the three complementary functional diversity metrics of Villéger et al. (2008). Functional richness (FRic) is estimated by calculating the area of the convex hull connecting species in trait space. Functional evenness (FEve) estimates the regularity of species' abundances along the minimum-spanning tree connecting species in trait space. Functional divergence (FDiv) represents the abundance-weighted divergence of species from the center of gravity in trait space. FDiv and FEve thus respectively characterise the regularity and divergence of species' abundances in trait space. In addition, we calculated an Integrated Distinctiveness Index (IntDi), to determine relative functional uniqueness of each taxon (Coulon et al. 2023). This method iterates and averages the Gower dissimilarity calculation over all possible combinations of 4+ traits for a resultant metric less sensitive to trait selection choices, which are inherently subjective and can alter the outcome of functional diversity studies (Beauchard 2023). This species-level metric allowed us to test whether species that are deemed ecologically unique based on their spatiotemporal variance (i.e., high SCBD values) are also functionally distinct (i.e., high IntDi) and vice versa. Pairwise functional dissimilarities between samples were visualised with NMDS, and the suite of NMDS-derived metrics described above for the compositional NMDS were also derived from the functional NMDS (hereafter fNMDS). We provide descriptions of all compositional and functional biodiversity metrics included in the present study in Table 2.

## 2.4 | Statistical Analyses

We created annual regional time-series for each biodiversity metric by calculating the mean and standard deviation of metric values for all samples within each region and year combination (mean  $\pm$  SD:  $30.86 \pm 15.02$  samples). Regional synchrony in biodiversity responses were then assessed by calculating Pearson's correlations between annual means of each metric in each region, with higher values implying shared biodiversity responses between regions. Differences in multivariate assemblage and functional trait structure between regions and clusters were tested with pairwise Permutational Analysis of Variance (PERMANOVA), using the 'adonis2' and 'pairwise.adonis2' function in the 'vegan' package (Oksanen et al. 2022), allowing for overall tests and pairwise partitioning of variance between individual regions and clusters. PERMANOVA tests were run with 999 unrestricted permutations using the above calculated dissimilarities as inputs. Post hoc comparisons  $p$ -values were Bonferroni-corrected for multilevel comparisons. Because PERMANOVA only tests for differences in location in multivariate space, these differences can be caused by differences in group dispersions. Thus, we also calculated permutational distance-based multivariate homogeneity of group dispersions (PERMDISP; 999 permutations) and tested for pairwise differences between groupings with Tukey's Honestly Significant Differences (Tukey's HSD) to aid interpretation of PERMANOVA results. To assess the amount of species richness represented by each region, we also calculated the percentage of the total species list

**TABLE 1** | Biological traits used in functional diversity analyses. Each trait was selected from a ‘Module’ of trait types in Gleiber, Hardy, Morganson, et al. (2024) and justified for use in the present study based on known relevance to groundfish and their relationship to oceanographic variability or ecosystem productivity. Additional trait metadata are available in Tables S1 and S2, and Gleiber, Hardy, Morganson, et al. (2024).

Module	Justification	Trait	Description	Type
Habitat & behaviour	Habitat-behavioural traits impact climate exposure, predator encounter rates and predation success	Max depth	Maximum recorded depth	Continuous
		Vertical habitat	Primary vertical habitat use; demersal, epipelagic, or mesopelagic	Fuzzy
		Horizontal habitat	Primary horizontal habitat use; coastal, continental shelf, continental slope, intertidal, reef-associated	Fuzzy
		Minimum temperature	Lower recorded temperature [°C]	Continuous
		Maximum temperature	Upper recorded temperature [°C]	Continuous
		Gregarious	Aggregation behaviour; solitary, shoaling, schooling	Categorical
		Refuge	Taxon use of reef habitat as refuge	Binary
		Diel migrant	Taxon daily vertical migration habit	Binary
		Seasonal migrant	Taxon seasonal migration habit	Binary
		Body shape	Compressiform, fusiform, depressiform, elongated, eel-like	Categorical
Morphology	Shape influences costs incurred by & success rate of predators; overall size limits consumptive ability (e.g., gape limitation) & mediates interactions with other species	Max length	Maximum length [cm] for the specific lifestage	Continuous
		Energy density	Energy density (kJ) per gram wet weight	Continuous
Nutritional status	Mediates prey selection by predators; reflective of environmental conditions and ecosystem health	Fished	Whether taxon is (1) or is not (0) commercially or recreationally fished	Binary
Population status	Modulates availability and abundance of species, indicative of ecosystem productivity			

(Table S1) represented in each region across all years, and annually on average. Similarly for functional trait diversity, we used the location of samples on the three fNMDS axes to calculate convex hull volumes around all samples, all samples in each region, and samples for each province-year combination, calculating the percentage of the volume occupied by each region in total and annually on average. All data wrangling and analyses were executed using R (v4.3, R Core Team 2023).

### 3 | Results

#### 3.1 | Integrative Ecoscapes of Groundfish Biodiversity

Our analysis included 1975 unique year-station combinations ( $n=3454$  hauls) across the CCLME from 1990 to 2023. Climatological means of richness, evenness, and LCDB depict differences in overall biodiversity patterns between the CCLME biogeographic provinces, with relatively high richness in the South and Central regions—particularly in the central California “Core” area (Figure 1). Evenness and LCBD was higher in the North, where richness was relatively low. Six compositionally distinct assemblages were identified with

hierarchical cluster analysis, with variations in species' abundance distributions and biodiversity metrics displaying the compositional drivers and differences in biodiversity within each assemblage (Figure 2; Figure S3). To aid in the interpretation of the cluster analysis, we provide synoptic descriptions of each assemblage below:

- **Assemblage I—‘Low CPUE/Biodiversity, Hake’** ( $n=375$ ). Driven by high Pacific hake CPUE relative to all other species, with lesser but notable contributions from flatfish taxa and shortbelly rockfish. Low diversity across both compositional and functional metrics.
- **Assemblage II—‘High CPUE/Biodiversity, Common Species’** ( $n=338$ ). Driven by high overall CPUE with high mean abundance of species that are relatively common across the study area: Pacific hake, sanddabs, shortbelly and chilipepper rockfish. High diversity across both compositional and functional metrics, including significantly greater FRic than other assemblages and the second highest mean ES(50) values. However, low LCBD values (Figure 2) and a central position in NMDS space (Figure S4) illustrate the relatively few contributions from rare species in this assemblage.

**TABLE 2** | Biodiversity metrics used to define juvenile groundfish ecoscapes in the present study.

Variable	Short_Name	Type	Level	Description
Species richness	—	Compositional	Community	# of species
CPUE	—	Compositional	Community	$\log(\text{CPUE} + 1)$
Diversity	H'	Compositional	Community	Shannon-Weaver Diversity index
Evenness	J	Compositional	Community	Pielou's Evenness index
Rarefied richness	ES(50)	Compositional	Community	Expected species richness from taxon accumulation curves
Local contributions to beta diversity	LCBD	Compositional	Community	Decomposition of total variance in taxon x abundance matrix by sample
Distance to regional NMDS centroid	CentroidDist	Compositional	Community	Euclidean distance of each sample to regional climatological centroid in NMDS space
Species contributions to beta diversity	SCBD	Compositional	Species	Decomposition of total variance in taxon x abundance matrix by species
Contribution to richness	—	Compositional	Regional	Percent of species represented in each biogeographic region in total and annually
Functional richness	FRic	Functional	Community	Convex-hull volume in functional trait space
Functional evenness	FEve	Functional	Community	Regularity of taxon abundances in trait space
Functional divergence	FDiv	Functional	Community	Divergence of taxon abundances in trait space
Distance to regional fNMDS centroid	fCentroidDist	Functional	Community	Euclidean distance of each sample to regional climatological centroid in trait-based NMDS (fNMDS) space
Integrated distinctiveness Index	IntDi	Functional	Species	Gower dissimilarity integrated from all combinations of 4+ traits
Occupancy of trait space	—	Functional	Regional	Percent of trait space represented in each biogeographic region in total and annually

- **Assemblage III**—‘Low CPUE/Biodiversity’ ( $n=421$ ). This assemblage—the most commonly observed across our time-series—had significantly lower mean CPUE values than all other assemblages. However, ES(50) values for this assemblage were similar to that of Assemblage I. Common species such as sanddabs, shortbelly rockfish, and Pacific hake had the highest mean abundances in this assemblage. However, the relatively high LCBD and FDiv values suggest this assemblage was ecologically unique despite low catches, with rare taxa often present at low abundances.
- **Assemblage IV**—‘Moderate Biodiversity/Low Uniqueness’ ( $n=373$ ). The most abundant species in this assemblage were relatively common across the study area, including sanddabs. This is reflected in the LCBD values, which were significantly lower than all assemblages except Assemblage II (Figure 2). Notably, widow rockfish had the fifth greatest mean abundance in this assemblage but did not rank in the top five in other assemblages, occurring at lower mean abundances.
- **Assemblage V**—‘Low CPUE, Northern species’ ( $n=357$ ). This assemblage had the second lowest mean CPUE and Shannon-Diversity values, which also corresponded with low FRic. However, ES(50) values were not significantly different from Assemblages II and IV which had relatively high CPUE/diversity values. Both compositional and functional evenness were greatest within this assemblage, suggesting a consistent composition in this cluster. This assemblage was typically comprised of taxa that

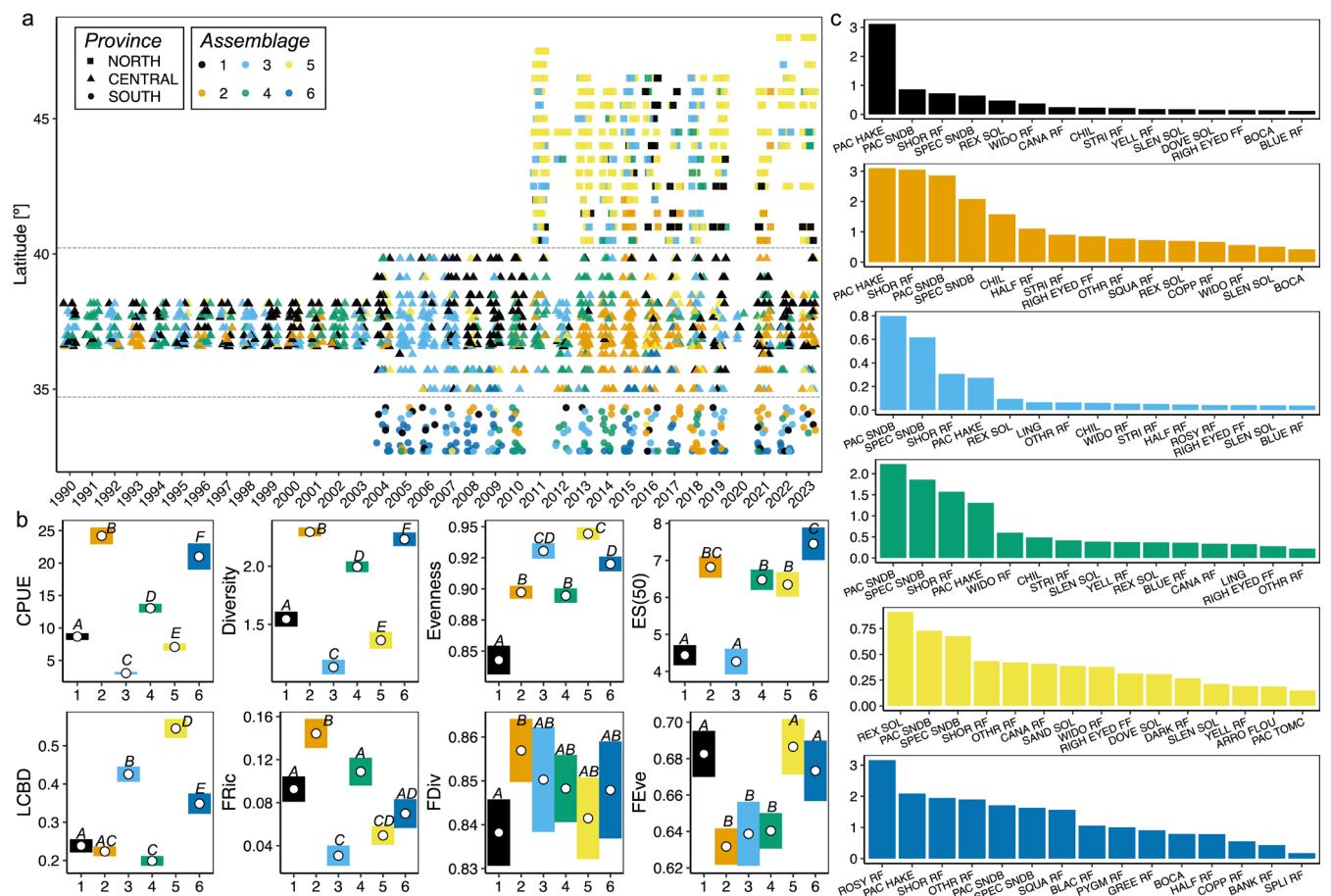
favour the North CCLME. Rex sole had the highest mean CPUE of this assemblage (Figure 2).

- **Assemblage VI**—‘High CPUE/Diversity, Rockfish’ ( $n=111$ ). This assemblage was the least commonly observed assemblage in our time-series, and was predominantly present in the South CCLME (Figure 2). Driven by high mean abundances of the rosy rockfish group and other rockfish taxa, with the second greatest CPUE/Shannon Diversity and the greatest ES(50) values of any assemblage. Rockfish represented three of the five most abundant taxa.

Biogeographic provinces were also supported by a general lack of regional synchrony in most biodiversity metrics found from correlations of annual means across regions (Table 3). However, annual means of FDiv were significantly correlated between the Central and South CCLME ( $p < 0.05$ ). There was some evidence of regional synchrony in CentroidDist covariance between North and Central regions ( $p < 0.1$ ); no metrics displayed regional synchrony between the South and North CCLME (Table 3).

### 3.2 | Compositional Diversity

The compositional variation in CCLME juvenile groundfish was depicted with the optimal NMDS solution (Figure 3a), which displayed assemblage variation in three dimensions (Stress = 0.19; Figure S4) and illustrated significant differences in composition



**FIGURE 2** | (a) Latitudinal distribution of assemblages over time from cluster analyses. Points represent abundance-based [ $\log(\text{CPUE} + 1)$ ] clusters from unique year-station combinations from juvenile groundfish surveys, with hypothesized biogeographic provinces depicted by point shapes and delineated with horizontal dashed lines. (b) Mean compositional (i.e.,  $\log(\text{CPUE} + 1)$ , Shannon Diversity, Evenness, LCBD) & functional (i.e., FRic, FDiv, FEve) biodiversity signatures ( $\pm 2 \text{ SE}$ ) of each cluster with significant groupings determined from Tukey's post hoc tests denoted with letters. (c) The 15 taxa with the highest mean abundance in each cluster.

**TABLE 3** | Contributions of each biogeographic region to total CCLME biodiversity (white) and correlation coefficients for annual mean biodiversity metric values between regions (grey). Contributions to richness represent the percentage of species present within a given region across all years (total) or annually. Occupancy of CCLME trait space represents the percent of trait space (i.e., the volume of a convex hull of all samples) represented by a convex hull around all samples in a given biogeographic province (total) or all samples in a given province-year combination on the three fNMDS axes (Figure 3).

Biogeographic region	Total contribution to richness (%)				Average annual contribution to richness (% $\pm \text{SD}$ )		Total occupancy of trait space (%)			Average annual occupancy of trait space (% $\pm \text{SD}$ )	
	Richness	CPUE	H'	ES(50)	J	CentroidDist	FRic	FEve	FDiv	fCentroidDist	
North		86.96			47.8 $\pm$ 10.7		58.69			19.1 $\pm$ 8.28	
Central		97.83			65.8 $\pm$ 19.9		82.72			41 $\pm$ 18.6	
South		82.61			51.7 $\pm$ 17.3		52.22			38.6 $\pm$ 15.3	
North-Central	0.22	0.22	0.12	0.52*	-0.22	0.54*	0.56*	0.21	-0.31	-0.34	
Central-South	0.09	0.15	0.07	0.13	0.38	0.41*	0.08	0.27	0.49**	-0.14	
South-North	0.09	0.14	0.01	-0.29	-0.24	0.31	0.21	0.48	-0.37	-0.25	

Abbreviations: # spec, species richness; centroid distance, distance to regional climatological NMDS centroid; CPUE, catch per unit effort; ES(50), rarefied richness; fCentroidDist, distance to regional climatological fNMDS centroid; FDiv, Functional Divergence; FRic, Functional Richness; H', Shannon Diversity; J, Pielou's Evenness.

\* $p < 0.1$ .

\*\* $p < 0.05$ .

between the regions (PERMANOVA;  $p < 0.05$ ,  $F_{2,1972} = 81.46$ ) that corresponds to the biogeographic breakpoints at Point Conception and Cape Mendocino. Despite these differences, there was notable overlap between the three regions (Figure 3a), with the greatest differences between the North and South (PERMANOVA;  $p < 0.05$ ,  $F_{1,700} = 82.74$ ). The mix of North- and South-dominant taxa that characterises the Central region (Santora et al. 2017) was evident in the central position of the region in the NMDS space (Figure 3a). Nearly all (~98%) of the examined taxa were present in the Central region at some point in the study period. This region was characterised by high variability; however, with only a portion (~66%) of the species pool represented per year on average (Table 3). Alternatively, the volume of the annual functional trait space of the North was, on average, half that of the Central or South despite containing similar species richness. Thus, while the average station-level FRic is higher in the North than the South, the low turnover between stations caused by the widespread prevalence of flatfish-driven assemblages in the North (Figure 2) leads to a small portion of CCLME-wide functional trait space being represented annually in this region, with approximately half the annual variability as the Central or South (Table 3).

As expected by the nature of agglomerative clustering, significant differences were also found between assemblage clusters (PERMANOVA,  $p < 0.05$ ,  $F_{5,1969} = 127.37$ ) and their multivariate dispersions from PERMDISP (Tukey's HSD,  $p < 0.05$ ; exception: pairs I-II and II-IV; Table S3). As group dispersions can contribute to the differences found by PERMANOVA, these results should be interpreted with caution; effect sizes (Table S3) should be used to discern the relative magnitude of group differences.

We also observed regional differences in climatological means and annual dynamics of biodiversity metrics (Figure S5). Climatological means of CPUE, richness, and diversity ( $H$ ) were all significantly lower in the North CCLME, although the regional means of rarefied richness [ES(50)] were similar. Climatological means of evenness were similar in all three regions, with notable departures occurring in the Central region in low-CPUE years (e.g., 2006, 2019; Figure S5). The only long-term linear trend found in annual means of compositional biodiversity metric was an increasing distance of assemblages from their climatological centroid (CentroidDist) in the Central CCLME (Linear Regression,  $p = 0.02$ , adj- $R^2 = 0.14$ ; Figure 3a). Even during well-documented coastwide events that led to depauperate (e.g., 2005) and diverse (e.g., 2015 and 16) years for YOY groundfish biodiversity (Santora et al. 2017), assemblage distributions were not uniform across metrics or regions. Assemblage VI, which was dominated by rockfish taxa and most prevalent in the South, emerged in the Central region in 2009 and was more pronounced in 2015–2017. Assemblage II, typically found in the South and Central CCLME, reached near ubiquity in the Central region and was relatively prevalent in the North during this same period, but was never observed in the North in consecutive years before or since (Figures S5 and S6).

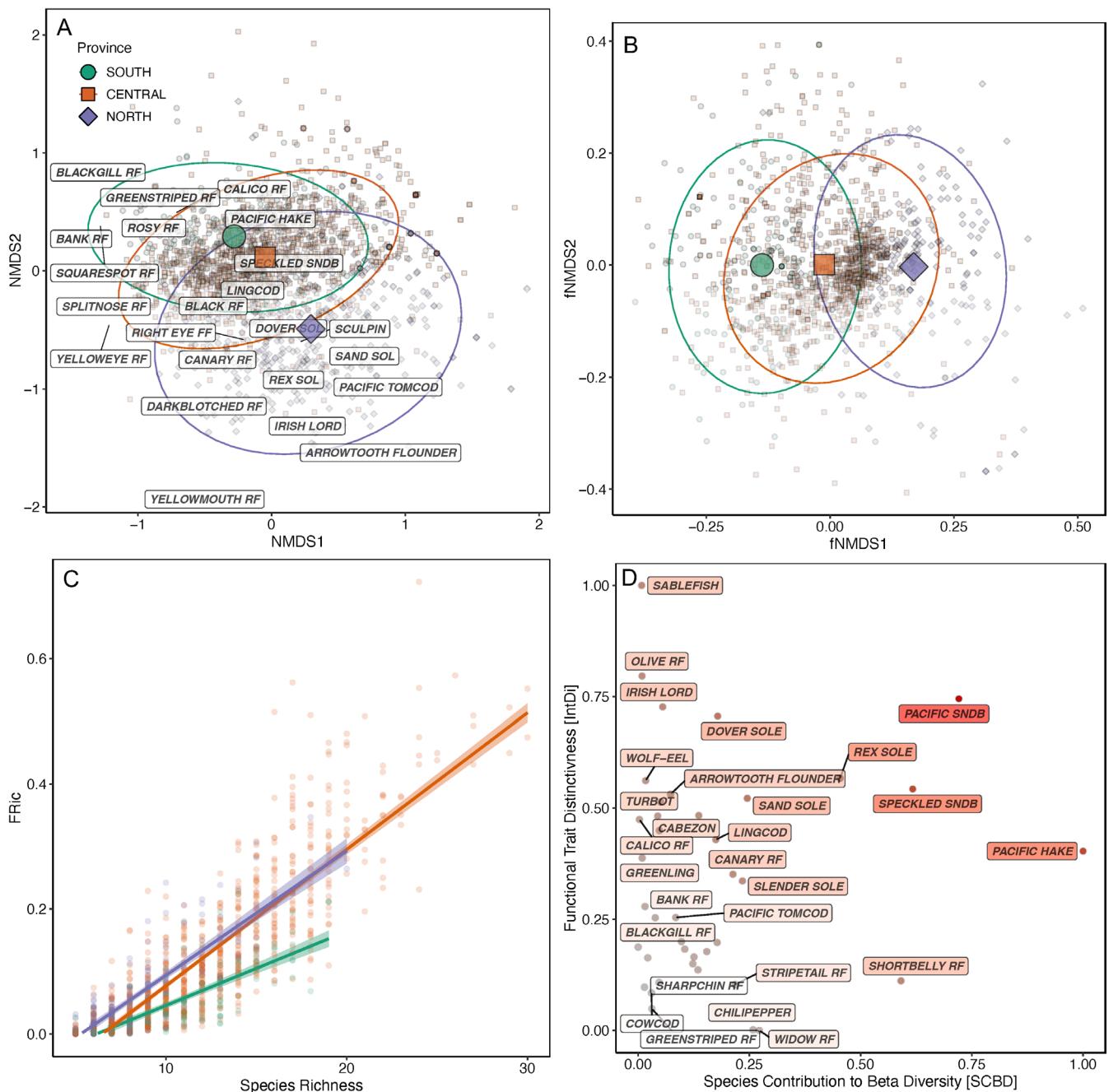
### 3.3 | Functional Diversity

Four PCoA axes were selected to calculate the functional trait space; this number of axes most appropriately balanced sample retention ( $n = 1333$  samples) and quality of the functional

space, as the difference between raw trait-based distances and those calculated in the functional space was low (Mean Absolute Deviation = 0.03) relative to solutions with fewer axes (Figure S2). PCoA1 explained 34% of the total variation in the functional space, and was significantly correlated with habitat and behavioural traits including vertical and horizontal habitat minimum temperature, and negatively correlated with species energy density and fished status. PCoA2 explained 20% of the total functional space variation, and was significantly correlated with the diel and seasonal migratory capacity of species (Figure S8). PCoA3 and PCoA4 explained 13% and 8% of the functional space variation, respectively. PCoA3 was significantly correlated with maximum depth, vertical habitat, maximum total length, and negatively correlated with minimum and maximum temperatures for species. PCoA4 was correlated with multiple habitat preference traits including a negative correlation with maximum depth (Figure S8) and positive correlations with the reef refuge trait (Figure S9). The four axes collectively explained 75% of the variance in trait expression, and species locations in the functional trait space also varied across the four axes according to their trait loadings (Figure S10).

We represented differences and overlap in functional composition between biogeographic regions and clusters with an optimal functional NMDS (fNMDS) solution (Figure 3b) that depicted the community-level trait variation in three dimensions (Stress = 0.14; Figure S11). Assemblages were functionally distinct between all three regions (PERMANOVA,  $p < 0.01$ ,  $F_{2,1330} = 26.96$ ; Table S4), and, to a lesser extent, by cluster (PERMANOVA,  $p < 0.01$ ,  $F_{5,1327} = 16.4$ ; Table S4). Effect sizes for pairwise functional differences between biogeographic regions were notably lesser than those based on compositional differences (Tables S3 and S4), as was the annual variation from long-term fNMDS centroids (Figure 4). The strongest assemblage-level functional differences between regions were observed between the South and North (PERMANOVA,  $p < 0.01$ ,  $F_{1,1383} = 35.4$ ; Figure 3a), while assemblage clusters II and V were the most functionally distinct from one another (PERMANOVA,  $p < 0.01$ ,  $F_{1,505} = 33.17$ ). There was a large degree of functional overlap between assemblage structures, however, with all cluster centroids besides V occurring in close proximity to one another (Figure S11). Significant differences in group dispersions from PERMDISP likely contributed to these differences, although assemblages I, II, and VI were not dispersed significantly differently from one another (Tukey's HSD,  $p > 0.05$ ; Table S4). ~83% of functional trait hypervolume were represented in the Central region at some point in the study period, with 41% represented per year on average (Table 3). Despite the highest mean CPUE, the South had the lowest station-level FRic values due to a preponderance of samples with highly and increasingly functionally even catch (Figure S12) dominated by rockfish taxa with similar traits (e.g., Assemblage VI) in most years (Figure 2). However, when assessed across all samples within each year, the South occupies a similar volume of the functional trait space as the Central region, indicating relatively high functional turnover between stations (Table 3).

Species' Integrated Trait Distinctiveness (IntDi) scores ranged from 0.25 to 0.45 (Table S1) with sablefish having the highest score, and

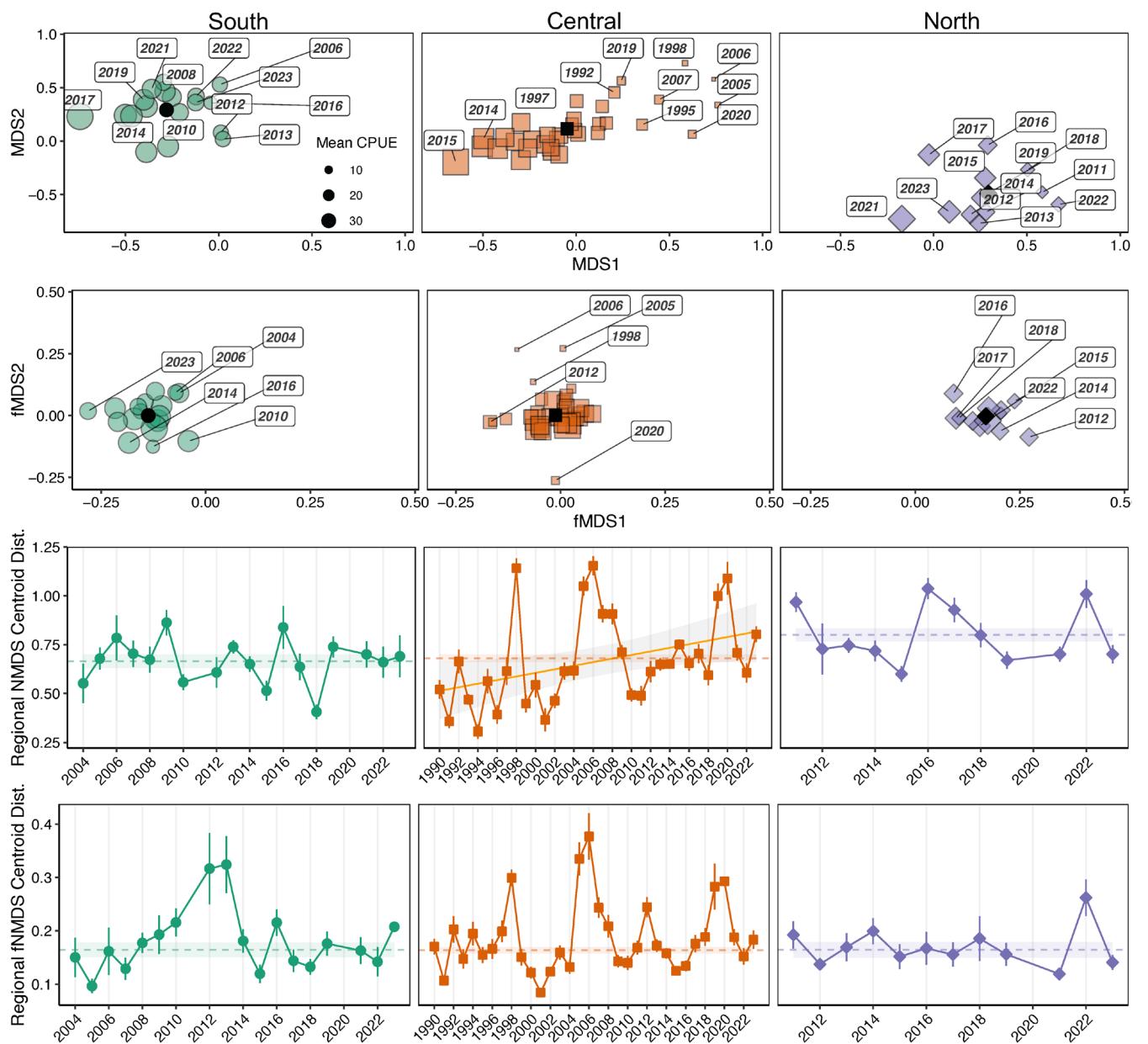


**FIGURE 3 |** Differences in biodiversity assessed with compositional and functional metrics. (a) Assemblage and (b) functional trait diversity differences shown via non-metric multidimensional scaling (NMDS). Individual points show unique year-station combinations, with colours and ellipses representing hypothesized biogeographic provinces. (c) The relationship between species and functional richness between provinces and (d) species contributions to beta diversity (SCBD) versus functional distinctiveness index at the species level. Labels are coloured to highlight species with relatively distinct traits (high IntDi) and high importance to community turnover (high SCBD).

rockfish taxa tending to have low scores (Figure 3d). IntDi scores were not correlated with species contributions to beta diversity (SCBD), indicating that, in general, species with high spatiotemporal turnover are not functionally rare or vice versa (Figure 3d). Sablefish, with the highest IntDi score of any species, for example, rarely occurred in surveys and thus had a low SCBD value. A few species, including Pacific and speckled sanddabs, rex sole, and Pacific hake had relatively high scores for both metrics. FRic and richness were significantly correlated (Linear Regression,  $p < 0.01$ ;

Table S5) in all three regions, although the slope and strength of the correlation was lesser in the South (Figure 3c).

Functional trait expression by assemblages was variable in time, with periods of notable departure from climatological means of community trait structure (Figure 4) and functional diversity metrics (Figure S12). For example, in the South region, the average annual distance from the regional centroid (fCentroidDist) was elevated in the period from approximately

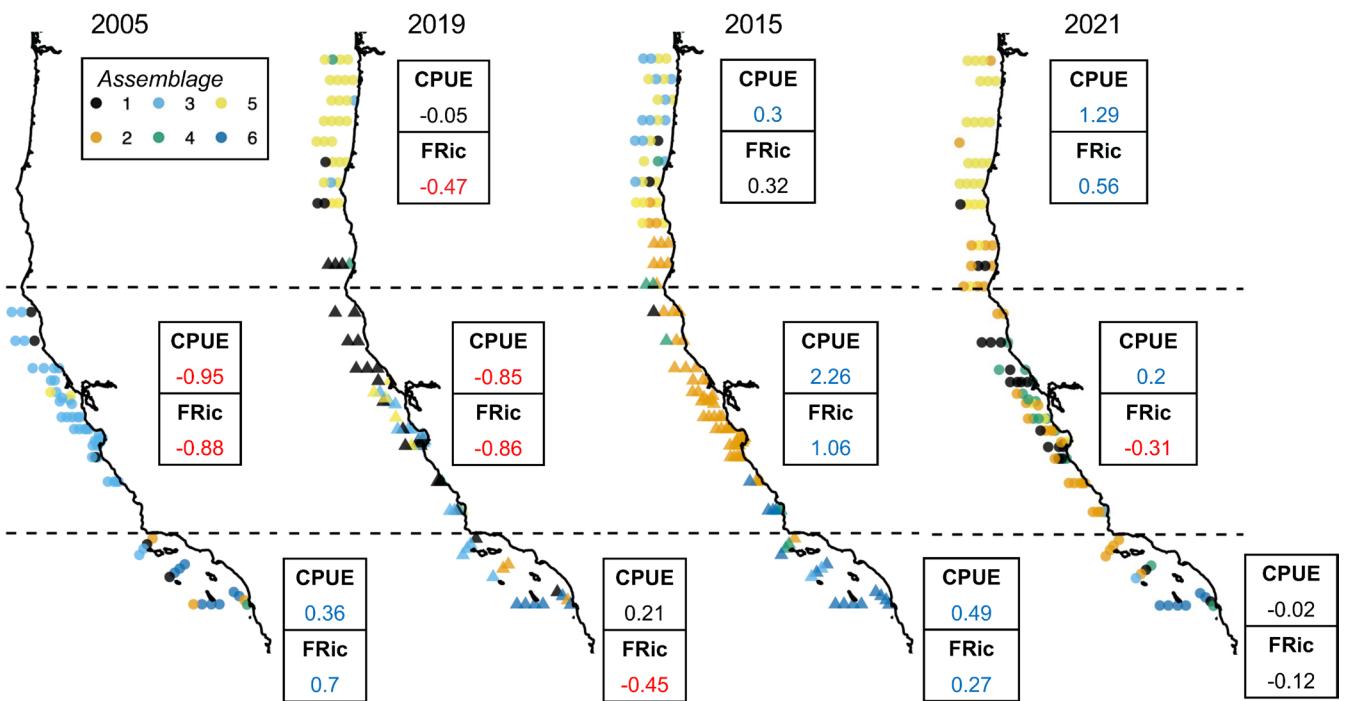


**FIGURE 4** | Annual differences in regional (columns) community composition and functional trait expression from NMDS (see Figure 3). The top two rows depict the annual position of NMDS and fNMDS centroids, respectively, with climatological centroids shown in black. Symbol size corresponds to annual mean CPUE ( $\log +1$ ), with relatively distinct years labelled. Bottom two rows show the mean ( $\pm \text{SE}$ ) Euclidean distance of each year's centroid to their corresponding regional compositional and functional climatological centroids (CentroidDist & fCentroidDist, respectively). Note that relatively few samples were obtained in the Central region in 2020, the North was not sampled in 2020, and the South was not sampled in 2011 and 2020.

~2009 to 2013 (Figure 4). This did not coincide with notable departures in any of the other regions. The same is true of the Central region in 2005–2006, associated with low-CPUE values and unusual assemblage structure with cluster III present throughout most of the region, while the South contained assemblages with relatively high CPUE and FRic values during the same time (Figure 5). Periods of functional departure in the Central region also occurred in 1998 and 2019–2020 and were also associated with low CPUE values. The Northern region did not experience any multi-year departures from climatological mean assemblage functional structure from 2011 to 2023.

#### 4 | Discussion

Our portfolio of annual biodiversity and species assemblage ecoscapes reveal the spatiotemporal assemblage structure, functional diversity, and turnover of YOY groundfish in the CCLME from 1990 to 2023. Such long-term datasets are rare for the pelagic juvenile life-stage of groundfish despite their importance in fisheries and ecosystem productivity. Our functional trait approach augments existing biodiversity baselines by providing links between biodiversity and ecosystem functioning and services, and insights into assemblage responses and resilience to climate variability that can aid biodiversity



**FIGURE 5** | Summary of juvenile groundfish ecoscapes in poor or below average (2005, 2019) and above average (2015, 2021) recruitment years. Points show the distribution of juvenile groundfish assemblages while boxes contain z-scores of CPUE and functional richness FRic metrics by biogeographic region (dashed lines). Z-scores significantly greater (less) than their respective regional climatological means (see Figures 3 and 4) are coloured blue (red).

monitoring and management. The differences between the patterns of functional and compositional diversity of assemblages highlight the potential of ecoscapes to resolve biogeographic patterns with promising applications for future studies. The latter includes parameterizations of ecosystem models (e.g., Gomes et al. 2024), and the development of predictive models for YOY groundfish assemblages and the assemblage-level expression of traits. Our ecoscape approach can also be applied to other ecosystem survey data and taxa, yielding a comparable set of metrics that may improve the management and conservation of marine biodiversity and fisheries in the CCLME and globally.

#### 4.1 | Biogeography of Juvenile Groundfish Compositional and Functional Diversity

Biodiversity metrics and community composition largely reflected known biogeographic provinces within CCLME. Our analyses revealed distinct scales of variability within each province that were distinguishable through the distribution of the six distinct YOY groundfish assemblages, with each region having distinct proportions of each assemblage present in a given year. Despite a high degree of variability and notable regional overlap in assemblage composition across the CCLME, the direction and magnitude of variability tended to be distinct between regions, as previously found for the abundance of several YOY rockfish taxa (Sakuma et al. 2006). The relatively high functional turnover between stations in the South may be associated with the presence of a faunal ecotone just south of Point Conception evident through high spatiotemporal variability in assemblage clusters associated with consistent eddy formation in this area

(Kim et al. 2011). Alternatively, the low variability of the North CCLME is consistent with previous studies that demonstrate the relative oceanographic and faunal stability on the relatively wide and gently sloping continental shelf of the North CCLME (Checkley and Barth 2009; Gottscho 2016).

High species richness may lead to the presence of functionally redundant species, which can act as ecological insurance against negative ecosystem consequences of compositional changes such as species losses (Naeem and Li 1997). The long-term changes in assemblage composition we observed in the Central region did not cause directional change in the functional space, suggesting that the notable variability and turnover within the Central region has led to different, but equally diverse, sets of traits being present and highlights the potential stabilising effect of high biodiversity. The relationship between FRic and richness is not as strong in the South CCLME, however, illustrating the higher functional redundancy within this region driven by the high prevalence of rockfish taxa. Functional redundancy may be a useful metric to monitor as a signal of warming-induced trait convergence (e.g., tropicalization; McLean et al. 2019).

Functional diversity measurements are also useful because a non-trivial amount of compositional diversity is uncharacterized due to the difficulty in identifying YOY rockfish to species. The Rosy Rockfish Group, for example, includes ~12 morphologically indistinguishable species. Thus, our compositional diversity measurements for the South—where they are primarily found—are likely underestimated. On the other hand, high trait redundancy of many rockfish suggests that most of their functional diversity was captured within our trait-based analyses by

co-occurring species. Thus, functional metrics are less biased by the taxonomic resolution of identifications, and may be more skilful indicators of assemblage responses to environmental variability (McGill et al. 2006). Given the benefits of incorporating trait-based diversity, an expanded ecoscape analysis may include invertebrates along with coastal pelagic and mesopelagic fishes caught in the same surveys, providing a broader scope to test hypotheses related to functional biogeography and the potential buffering effects of biodiversity with climate change.

## 4.2 | Functional Diversity in a Changing Climate

The differences we found between compositional and functional diversity of YOY groundfish highlight the potential benefits that may emerge from incorporating the functional facet of biodiversity into conservation and fisheries management, especially in light of climate change (Villéger et al. 2017). This need has been widely recognised in terrestrial ecosystems (Pollock et al. 2017) and for coral reef fish (Stuart-Smith et al. 2013; Grenié et al. 2018), but is just emerging for groundfish. Coulon et al. (2023), for example, demonstrated that threatened demersal taxa tend to be functionally rare, with extinction risk associated with higher trophic levels and long-lived taxa. Functionally distinct demersal taxa also tend to be more affected by fishing pressure (Murgier et al. 2021). Our results provide an important first step in quantifying patterns in the spatiotemporal diversity of YOY groundfish traits expressed at the assemblage level. Moreover, the index of species' functional trait distinctiveness (IntDi) may be used in future to determine linkages between functional trait rarity and species vulnerability.

In theory, the spatial heterogeneity in functional diversity creates a metacommunity that buffers against compositional changes for ecosystem functioning and services (Loreau et al. 2003). Over time, asynchrony in species responses to environmental variability—mediated by the diversity of their functional traits—leads to higher ecosystem stability (de Mazancourt et al. 2013). However, as environmental stressors related to climate change (e.g., warming and deoxygenation; Somero et al. 2016) intensify, the availability of functional niches may dictate the path of community reorganisation (Miller et al. 2023). Climate change will tend to favour fast-growing, smaller fish species (Cheung et al. 2013), and trait-based metrics are more likely to detect emergent climate change signals than taxonomic composition, as traits are directly filtered by climate variables (Sentis et al. 2024). Variation in the assemblage-level expression of traits can be measured by weighing trait values by species abundances (i.e., community-weighted mean traits), providing an indicator of ecosystem status in a changing climate (Beukhof et al. 2019). Future work may examine the relation between community-weighted means of traits we examined (e.g., energy density, maximum total length) and ecosystem productivity, or to elucidate assemblage functional responses to extreme events such as more frequent marine heatwaves (Di Lorenzo and Mantua 2016).

In contrast to other studies indicating that functionally distinct taxa are more vulnerable to climate change (Murgier et al. 2021; Coulon et al. 2023), flatfish may benefit from shifting climate in the CCLME, and increases in their abundance could lead to

changes in YOY groundfish functional diversity given their high IntDi scores relative to most rockfish. Juvenile speckled sanddabs, for example, have relatively high hypoxia tolerance compared to other groundfish (Cornett et al. 2024). Similarly, slender sole emerge as winners in benthic assemblages subjected to seasonal and multi-year low-oxygen events (Gasbarro et al. 2019) and have increased in the ichthyoplankton over the last several decades (Tunnicliffe et al. 2020). This resiliency is underpinned by functional traits including biochemical and behavioural adaptations that allow them to forage and persist for extended periods in severely hypoxic waters (Chu and Gale 2017). Notable YOY flatfish abundances were recorded in the Central CCLME during the marine heatwave years of 2015–2016, which may be indicative of their abundances in future, warmer conditions. Despite harbouring the least compositional and functional diversity annually, the relatively high prevalence of flatfish in the North region may foster resilience to environmental perturbation. This may contribute to the relatively low year-to-year assemblage variability in this region, where Assemblage V is dominant in most years. Increased flatfish abundance in the future may have ecosystem-level effects, particularly in the North CCLME where relatively high YOY flatfish abundance has been associated with increased species interactions in shared foraging habitat, leading to decreased condition and growth of Chinook salmon (*Oncorhynchus tshawytscha*), as well as an increased potential for bycatch of older salmon in the Pacific hake fishery (Wells et al. 2024). Meanwhile, the large size, slow maturation rate, and long lifespan of adult rockfish are traits that suggest high vulnerability to climate change (Magnuson-Ford et al. 2009). In addition, climate induced habitat compression is likely to affect rockfish differently across their ontogenetic stages. Shoaling of the extensive oxygen minimum zone of the Northeast Pacific may affect deeper dwelling adults (Keller et al. 2015), while YOY rockfish may be more affected by warming-related shoaling of the mixed layer (Hu et al. 2024) in addition to horizontal compression associated with the availability of cool-water upwelling habitat (Schroeder et al. 2022). Thus, there is an urgent need for models that represent responses to climate variability across rockfish life-stages, and the interrelations between these responses that affect their observed distributions.

## 4.3 | Predictive Ecoscapes of Biodiversity and Community Composition

Functional traits may improve the predictive ability of models relating environmental variables with species presence or abundance (i.e., species distribution models) by providing mechanistic links to community dynamics (i.e., species positive and negative associations) and species' responses to environmental forcing (Chalmadrier et al. 2022; Green et al. 2022). Such links are notably absent in the vast majority of distribution models, with potentially large ramifications for the realism and reliability of predictions (Wisz et al. 2013; Evans et al. 2015). Though outside the scope of this study, the integrative YOY ecoscapes hold promise for a number of potential predictive applications. For example, joint species distribution models that incorporate functional trait, phylogenetic, and species co-occurrence information may help disentangle the various community assembly processes driving marine fish assemblages, leading to more realistic biodiversity predictions than from summing outputs from

individual species models (Ovaskainen et al. 2017; Montanyès et al. 2023). Potential outputs from these models include spatial predictions for individual taxa, but also community-level predictive surfaces of biodiversity across the full spectrum of ecoscape indices. Joint modelling approaches are especially powerful for rare taxa (Zhang et al. 2020), which could improve predictions for a number of infrequently occurring YOY groundfish. However, accurate CCLME-wide species distribution models for YOY groundfish have remained elusive (but see Tolimieri et al. 2020 for models of combined YOY and age-1 juveniles), as their distribution and abundance in the CCLME is linked to source waters and transport mechanisms, not surface conditions at the time of sampling, and their extreme spatial patchiness in abundance is difficult to capture in models (Schroeder et al. 2019; Santora, Schroeder, et al. 2021). Assemblage-level distribution models using the clusters may bypass the taxonomic uncertainties and myriad data issues associated with species-level models for YOY groundfish. Based on our ecoscapes, the assemblage distributions in such models could be readily linked to functional and compositional biodiversity signatures, or used to forecast YOY groundfish assemblages based on winter upwelling conditions prior to spring surveys. While climate projections for northeast Pacific groundfish have been limited to adults (Thompson et al. 2023), such integrated ecoscape modelling could be expanded to project assemblage distributions in scenarios of climate change to define climate-proactive priority conservation areas for future recruitment habitat.

Despite their promise, the power of predictive trait-based approaches for groundfish face limitations imposed by the rarity of baseline trait data, specifically the lack of intra-specific data and non-morphological trait values specific to the juvenile life stage. However, these problems are common in trait-based ecology and more pronounced in marine taxa and fish (Villéger et al. 2017). Without trait measurements with sufficient spatiotemporal and taxonomic coverage, and uptake of resultant trait data into public databases, data scarcity will remain a major hurdle for including traits in predictive models (Barnett et al. 2019). Biodiversity monitoring should thus prioritise monitoring of traits to increase the ecological realism of trait inputs into models and to create species-level trait indicators for assessing climate impacts (e.g., Vasconcelos et al. 2024). That being said, our study uses the best information available, and we conceive a number of routes for our ecoscape metrics to contribute to biodiversity monitoring and management.

#### 4.4 | Juvenile Groundfish Biodiversity in Context of Exploitation History and Contemporary Management Needs

The unique biodiversity markers and assemblages identified may facilitate ecosystem monitoring and potentially provide a multispecies perspective that improves recruitment estimation and forecasting. Detecting and communicating the geographic extent and nuances of above- and lower-than-average years of YOY groundfish abundance is critical for ecosystem monitoring and informing fishery management councils and stakeholders, including the public. Relatively productive years are characterised by high diversity, elevated catch rates, and high prevalence of Assemblage II in the Central region extending into the North

(e.g., 2015). Meanwhile, unproductive years, such as those associated with delayed upwelling (e.g., 2005; Bograd et al. 2009), are typified by widespread prevalence of Assemblage III and overall low CPUE and compositional biodiversity, and high functional distinctiveness (FDiv). Generation of these and the wider suite of ecoscape indices can be automated in future years to provide management relevant indices to, for example, the California Current Integrated Ecosystem Assessment that delivers an annual report on ecosystem status to the Pacific Fisheries Management Council. In addition, YOY ecoscapes can provide critical evaluation data for other biodiversity monitoring programs and models in the CCLME, including for eDNA (e.g., Closek et al. 2019), acoustics (e.g., Santora et al. 2018), predator observations (e.g., Wells et al. 2017), and species distribution model outputs for groundfish and the taxa that interact with them.

As with most temperate marine ecosystems, the CCLME has an extensive exploitation history, with over 200 years of industrial-scale impacts to the biota of this ecosystem that began with marine mammals and salmonids but included many forage fishes (e.g., the Pacific sardine [*Sardinops sagax*]), highly migratory species, groundfishes, a wide range of invertebrates and other species over time (McEvoy 1996; Miller et al. 2017; Pacific Fishery Management Council 2022). While groundfish have long been an important component of subsistence, commercial and recreational fisheries, the period of greatest groundfish exploitation began in the 1950s (for flatfish) and 1960s (for Pacific hake, rockfish and species such as lingcod and sablefish). Fisheries landings and fishing intensity reached a peak in the 1980s and 1990s, associated with a growing diversity of fisheries target species and an expansion of fisheries effort into deeper and more offshore habitats (Miller et al. 2014), exploitation patterns that could favour the extraction of a wider set of functional traits from deep sea and mesopelagic taxa (Trindade-Santos, Moyes and Magurran, 2022). Consequently, many populations were at very low levels during the early part of the time period analysed here, and the vast majority have recovered to or above ‘target’ levels in the past few decades in response to management actions (Hilborn et al. 2020). Disentangling the impacts of fishing from a historically variable and a monotonically changing climate remains a challenge with respect to interpreting many of the temporal signals within these time-series (but see Thompson et al. 2022). At the same time, the observation of high synchrony in abundance patterns of both heavily exploited and unexploited YOY rockfishes (Ralston et al. 2013; Schroeder et al. 2019) suggests that the climate and ecosystem factors that contribute to variable abundance and year class strength are likely greater than the variability in pelagic YOY abundance that might result from fishing-induced changes in spawning output alone.

It is important to recognise that oceanographic processes likely influence YOY groundfish distributions and biodiversity patterns, as this relationship suggests considerable potential to improve recruitment estimation or forecasts by evaluating the entire YOY assemblage rather than the current practice of using species-specific information on YOY abundance. The surveys from which our analyses were drawn were developed with the objective of improving knowledge of the mechanisms that lead to strong or weak year classes for species important for commercial and recreational fisheries, as well as for directly informing stock assessments (Ralston and Howard 1995; Ralston et al. 2013; Ward

et al. 2024). This remains a primary objective of these surveys, with recognition that among the most challenging components of contemporary assessment models involves how best to forecast short-term recruitment, which is rarely well explained by adult spawning biomass and typically assumed to be much more influenced by a complex suite of climate and oceanographic drivers that influence early life-history survival (Cury et al. 2014; Szuwalski et al. 2015). Species richness and diversity within the YOY groundfish assemblage is closely associated with the influx of sub-Arctic waters at depth (Santora et al. 2017; Schroeder et al. 2019), and previous studies have also linked both YOY indicators and realised (from stock assessment) recruitment patterns with large-scale circulation patterns in the California Current (Ralston et al. 2013; Stachura et al. 2014; Tolimieri and Haltuch 2023). If the oceanographic factors responsible for a large fraction of the observed variability in the pelagic YOY communities are also influential to the realised recruitment to the adult population and fisheries, then there should be the potential to either quantitatively or qualitatively inform either fisheries models or fisheries managers with respect to the direction and magnitude of incoming year classes, information that should greatly improve management advice and ultimately sustainability (Stige et al. 2013; Le Pape et al. 2020; Ward et al. 2024). A rigorous analysis of the relationships between the diversity markers and assemblages developed here with oceanographic drivers, as well as realised recruitment estimates from stock assessments, is a critical next step for evaluating how metrics of biodiversity and assemblage structure may inform stock assessments or ecosystem status reports on the relative strength and magnitude of new productivity for commercially and ecologically important species.

## Author Contributions

Conceptualization: R.G., J.A.S., M.C., A.S., S.J.B., E.L.H., J.C.F.; data curation: R.G., A.S.; Formal analysis: R.G.; funding acquisition: J.A.S., M.C., S.J.B., E.L.H., B.K.W., J.C.F.; investigation: R.G., J.A.S., B.K.W., J.C.F.; methodology: R.G.; software: R.G.; supervision: J.A.S., M.C., S.J.B., E.L.H., B.K.W., J.C.F.; validation: R.G.; visualization: R.G.; writing – original draft: R.G., J.A.S., J.C.F.; writing – review and editing: All authors.

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## Conflicts of Interest

The authors declare no conflicts of interest.

## Data Availability Statement

All processed (i.e., station-level averaged) trawl data used in all analyses and outputs from biodiversity analyses are available on Dryad (<https://doi.org/10.5061/dryad.w0vt4b92x>). Raw trawl data from RREAS is available on ERDDAP ([https://coastwatch.pfeg.noaa.gov/erddap/tabledap/FED\\_Rockfish\\_Catch.html](https://coastwatch.pfeg.noaa.gov/erddap/tabledap/FED_Rockfish_Catch.html)) and can be accessed using the 'RREAS' R package (<https://github.com/tanyalorge/rs/RREAS>). Raw trawl data from the NOAA Northwest Fisheries Science Center's pre-recruit survey is available upon reasonable request. Functional trait data from the Pelagic Species Traits database (Gleiber, Hardy, Morganson, et al. 2024) can be accessed at the following URL: <https://borealisdata.ca/dataset.xhtml?persistentId=doi:10.5683/SP3/0YFJED>.

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### Supporting Information

Additional supporting information can be found online in the Supporting Information section.