



## Epibenthic faunal community dynamics and seasonal species turnover in a deep-sea coral ecosystem

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### ABSTRACT

Deep-sea coral ecosystems represent oases of life in the deep ocean, often hosting abundant and diverse faunal communities. Although mounting evidence indicates that deep-sea benthic communities are highly dynamic and can change over scales of a few hours to seasons or years, such dynamics have never been characterized in deep-sea coral ecosystems. We used a time-lapse camera deployed for a year at a depth of 1230 m on Sur Ridge (Monterey Bay National Marine Sanctuary) to characterize hourly changes in megafaunal abundance and diversity in a deep-sea coral assemblage. The response of community dynamics to variation in environmental factors, including surface net primary production as well as current speed/direction, temperature and acoustic backscatter (a proxy for particle and zooplankton density) at depth, was also evaluated. Overall, 33 taxa from 6 phyla, including multiple commercially valuable species, were observed throughout the study period. The strong seasonal pattern and periodicities in the occurrence of the most abundant taxa likely drove the observed temporal trends in overall abundance and diversity. Fluctuations in food availability may have, at least partially, driven these trends, as indicated by the significant relationship between community dynamics, surface net primary production and acoustic backscatter at depth. However, the low explanatory power of environmental parameters tested here suggest that biotic factors such as individual behaviors and species interactions had a strong influence on community dynamics. This study emphasizes the role of deep-sea coral as habitat and the need for monitoring to better understand how environmental and biological processes interact to shape associated faunal communities.

### 1. Introduction

Most marine environments fluctuate through time, forcing organisms to constantly cope with variations in abiotic conditions occurring at scales of hours (e.g., tidal processes) to decades (e.g., Pacific Decadal Oscillation). While environmental variability can drive ecological change (Poloczanska et al., 2013; Stenseth et al., 2002), disentangling the roles of natural and anthropogenic factors is often difficult (Magurran et al., 2010). To predict marine organisms' response to future environmental changes and better tease apart natural from anthropogenic causes, the collection of baseline information on the relationship between marine communities and their physical environment is key (Magurran et al., 2010).

The need for biological and ecological baseline data is particularly acute for the management and protection of vulnerable ecosystems. This

includes ecosystems defined as vulnerable marine ecosystems (VMEs; UNGA, 2009) and ecologically or biologically significant marine areas (EBSAs; Convention on Biological Diversity, 2008) due to their ecological importance and vulnerability to anthropogenic activities (Ardron et al., 2014). Although much effort has been put into mapping the spatial distribution of these ecosystems (Vierod et al., 2014), monitoring studies remain comparatively rare. This is particularly true for the deep sea (depths greater than 200 m) where most temporal studies have focused on annual or multi-annual time scales (Bohlukos et al., 2019; Etnoyer et al., 2022; Girard and Fisher, 2018; Glover et al., 2010; Sen et al., 2014) and little information on intra-annual dynamics are available (Aguzzi et al., 2010; Girard et al., 2020, 2022; Lelièvre et al., 2017).

Among VME/EBSAs, deep-sea coral ecosystems have been a recent focus of research. Deep-sea corals, including reef-forming scleractinians and octocorals, are ubiquitous worldwide and have been reported over a

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wide range of depths (Watling et al., 2011). By increasing the structural complexity of the sea floor, they provide habitat to various species, including species of high commercial value (Buhl-Mortensen et al., 2010; du Preez and Tunnicliffe, 2011; Roberts et al., 2006). For these reasons deep-sea corals are widely considered as abundance and diversity hotspots (Henry and Roberts, 2016). However, due to their slow growth and recovery rates, they are also particularly vulnerable to anthropogenic impacts (Andrews et al., 2002; Girard and Fisher, 2018; Roark et al., 2009). Specifically, bottom trawling represents the main threat to deep-sea coral ecosystems, often targeted for the commercially valuable species that they host (Clark et al., 2016). To predict the response of coral ecosystems to the multiple anthropogenic stressors they face (fishing but also oil and gas extraction activities (Cordes et al., 2016) and climate change (Levin and le Bris, 2015; Morato et al., 2020)), a better understanding of their response to natural environmental change is needed.

To date, most temporal studies in deep-sea coral ecosystems have focused on the coral themselves, investigating temporal dynamics in coral cover (Bohlukos et al., 2019), recovery (Girard and Fisher, 2018; Huvenne et al., 2016) or feeding activity (Girard et al., 2022; Osterloff et al., 2019; Zuazo et al., 2020). Overall, intra-annual studies have emphasized the strong connection between surface waters and the deep sea, showing an influence of tides and seasons on the biology of deep-sea corals (Girard et al., 2022; Johanson et al., 2017; Maier et al., 2020; Zuazo et al., 2020). As for most deep-sea ecosystems, deep-sea corals and their associated fauna rely on food produced at the surface that subsequently sinks to the sea floor (Ramirez-Llodra et al., 2010). As a result, variation in surface primary production and processes influencing the sinking flux of particulate organic matter (POM) can drive food availability at depth (Boyd et al., 2019; de Froe et al., 2022). Although these processes have been shown to influence the temporal dynamics of deep-sea benthic communities at intra-annual time scales (Aguzzi et al., 2010, 2018; Doya et al., 2017; Lelièvre et al., 2017), no information is currently available for megafauna associated with deep-sea corals.

Here we analyzed data collected hourly by a time-lapse camera deployed for a year on Sur Ridge (northeast Pacific) to 1) characterize temporal changes in megafauna abundance and diversity in a deep-sea coral ecosystem within Monterey Bay National Marine Sanctuary (MBNMS), 2) evaluate the relationship between changes in environmental condition and community structure and 3) identify potential indicator species for future monitoring within the sanctuary (Office of National Marine Sanctuaries, 2015).

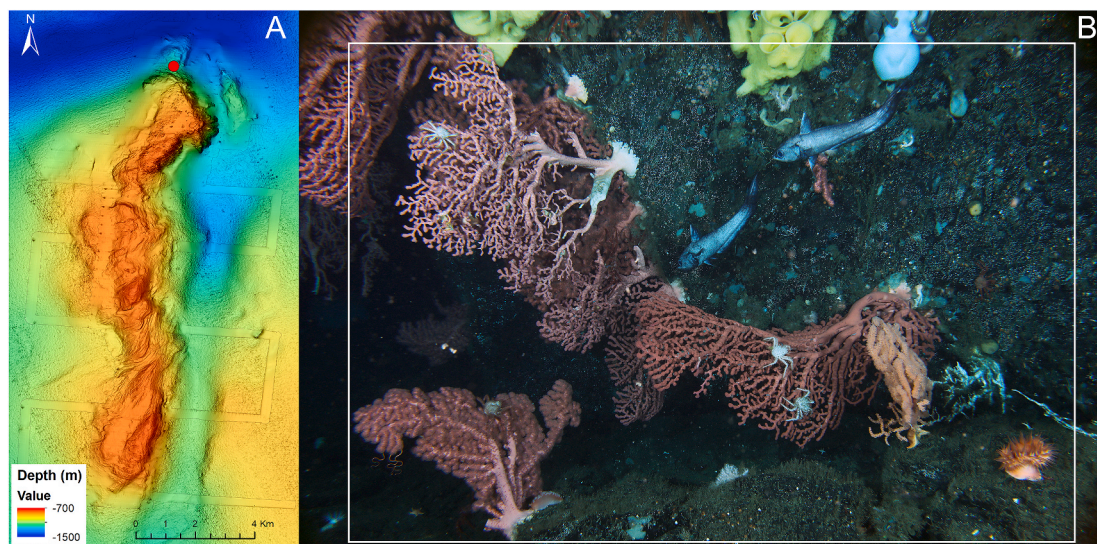
## 2. Materials and methods

### 2.1. Data collection

Community dynamics were characterized in a deep-sea coral and sponge ecosystem in the north end of Sur Ridge (depth range: 800 – 1500 m; Fig. 1A), located off the central California coast within MBNMS. A time-lapse camera (Canon EOS 5D Mark IV) mounted on a steel-frame lander was deployed on March 6, 2020 at a depth of 1230 m in front of a large boulder hosting several coral species (Fig. 1B). The camera system, which included two strobe lights mounted on both sides of the camera and a remotely releasable anchor weight for recovery, remained in place until March 16, 2021, for a total of 375 days. Except between late September and early November when occasional camera failures occurred (77 images lost), the camera consistently took one image every hour throughout the study period (8866 images).

All mobile megafauna visible on the images were annotated using the PAPARA(ZZ)I version 2.8 software application (Marcon and Purser, 2017). To limit the effect of changes in the field of view due to the camera being moved slightly during periods of strong currents, only organisms visible within the central section of the images were annotated (Fig. 1B). Overall, 4439 images, corresponding to one image every 2 h, were analyzed. All mobile fauna were counted and identified to the lowest taxonomic level possible using the Sur Ridge field guide (Burton et al., 2017) and MBARI deep-sea guide (Jacobsen Stout et al., 2016). No attempt was made to account for the same individual appearing in multiple images; such an individual was counted once for each image in which it appeared. For benthic species, the location (on sea-floor/boulder vs on coral) of observed individuals was recorded.

Additionally, a 1-MHz Acoustic Doppler Current Profiler (ADCP; Nortek Aquadopp profiler) was deployed next to the camera between March and December 2020. This ADCP measured bottom pressure, current speed and direction, bottom temperature, and acoustic backscatter with a temporal resolution of 30 min and bin size of 50 cm over a depth range of 6 m. Raw ADCP data were processed using the Surge version 1.15.03 software program. Because the goal of this study was to characterize environmental conditions within the coral community, only data collected between 1.5 and 2.5 m above the seafloor were used in the analyses. Therefore, measurements recorded within that range (two bins) were averaged. In addition, backscatter intensity averaged over all three beams was used as a proxy for suspended particle and zooplankton densities. A subset of the environmental time series that



**Fig. 1.** Study area and time-lapse camera field of view. (A) Camera location on Sur Ridge represented by a red dot. (B) Field of view of the camera ( $\sim 4.7 \text{ m}^2$ ). All mobile organisms visible within the study area (white rectangle) were counted and identified to the lowest taxonomic level possible.

matched image time points (every 2 h) was then extracted for comparison with community data.

Finally, to investigate the relationship between surface primary productivity and faunal community structure at depth, a time series (8-day averages) of net primary productivity (NPP) between March and November 2020 was exported from the Ocean Productivity website (<http://sites.science.oregonstate.edu/ocean.productivity/>). These NPP values were estimated using the Vertically Generalized Production Model, based on VIIRS Chlorophyll-a concentration data, available light and temperature-dependent photosynthetic efficiency (Behrenfeld and Falkowski, 1997). For each timepoint, NPP values estimated within a  $100 \times 100$  km area centered above Sur Ridge were averaged and used in the analyses.

## 2.2. Data analysis

Time series of abundance were computed for the most common species (>90% of total mobile fauna abundance observed over the study period). Periodograms were then calculated using a fast Fourier transform to identify potential periodicities in faunal abundance. Missing data points, resulting from camera failure, were imputed by linear interpolation using the *imputeTS* R (R Core Team, 2020) package (version 3.2) prior to analysis.

To characterize temporal dynamics of species diversity and evenness, the Shannon-Wiener and Pielou indices, respectively, were calculated using the R package *vegan* (version 2.5.7). In addition, local contributions to beta diversity (LCBD) indices were computed over the study period. Temporal LCBD indices are indicators of ecological uniqueness, large values indicating time points that strongly differ from the mean community (Legendre and Gauthier, 2014). Species contributions to beta diversity (SCBD) were then estimated to identify species driving differences in LCBD values. LCBD and SCBD values were computed using the *adespatial* R package (version 0.3.14).

For all the following analyses, taxa defined as rare (<1% of the community over the study period) were removed from the community matrix. Data were then Hellinger-transformed to reduce the weight of highly abundant taxa.

To visualize species turnover between March 6, 2020 and March 16, 2021, redundancy analysis (RDA) examining the relationship between Hellinger-transformed abundances and a second-degree polynomial function of time was performed. As in previous studies (Legendre and Salvat, 2015), a polynomial rather than linear function of time was chosen to facilitate data visualization.

Distance-based Moran's eigenvector maps (dbMEMs) were used to identify the temporal structure in community composition over the study period. This analysis, initially developed in a spatial context and subsequently extended to multivariate temporal datasets, decomposes series of observation time points into eigenvectors that can then be used as predictors to model temporal correlation (Legendre and Gauthier, 2014; Peres-Neto and Legendre, 2010). Positive and negative dbMEM eigenfunctions, depicting positive and negative temporal correlations, respectively, were first obtained by principal coordinate analysis of a Euclidian distance matrix computed among the observation time points. Second, RDAs were performed to model the relationship between detrended Hellinger-transformed abundances and positive/negative dbMEMs. Significant dbMEMs were then selected through forward selection and arbitrarily divided into three sub-models representing different temporal scales (broad, medium and fine) following inspection of the dbMEM scalogram. Periodograms were plotted for each sub-model to identify dominant periods corresponding to the different temporal structures. All dbMEM analyses were performed using the *adespatial* R package.

To quantify the contribution of environmental variables (bottom temperature, acoustic backscatter, northward and eastward flow speeds, mean NPP and NPP standard deviation (SD)) and the three different temporal sub-models to the variability in community composition, a

variation partitioning analysis was performed. The *vegan* package was used for this analysis, which breaks down the variance explained by predictor variables in RDA and illustrates it through a Venn diagram. The significance of time-dependent relationships between faunal communities and individual environmental variables was then assessed with partial RDA.

## 3. Results

### 3.1. Community composition

Between March 6, 2020 and March 16, 2021, 33 operational taxonomic units (OTUs) were observed (Table 1). Sessile taxa including coral, anemone and sponge OTUs were recorded but not included in the analyses.

In total, 41326 individuals belonging to 26 OTUs of mobile organisms were identified throughout the study period. In particular, nine OTUs represented over 90% of all observations: red crab *Paralomis multispina*, sea stars *Hippasteria* spp., king crabs from the *Neolithodes-Paralithodes* Complex, squat lobster *Munidopsis* sp., grenadiers *Coryphaenoides* spp., shrimp *Pandalus amplus*, nudibranch *Tritonia tetraquetra*, soles *Microstomus* spp. and snails from the *Neptunea-Buccinum* Complex; hereafter referred as common taxa. *P. multispina* was the most abundant species (39% of all observations; Table 1).

While most taxa were observed on the sea floor, nine were also regularly seen on corals. Several OTUs such as the king crab *Lithodes couesi* and species from the *Neolithodes-Paralithodes* complex showed a clear association with corals (69% and 83% of observations on corals, respectively; Table 2). Conversely, tanner crab *Chionoecetes tanneri*, soles *Microstomus* spp., *Hippasteria* spp., *Tritonia tetraquetra*, *Munidopsis* sp. and *Pandalus amplus* were more frequently observed on the sea floor (Table 2). No substrate preference was exhibited by *Paralomis multispina*. No OTU was found exclusively on corals.

### 3.2. Temporal changes in abundance, diversity and community structure

The abundance of common taxa varied throughout the study period (Fig. 2). Spectral analysis revealed that the abundance of several taxa was cyclic. Specifically, periodic variations of several days were detected for *Paralomis multispina*, *Neolithodes-Paralithodes* Complex, *Munidopsis* sp. and *Microstomus* spp. (Table 1). Furthermore, the abundance of *Munidopsis* sp. and *Coryphaenoides* spp. varied with the diurnal (O1, period of 25.82 h; both taxa) and lunar semi-diurnal (M2, period of 12.42 h; *Coryphaenoides* spp.) tides, as well as shallow water terdiurnal (MK3, period of 8.18 h; both taxa) and shallow water overtides of principal lunar constituent (M4, period of 6.21 h; *Coryphaenoides* spp.).

While *Paralomis multispina*, *Hippasteria* spp., *Neolithodes-Paralithodes* Complex, and *Munidopsis* sp. were present year-round, other species were seasonal (Fig. 2). Abundances of grenadiers *Coryphaenoides* spp. and shrimp *Pandalus amplus* followed opposite trends; grenadiers were primarily observed between late May and mid-December, and *P. amplus* in March–June 2020 and January–March 2021. The nudibranch *Tritonia tetraquetra* and snails from the *Neptunea-Buccinum* Complex were more abundant in the fall/winter season (November–January and October–mid-January, respectively). Finally, the abundance of soles (*Microstomus* spp.) peaked from July to October and November to mid-January (Fig. 2).

Total megafauna abundance and diversity were highly variable over the study period (Fig. 3). Total abundance ranged between 1 and 25 individuals per image (mean =  $9.31 \pm 3.36$  SD) with the highest abundances detected in April, late June–early September and late October–late November. Similarly, the time series of the Shannon index revealed peaks in diversity in June–July and September–November 2020. Overall, the faunal community remained relatively even throughout the study period with a mean Pielou index of  $0.89 \pm 0.078$  SD. Periods of lower taxa evenness could be detected in April 2020,



**Table 1**

List of megafauna observed on the time-lapse camera images between March 6, 2020 and March 16, 2021. Dominant periods identified in the abundance time series are represented for the nine most abundant operational taxonomic units (OTUs; in bold). Temporal dynamics of abundance were not analyzed for the other OTUs (indicated by NA: not applicable). Sessile organisms and rare species (<1% of observations) are indicated by asterisks (\* and \*\*, respectively). All OTUs were identified to the lowest taxonomic level possible.

Phylum	OTU name	Total number of observations	Dominant periods	
Arthropoda	<i>Chionoecetes tanneri</i> Rathbun, 1893	275	NA	
	Decapoda indet.**	27	NA	
	<i>Lithodes couesi</i> Benedict, 1895**	36	NA	
	<b><i>Munidopsis</i> Whiteaves, 1874 sp.</b>	1950	23.4, 5.07 days	
			25.7 h, 8.16 h	
	<b>Neolithodes-Paralithodes Complex – <i>N. diomedae</i> (Benedict, 1895) &amp; <i>P. rathbuni</i> (Benedict, 1895)</b>	4534	23.4, 5.95 days	
	<b><i>Pandalus amplus</i> (Spence Bate, 1888)</b>	1425	No significant period	
	<b><i>Paralomis multispina</i> (Benedict, 1895)</b>	16014	62.5, 17.1, 8.72, 3.91 days	
	Chordata	Actinopterygii indet.**	33	NA
		<i>Anoplopoma fimbria</i> (Pallas, 1814)**	5	NA
<i>Antimora microlepis</i> Bean, 1890**		1	NA	
<i>Bothrocara brunneum</i> (Bean, 1890)**		3	NA	
<i>Careproctus</i> Krøyer, 1862 spp.**		79	NA	
<b><i>Coryphaenoides</i> Gunnerus, 1765 spp.</b>		1437	25.9, 12.4, 8.17, 6.18 h	
<b><i>Microstomus</i> spp. – <i>M. bathybius</i> (Gilbert, 1890) &amp; <i>M. pacificus</i> (Lockington, 1879)</b>		800	53.6 days	
			12.4 h	
<i>Pyrosoma</i> Péron, 1804 sp.		247	NA	
<i>Sebastolobus</i> spp. – <i>S. altivelis</i> Gilbert, 1896 & <i>S. alascanus</i> Bean, 1890		308	NA	
Unidentified species**		141	NA	
Cnidaria		<i>Clavularia grandiflora</i> (Nutting, 1908)*	3	NA
		<i>Keratois</i> Wright, 1869 sp.*	1	NA
	<i>Paragorgia arborea</i> (Linnaeus, 1758)*	7	NA	
	<i>Stomphia</i> (Gosse, 1859) sp.*	1	NA	
	Echinodermata	Asteroidea indet.	1271	NA
Goniasteridae spp.**		103	NA	
<i>Henricia</i> Gray, 1840 spp.		416	NA	
<b><i>Hippasteria</i> spp. – <i>H. californica</i> Fisher, 1905 &amp; <i>H. lepidonotus</i> (Fisher, 1905)</b>		9073	No significant period	
<i>Solaster hypothyrsus</i> Fisher, 1910		537	NA	
Zoroasteridae spp.**		9	NA	
Mollusca		<i>Graneledone boreopacifica</i> Nesis, 1982	416	NA
		<b><i>Neptunea</i> Röding, 1798 - <i>Buccinum</i> Linnaeus, 1758 Complex</b>	775	No significant period
	<b><i>Tritonia tetraquetra</i> (Pallas, 1788)</b>	1411	No significant period	
Porifera	Encrusting Porifera*	NA	NA	
	Porifera indet.*	2	NA	
	<i>Staurocalyptus solidus</i> Schulze, 1899*	2	NA	
	<i>Thenea muricata</i> (Bowerbank, 1858)*	3	NA	

matching the first peak in abundance, and from mid-July to early August.

As for abundance and alpha diversity, beta diversity varied throughout the study period (Fig. 3). While multiple peaks in LCBD values were detected, no clear intra-annual patterns emerged. The SCBD values of eight taxa were higher than the mean of the community assemblage: *Neolithodes-Paralithodes* Complex, *Paralomis multispina*, *Munidopsis* sp., *Pandalus amplus*, *Hippasteria* spp., *Coryphaenoides* spp., *Tritonia tetraquetra* and Asteroidea indet. (Fig. 4A).

Different taxa contributed to beta diversity depending on the time period considered (Fig. 4B). The predatory sea stars *Hippasteria* spp. were associated with the beginning of the time series, in the spring of 2020, while grenadiers (*Coryphaenoides* spp.) drove beta diversity in the summer. Several taxa, including king crabs *Neolithodes-Paralithodes*, soles *Microstomus* spp., nudibranch *Tritonia tetraquetra* and sea star *Solaster hypothyrsus* all correlated with the fall season. Finally, the shrimp *Pandalus amplus* was primarily associated with the end of the time series (late fall–winter period).

### 3.3. Changes in environmental conditions

Variations in bottom temperature as well as acoustic backscatter, current speed and direction 2 m above the sea floor between March and November 2020 have been described in detail in a previous study

(Girard et al., 2022). In short, bottom temperature varied between 3.0 and 3.7°C (mean: 3.3°C ± 0.099SD) while current speed varied between 0.071 and 46 cm/s (mean: 16 cm/s ± 8.8SD) along dominant southeast-southwest directions. Timeseries of bottom temperature, current speed and direction all displayed cyclic patterns with periods matching those of the diurnal and semi-diurnal tides. Although periodic variations were also detected for acoustic backscatter, these appeared to be driven by spring/neap tidal oscillations (14.8 days) rather than diurnal or semi-diurnal tides.

NPP varied seasonally, with three main peaks identified in May, June

**Table 2**

Proportion of individuals observed on coral colonies over the study period (March 6, 2020 to March 16, 2021). Only taxa occurring on both corals and sea floor are represented here.

OTUs	Proportion observed on corals
<i>Neolithodes-Paralithodes</i> Complex	0.83
<i>Lithodes couesi</i>	0.69
<i>Paralomis multispina</i>	0.51
<i>Pandalus amplus</i>	0.32
<i>Hippasteria</i> spp.	0.29
<i>Tritonia tetraquetra</i>	0.24
<i>Chionoecetes tanneri</i>	0.22
<i>Microstomus</i> spp.	0.17
<i>Munidopsis</i> sp.	0.06

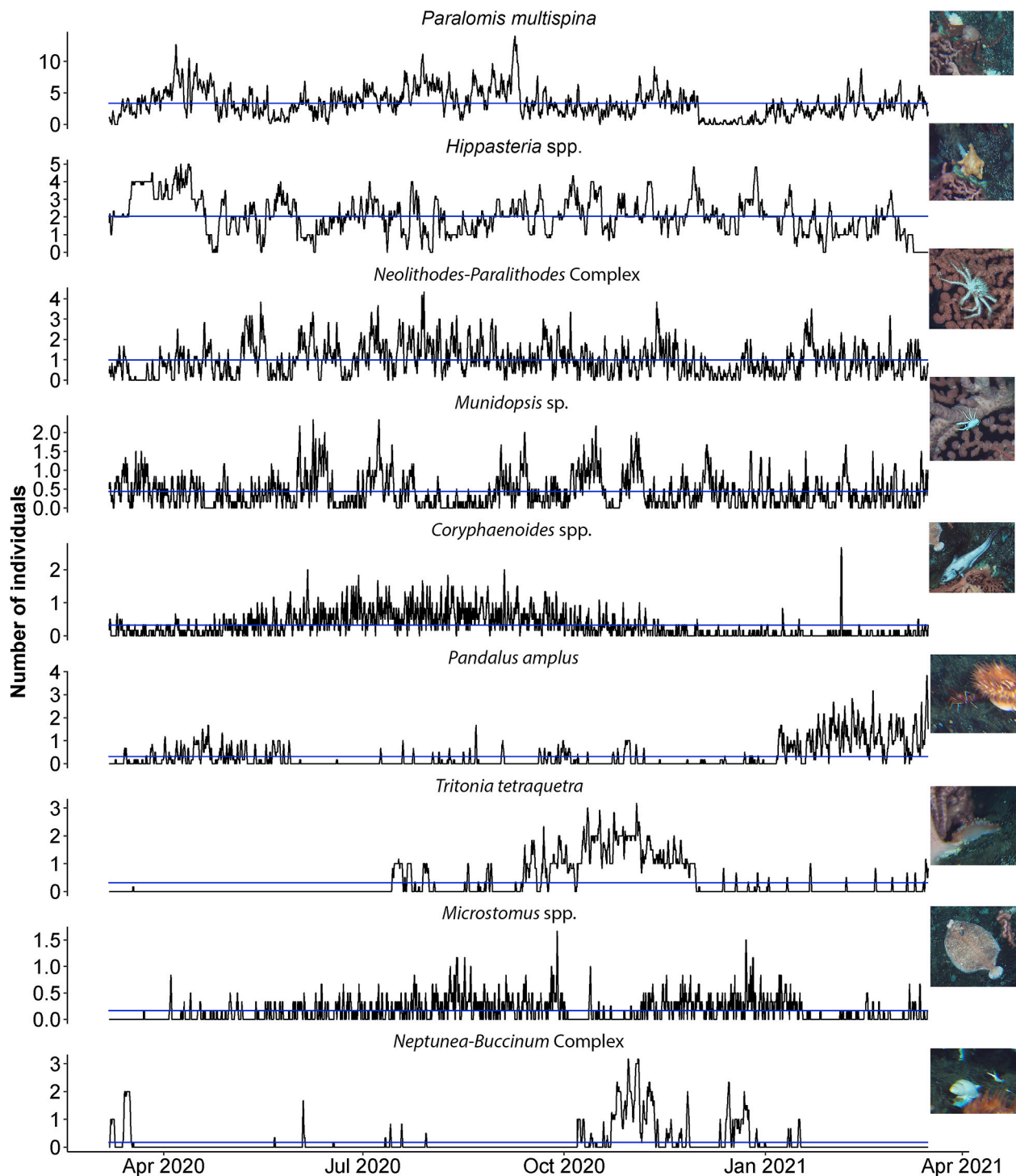


Fig. 2. Time series of common taxa abundance at Sur Ridge between March 6, 2020 and March 16, 2021. Only the nine most abundant taxa are represented. Moving averages over 12h are shown. Blue lines represent the mean number of individuals computed over the entire study period.

and September 2020 (Supplementary Fig. 1).

### 3.4. Drivers of change in community composition

Overall, 868 positive and 2151 negative dbMEMs were identified. However, RDA analysis indicated that only the temporal model with positive autocorrelation significantly explained community variation (positive dbMEM:  $p$ -value = 0.001,  $R^2_{adj}$  = 0.51; negative dbMEM:  $p$ -value = 0.22). Therefore, only positive dbMEMs were considered in the following analyses.

Of the 868 positive dbMEMs, 125 were selected by forward selection and sorted into three sub-models of different temporal resolution (Supplementary Fig. 2; Table 3). While all three models were statistically significant ( $p$ -values < 0.001), the broad scale sub-model explained most of the variance in community composition ( $R^2_{adj}$  = 0.17) compared to the medium- ( $R^2_{adj}$  = 0.13) and fine-scale ( $R^2_{adj}$  = 0.052) models. Cycles were identified in the different sub-models with periods of 19.7 days for the broad-scale sub-model, 6.92 days for the medium-scale sub-model and 4.06 days and 25.6 h for the fine-scale sub-model (Table 3).

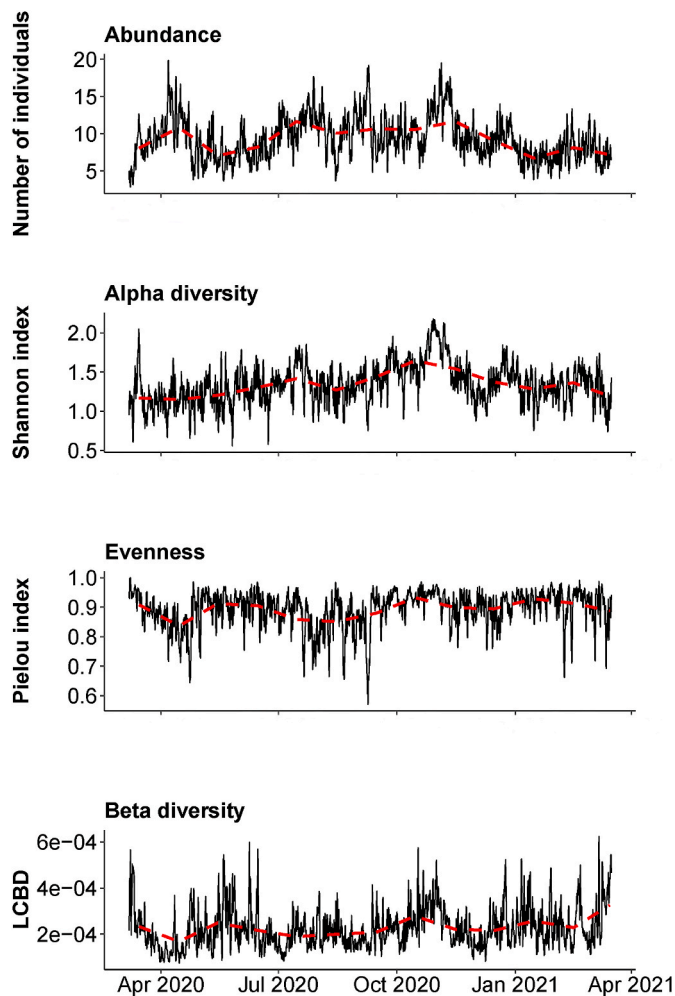


Fig. 3. Temporal dynamics of abundance, alpha and beta diversity between March 6, 2020 and March 16, 2021. Time series of abundance, Shannon index, Pielou index and local contributions to beta diversity (LCBD) are represented with associated monthly means (red dashed lines).

Variation partitioning analysis indicated that environmental and dbMEM predictors explained 41% of the variability in community composition over the study period (Fig. 5). As shown by the Venn diagram, the environment alone explained only 1% of the variance in community data, whereas broad-, medium- and fine-scale temporal structures individually accounted for 17, 13 and 5% of the variance, respectively. Shared effects of environmental variables and the different temporal sub-models explained 2% of the variance in community data for all three models.

Community response to environmental variability differed based on the temporal model considered. None of the environmental variables included in this study significantly explained community variability at the global level. However, the mean and standard deviation of NPP were significant at all three temporal scales. Acoustic backscatter structured community composition at medium and fine temporal scales.

#### 4. Discussion

This study, the first to document intra-annual dynamics of faunal communities associated with deep-sea corals, emphasizes the ecological importance of coral habitats and the influence of seasonality on community dynamics at a depth greater than 1000 m. By characterizing changes in abundance, diversity and community structure at different temporal scales, this study provides important baseline information on

the ecology of vulnerable deep-sea coral ecosystems.

##### 4.1. Species associated with deep-sea corals at Sur Ridge

In total, 26 megafauna taxa were identified during the study period (March 2020 to March 2021), indicating a diverse community at Sur Ridge, comparable to image-based estimates in other deep-sea coral ecosystems (Buhl-Mortensen et al., 2017; Krieger and Wing, 2002; Lesard-Pilon et al., 2010). While most taxa were observed on the sea floor, nine were also detected on *Paragorgia arborea* and *Keratoisis* sp. colonies, including three lithodid (king crabs; *Paralomis multispina*, *Neolithodes-Paralithodes* Complex and *Lithodes couesi*) taxa showing a clear association with these corals with more than 50% of observations recorded on coral colonies. Associations between king crabs and benthic epifauna (coral and sponges) have been documented in other studies (Auster et al., 2014; Stone, 2006). Notably, these associations were particularly strong for juvenile king crabs, highlighting the importance of corals as habitat for early life stages (Stone, 2006). Similarly, almost all individuals from the *Neolithodes-Paralithodes* Complex, which presented the strongest association with corals, were juveniles (e.g., Fig. 1). Although less frequently observed on coral colonies, several known coral predators such as the nudibranch *Tritonia tetraquetra* and sea stars *Hippasteria* spp. were also commonly recorded.

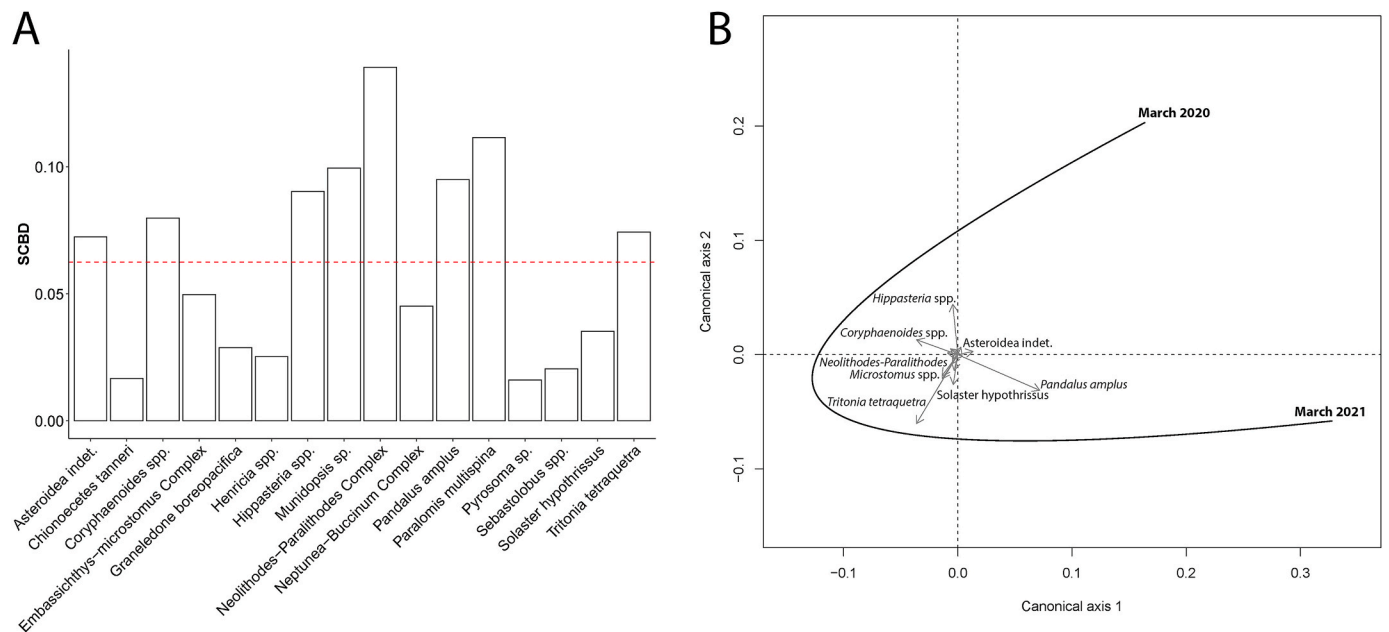
##### 4.2. Seasonal dynamics of abundance, diversity and community composition

Seasonality in benthic community dynamics, as reported here for the faunal assemblage in a deep-sea coral ecosystem, has been documented in various deep-sea ecosystems and linked to seasonal variability in food supply to the sea floor (Billett et al., 1983; Chauvet et al., 2018; Juniper et al., 2013; Sumida et al., 2022). The coral community at Sur Ridge is located within the California Current System, characterized by seasonal upwelling bringing deep, cold and nutrient-rich water to the ocean's surface, fueling primary production (Pennington and Chavez, 2000). Regionally, the peaks in primary production generally occur in June–July and November (Pennington and Chavez, 2000), correlating with periods of high megafaunal abundance and diversity at depth.

Similar seasonal changes in deep benthic communities have been previously reported in the northeast Pacific (Chauvet et al., 2018; Chu et al., 2018; Doya et al., 2017; Juniper et al., 2013). In these studies, as we observed at Sur Ridge, some species were observed throughout the year, while others showed clear seasonal patterns in abundance, driving changes in diversity patterns over time.

Notably, the abundance of some very common species varied seasonally at Sur Ridge. Specifically, grenadiers (*Coryphaenoides* spp.) were most abundant between late May and November, significantly contributing to temporal beta diversity during the summer/early fall (Fig. 4B). Similarly, baited camera deployments in the north Pacific have revealed higher grenadier activity, suggestive of higher densities, during the summer/fall period (Armstrong et al., 1991; Priede et al., 1994). Lower fish densities in the winter were likely due to food limitation, as grenadiers appear to lead a more pelagic existence during oligotrophic conditions (Armstrong et al., 1991). Grenadiers prey on a broad range of fish and benthic invertebrates (Pearcy and Ambler, 1974), and thus increased POM flux during periods of high surface primary productivity may indirectly promote higher fish abundance through an increase in the number of benthic suspension or deposit feeders (Milligan et al., 2020).

The pandalid shrimp, *Pandalus amplus*, showed the opposite abundance pattern than grenadiers, with a higher number of individuals observed in March–early June 2020 and January–March 2021. Although data presented here are not sufficient to infer a predator-prey relationship between these species, previous observations of negative correlations between grenadier species and their prey (Bailey et al., 2006) along with observations of predation attempt during ROV dives on Sur Ridge (author personal observation) suggest a possible predator-prey



**Fig. 4.** Temporal beta diversity. (A) Species contributions to beta diversity. The red dashed line represents the mean SCBD of the community assemblage. (B) Redundancy analysis (RDA) of community composition by time (curved line with start and end dates). Grey arrows indicate the sequential importance of different taxa in driving temporal beta diversity. Species that clustered near the origin have been removed to facilitate data visualization.

**Table 3**

Significance of temporal and environmental drivers of community changes between March 6, and November 18, 2020. 125 positive dbMEMs were selected and sorted into three sub-models (broad-, medium- and fine-scale) to explain variation in the community matrix. Significant periods identified for the different sub-models are indicated. \*\*\* p-value <0.001; - variable not tested as  $R^2 < 0.01$ .

	Global model	Broad	Medium	Fine
Significant periods		19.7 days	6.92 days	4.06 days and 25.6 h
Bottom temperature	-	-	-	-
Acoustic backscatter	-	-	***	***
Eastward flow speed	-	-	-	-
Northward flow speed	-	-	-	-
Mean NPP	-	***	***	***
NPP SD	-	***	***	***

interaction. Other species, including the predatory nudibranch *Tritonia tetraquetra* and deep-sea soles *Microstomus* spp. also varied in abundance throughout the year, contributing to temporal beta diversity in the fall. Although little information exists on the temporal dynamics of these species, seasonal patterns in abundance could be due to annual migrations related to the species' life cycle (e.g., spawning migrations in the case of the dover sole *Microstomus pacificus* and grenadiers (Abookire and Bailey, 2007; Novikov, 1970; Tuponogov, 1997, 1986);) or food availability.

**4.3. Environmental and biological influence on community dynamics at multiple temporal scales**

Overall, the influence of food availability was evident from the significant relationship between community composition and surface NPP (all time scales) as well as acoustic backscatter at depth, a proxy for particle and zooplankton density (medium and fine time scales).

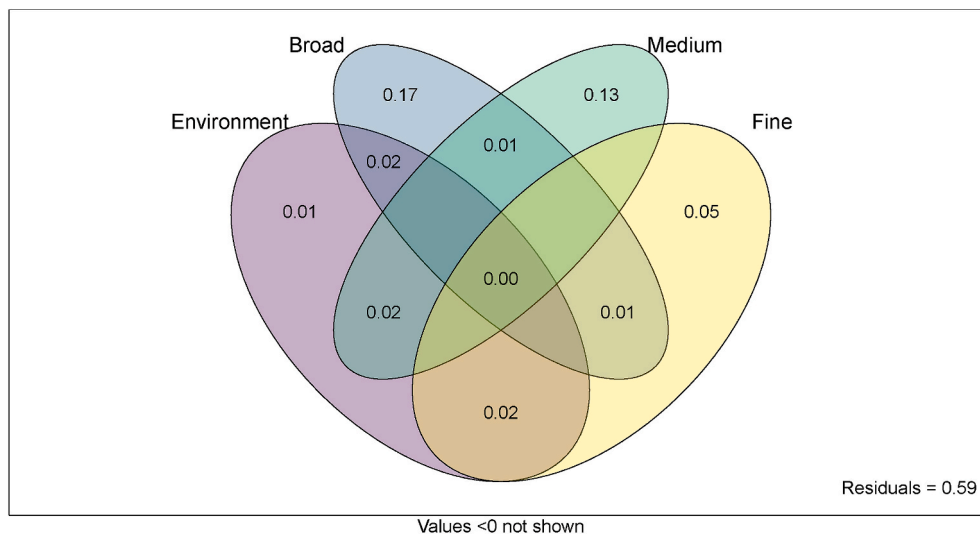
Temporal variability in community structure may have been driven in part by periodic changes in the abundance of the red crab *Paralomis multispina*. This species was by far the most abundant throughout the

year and, as suggested by the combined lower species evenness and high *P. multispina* abundance, dominated the community in April and July–August 2020. Moreover, the abundance of red crabs showed significant cyclic patterns with periods of ~ 4, 9, 17 and 62 days. The complex rhythmic activities detected for *P. multispina*, but also *Neolithodes-Paralithodes* Complex and *Munidopsis* sp., are difficult to explain and could result from the combined effects of multiple factors (i.e., tides, inertial current, benthopelagic coupling, seasons) acting on behavioral rhythms or arrhythmia between individuals, as common for decapods (Aguzzi et al., 2011).

Over fine time scales (few hours), variations in the abundance of several taxa were likely influenced by tides and seemed to be coupled with individual behavior rather than a population response. In the case of *Munidopsis* sp. it appeared that the same individuals remained at the study site between March 2020 and 2021 but were only visible when out of their shelter (likely rock crevices at the base of *Paragorgia arborea* colonies and *Staurocalyptus solidus* sponge). Tidally controlled flow change has been shown to influence the emergence behavior of multiple decapod species, and may explain the detected diurnal signal (Aguzzi et al., 2011). Changes in current direction and speed related to tides affect coral feeding activity at Sur Ridge by regulating food delivery (Girard et al., 2022). Similarly, currents may influence food available to *Munidopsis* sp., for instance by affecting turbulence regimes near the sea floor, and thus resuspension. *Munidopsis* squat lobsters are opportunistic feeders (Hoyoux et al., 2012; Janßen et al., 2000) and likely emerge from their shelter to take advantage of favorable feeding conditions. Finally, tidally driven hydrodynamic changes may also influence the number of grenadiers visible in the field of view of the camera by affecting their swimming behavior (Wilson and Smith, 1984).

The fact that more than half of the variability in community structure remained unexplained in this study indicates that currently unknown factors may play a large role in shaping community patterns over time. For instance, changes in physical properties (e.g., oxygen levels) are associated with variation in community dynamics in seasonally hypoxic environments (Chu et al., 2018). Although hypoxic conditions have not been documented at Sur Ridge, variations in oxygen concentrations may still have affected community structure. In addition, biotic factors including species interactions (e.g., predator-prey, competition) or





**Fig. 5.** Variation partitioning of the effects of environmental variables and positive temporal autocorrelation on megafauna community structure at Sur Ridge. The proportion of the variance explained by the different factors (environment, broad-, medium- and fine-scale temporal structures) are indicated within the Venn diagram. Overlap between circles indicates shared effects.

migrations related to the species life cycle may explain part of the observed temporal variability (Åkesson et al., 2021). Dover soles, buccinid snails and tanner crabs can each form large aggregations for reproduction, affecting their spatial distribution (Abookire and Bailey, 2007; Himmelman and Hamel, 1993; Keller et al., 2012). Notably, in the northeast Pacific, high densities of buccinids have been previously documented in the winter (February) coinciding with the period of most pronounced downwelling (Doya et al., 2017). Finally, it is important to note that only a limited area of the sea floor was visible in the field of view of the camera ( $\sim 4.7 \text{ m}^2$ ). Some of the observed trends may thus not be generalizable or be the result of dynamics occurring over broader spatial scales. Moreover, faunal communities on nearby rocky areas where other coral species occur may differ from the community described here. Therefore, additional studies covering different coral habitats will likely shed a new light on processes driving community dynamics in deep-sea coral ecosystems.

#### 4.4. Importance of monitoring vulnerable marine ecosystems

Many species reported here, including the most abundant species (e.g., king crabs, grenadiers, pandalid shrimps, soles) are commercially valuable and targeted by the fishing industry. This study further emphasizes the ecological importance of deep-sea coral habitats for these species throughout, or during part of their life cycle. Therefore, providing knowledge of their temporal dynamics within a vulnerable marine ecosystem enhances our ability to sustainably manage these resources.

Beyond their economic value, red crab *Paralomis multispina*, and other large decapods observed here can play a keystone role in structuring benthic communities through predation (Boudreau and Worm, 2012). Moreover, because of their abundance and clear association with corals, red crabs may be a robust indicator of ecosystem health within MBNMS. Accordingly, due to their generally slow metabolism, trophic level and ubiquity, deep-sea crabs (e.g., Atlantic red crab *Chaceon quinqueidens*) have been proposed as sentinel species useful as indicators of human impacts (i.e., contaminants) in the deep sea (Douglas et al., 2018).

## 5. Conclusions

Results reported here are the first to show the complex effect of environmental and biological processes acting over multiple temporal

scales on the dynamics of megafauna associated with a deep-sea coral community. Though more than 50 percent of the variability in community structure remained unexplained, our results suggested that seasonal changes in surface primary production may be a key driver of community dynamics (abundance and diversity) at depth. Moreover, the identified cycles in species' abundances indicated that their life histories, along with biological interactions, likely resulted in significant species turnover during the study period. Overall, these results highlight the need for more intra- and inter-annual studies in vulnerable marine ecosystems to better understand their resilience to natural and anthropogenic environmental change.

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#### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

#### Data availability

Data will be made available on request.

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#### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.dsr.2023.104048>.



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