



Spatiotemporal variability in the structure and diversity of understory faunal assemblages associated with the kelp *Eisenia cokeri* (Laminariales) in Peru

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Abstract

Kelp species function as foundation organisms in coastal marine ecosystems, where they alter environmental conditions and promote local biodiversity by providing complex biogenic habitat for an array of associated organisms. The structure and functioning of kelp forest ecosystems in some regions, such as along the Peruvian coastline, remain critically understudied. We quantified the structure and diversity of faunal assemblages within both holdfast and understory reef habitats within *Eisenia cokeri* forests. We sampled both habitat types within four subtidal kelp forests on multiple occasions between 2016 and 2020, and quantified fauna at a fine taxonomic level (mostly species). We recorded a total of ~55,000 individuals representing 183 taxa across the study, with holdfast assemblages typically exhibiting higher richness, abundance and biomass values compared with understory reef-associated assemblages. Holdfast assemblages were structurally and functionally dissimilar to those on reef surfaces and were less variable and consistent across sites and sampling events. Even so, assemblages associated with both habitat types varied significantly between sites and sampling events, with variation in upwelling strength, ocean currents, and grazing pressure among potential drivers of this ecological variability. Overall, *E. cokeri* supports diverse and abundant holdfast assemblages and functions as a foundation organism in Peru. Given that no other habitat-forming kelp species persist at the low latitudes of *E. cokeri* in mid-to-north Peru, the lack of functional redundancy suggests that effective management and conservation of this species is vital for wider ecosystem processes and biodiversity maintenance.

Keywords Temperate reefs · Kelp forest ecosystems · Benthic communities · Marine biodiversity · Humboldt current system · ENSO

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Introduction

Marine foundation species (e.g., seagrasses, reef-building corals and large macroalgae) maintain biodiversity and structure local communities (Bruno and Bertness 2001; Angelini et al. 2011) by modifying environmental conditions (Miller et al. 2018), increasing food availability (Muthukrishnan et al. 2020), and directly providing biogenic habitat for a vast array of associated species (Teagle et al. 2017; Thomsen et al. 2022). In many regions, however, they are increasingly impacted by a range of human-mediated stressors, such as ocean warming (Thomson et al. 2015; Sorte et al. 2017), habitat degradation (Lenihan and Peterson 1998; Cheevaporn and Menasveta 2003) and direct extraction (Lorentsen et al. 2010; Gouraguine et al. 2021), at times diminishing their functional role within coastal ecosystems. Therefore, there is a critical need to understand how marine foundation species structure associated communities and influence local biodiversity patterns to better inform and improve their management and conservation.

Kelps (large canopy-forming macroalgae belonging to the order Laminariales) are distributed across one-third of the world's coastlines (Jayathilake and Costello 2020; Duarte et al. 2022) and the forests they form represent some of the most diverse and productive habitats on Earth (Steneck et al. 2002; Pessarrodona et al. 2022) that in turn provide a wealth of ecosystem services to human society (Bennett et al. 2016; Eger et al. 2021). Kelp-associated communities are typically diverse, abundant and variable (Anderson et al. 2005; Arkema et al. 2009; Teagle et al. 2018; Bué et al. 2020; King et al. 2021)—being structured by a range of processes operating across multiple spatial and temporal scales—and play a central role in overall ecosystem functioning (Byrnes et al. 2006; Schaal et al. 2016). However, the distribution and structure of kelp populations and their associated communities are strongly influenced by environmental change factors, including ocean warming (Smale 2020), decreased water quality (Desmond et al. 2015), extreme storm events (Byrnes et al. 2011), disease outbreaks (Eisaguirre et al. 2020), overfishing (Ling et al. 2009), overgrazing by sea urchins (Ling et al. 2015), and the spread of invasive non-native species (Levin et al. 2002).

To effectively predict and manage the impacts of environmental change, a robust understanding of current biodiversity patterns and key processes that structure communities is required. In many regions, such as California, the Great Southern Reef in Australia, and parts of northwest Europe, variability in the structure of kelp forest ecosystems has been well-documented, providing reliable baselines against which to detect change (e.g., Reed et al. 2011;

Wernberg et al. 2011; Smale and Moore 2017). However, kelp forest ecosystems in other regions, such as the Humboldt Current system in the southeast Pacific, are less well studied (but see Pérez-Matus et al. 2017; Gouraguine et al. 2021), resulting in pressing knowledge gaps that hinder approaches to kelp forest management and conservation.

The vast (~2500 km) coastline of Peru is bathed in cool, nutrient-rich waters associated with wind-driven upwelling characteristic of the Humboldt Current system (HCS) (Chavez et al. 2008). These waters support extensive biological production, fueling food webs and maintaining fisheries such as the Peruvian anchoveta (*Engraulis ringens*) and Humboldt squid (*Dosidicus gigas*), which are vital for regional economies (Gozzer-Wuest et al. 2021). Shallow subtidal habitats are known to support extensive stands of several kelp species (i.e., *Macrocystis pyrifera* and *Lessonia trabeculata*, which are restricted to southern Peru, and *Eisenia cokeri*, which extends further north) that are likely to underpin rich and productive ecosystems. However, patterns of local biodiversity and variability in the structure of kelp populations and their associated communities remain almost entirely unknown for this system (but see Carbajal et al. 2022; Uribe et al. 2022). This is a particularly pressing knowledge gap, as seaweed harvesting in Peru has intensified markedly in recent years, primarily to meet increasing demand from the alginate industry (Avila-Peltroche and Villena-Sarmiento 2022). As such, understanding how kelp species here function as foundation species is vital to inform effective management and conservation.

Here, we examined the diversity and structure of faunal assemblages associated with the forest-forming kelp *Eisenia cokeri*, an understudied kelp species which is distributed in discrete patches of high densities along the Peruvian coast (Howe 1914; Acleto 1971), across multiple sites, seasons, and years in the north-center of Peru. The overall aims of the study were to: (i) document spatiotemporal patterns in ecological structure; (ii) compare the diversity, abundance, and structural and functional variability of assemblages associated with *E. cokeri* holdfasts to those on adjacent understory reef surfaces; and (iii) provide a robust and reliable baseline of kelp forest diversity that can serve as a benchmark against which to detect any future ecological change.

Methods

Study area

This study was conducted along the coastline of the Ancash region in Peru (Fig. 1), which is characterized by cliffs, small inlets, and abundant shallow rocky reefs that are moderately-to-fully exposed to wave action. The rocky seabed is typically heterogeneous, forming a mosaic of volcanic rock

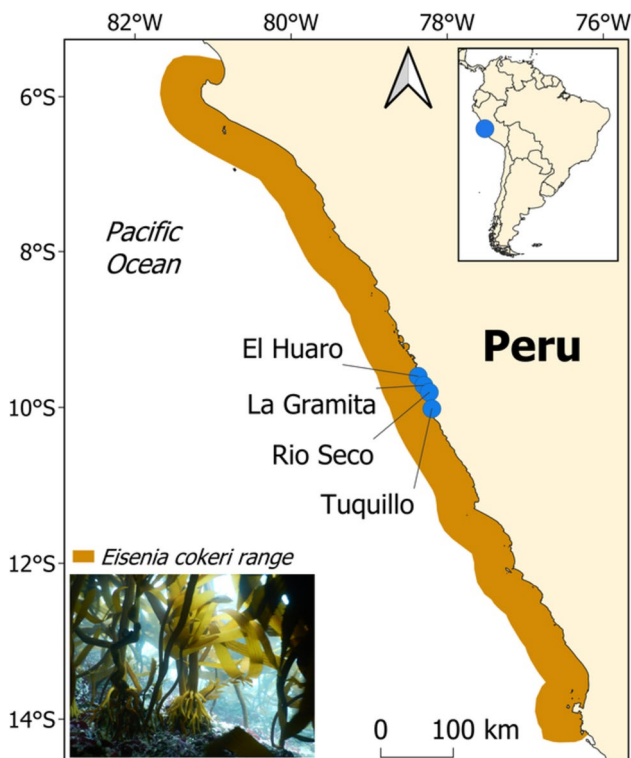


Fig. 1 Location of the study sites in the Ancash region of Peru. Inset map shows position of study area within South America and inset image depicts a typical *Eisenia cokeri* forest sampled during the study. Approximate distribution of *E. cokeri* also shown (light brown shading) as described by Howe (1914) and Acleto (1971)

platforms, small and large boulders and rocks, patches of sand, and accumulations of shells and pebbles extending to depths of ~12 m (Uribe et al. 2022). At higher latitudes in Peru, the distribution of *E. cokeri* overlaps with other habitat-forming kelp species (i.e., *Macrocystis pyrifera*, *Lessonia trabeculata*). However, in the Ancash region and further north, *E. cokeri* is the only kelp species present within the ecosystem. Site selection was based on previous explorations and the knowledge of local artisanal fishermen. Sampling was conducted at four subtidal reef sites distributed across 60 km of coastline (Fig. 1). Each site (from north to south: El Huaro, La Gramita, Rio Seco, Tuquillo) was characterized by extensive monospecific stands of *Eisenia cokeri* and was not obviously impacted by local stressors such as excessive sediment loading or nutrient/pollutant inputs. All sites are located within the Northern Humboldt Current System (NHCS) and are influenced by cool, nutrient-rich waters drawn to surface by intense coastal upwelling (Tarazona and Arntz 2001). Environmental conditions are strongly mediated by the El Niño Southern Oscillation (ENSO) which drives pronounced interannual variability with both warm (El Niño) and cool (La Niña) periods (Tarazona and Arntz 2001).

Sampling procedure and laboratory analyses

Sampling was conducted by divers using ‘Hookah’ (i.e., surface air supply) during a total of six sampling events between 2016 and 2020, with each site sampled at least five times. At each site and on each sampling event, nine adult kelp without fused holdfasts were selected from within *E. cokeri* stands at ~5–8 m depth. Each kelp stipe was cut at the first growing meristem and a numbered plastic bag was placed over the holdfast to ensure macroinvertebrates did not escape, before it was carefully removed from the substrate using a knife and chisel. Assemblages on understory reef surfaces adjacent to holdfasts were sampled using a 25 × 25 cm (i.e., 0.625 m²) quadrat ($n=9$) and a putty knife carefully removing all macroinvertebrates from the rock which were collected and placed in numbered plastic bags. At the surface, samples were fixed with 96% ethanol and stored for subsequent processing. In the laboratory, samples were sieved through a 0.5 mm mesh. Individual haptera were dissected to remove organisms inhabiting interstices of the holdfasts. Macrofauna were identified to the lowest possible taxonomic level (usually species), enumerated (number of individuals) and weighed (fresh weight biomass). Only taxa that could be enumerated by individual density were recorded; encrusting or colonial taxa (i.e., sponges, ascidians, turf red algae, bryozoans) were not included in the current study. Taxa were also assigned to coarse taxonomic and trophic groupings (based on expert knowledge and regional taxonomic keys).

Environmental conditions

A range of biological and physical factors were measured to define the environmental conditions at each site and for each sampling event. The densities of key herbivores known to graze kelp plants (specifically the urchins *Tetrapygus niger* and *Caenocentrotus gibbosus* and the gastropod *Tegula* spp.) were quantified within ~9 haphazardly placed 1 m² quadrats. The depth of each of the nine holdfasts collected was recorded, corrected for the tide, and averaged. Satellite-derived sea surface temperature (SST) data were obtained from the National Oceanic and Atmospheric Administration (NOAA) Optimum Interpolation Sea Surface Temperature (OISST) v2 high-resolution gridded data set. Eckman upwelling data were obtained from wind velocity measurements processed by NOAA CoastWatch, using data extracted from the Advanced Scatterometer (ASCAT) data set on Meteorological Operational (MetOp)-B obtained from the European Organisation for the Exploitation of Meteorological Satellites (EUMETSAT) Ocean and Sea Ice Satellite Application Facility (OSI SAF) provided through the Royal Netherlands Meteorological Institute (KNMI). All data were downloaded from NOAA CoastWatch (<https://coast>

watch.pfeg.noaa.gov/data.html). Both data sets (i.e., SST and Eckman upwelling) have a spatial resolution of 0.25 degrees. OISST data have a temporal resolution of 1 day, while ASCAT MetOp-B data have a temporal resolution of six hours. For each location, daily measurements were averaged over a 3-month period prior to each sampling event, with El Huaró and La Gramita falling into the same 0.25 degree spatial grid, and Río Seco and Tuquillo occupying independent 0.25 degree spatial grids. Wave exposure values were obtained from a wave fetch model (Burrows et al. 2008), based on distances to the nearest land in all directions around each 200 m coastal cell for the Peruvian coastline.

Statistical analyses

Patterns were initially explored by generating mean values (\pm standard error) for assemblage-level metrics (i.e., taxon richness, total abundance, and biomass) and by comparing the relative abundances of coarse taxonomic and functional (trophic) groups. Variability in abundance, biomass and richness was then formally examined via univariate Permutational Analysis of Variance (PERMANOVA) (Anderson 2001), based on Euclidean distances of untransformed data and implemented in PRIMER with the PERMANOVA add-on. Models consisted of the factors ‘habitat’ (fixed, two levels; holdfast and understory reef), ‘site’ (random, four levels; El Huaró, La Gramita, Río Seco, Tuquillo) and ‘event’ (random, Nov-16, Mar-18, Aug-18, Feb-19, Jul-19 and Feb-20, nested within site to account for the hierarchical sampling design), with significance accepted at $p < 0.05$ and based on 9999 permutations. Differences in multivariate assemblage structure were examined using PERMANOVA based on Bray–Curtis dissimilarity and square-root transformed abundance data, with permutations conducted under the model described above. The multivariate dataset was square-root transformed prior to analysis to down-weight the importance of highly-abundant taxa. For both univariate and multivariate analyses, post hoc pairwise tests (comparable to pairwise Student t-test) were performed to determine where significant differences lay between habitat type and sites ($p < 0.05$). Although sites were initially chosen randomly to be representative of a wider pool (and, therefore, considered a random factor), it was also of interest for ecological and biogeographic reasons to compare these specific locations, and so pairwise post hoc tests were conducted where appropriate (Anderson et al. 2005). Whilst the sampling techniques differed between habitat types (i.e., holdfast collection versus quadrat clearances on reef surfaces), the typical volume/area/biomass of samples was broadly comparable between habitats. However, as this discrepancy in sampling technique could have led to biases in terms of absolute values, we also calculated the relative (i.e., proportional) abundances of coarse taxonomic/trophic groups, effectively standardizing

for sample size, to compare assemblages across habitats, sites and events.

Results

Site characteristics

Across the study, the depth of sampling ranged from 5.3 to 8.3 m and was broadly comparable across sites and events (Table 1). SST ranged from 17.5 to 21.8 °C and maximum within-site range was 4.0 °C. Upwelling intensity varied by several orders of magnitude across sampling events, with particularly strong upwelling observed in August 2018 and July 2019 at all sites (Table 1). Wave fetch was broadly comparable across sites, with El Huaró being the most sheltered and La Gramita being the most exposed to wave action (Table 1). The densities of sea urchins and gastropod grazers were highly variable across sites and events and reached maximum values of 29 and 315 inds.m⁻², respectively. However, average total grazer density was typically greater at El Huaró (~130 inds.m⁻²) and Río Seco (~140 inds.m⁻²) compared with La Gramita (~45 inds.m⁻²) and Tuquillo (~70 inds.m⁻², Table 1). The size of holdfasts was also variable across sites and events, with the lowest average holdfast weight (92.3 g) and volume (85.6 ml) recorded in November 2016 at Tuquillo and the highest average weight (303.4 g) and volume (252.3 ml) recorded in July 2019, also at Tuquillo (Table 1). That said, holdfast parameters were comparable between sites when averaged across sampling events, with wet weight ranging from ~150 g (La Gramita) to ~180 g (El Huaró) and volume ranging from 126 ml (La Gramita) to 155 ml (El Huaró).

Macrofaunal assemblage structure

Across the study and both habitat types (i.e., holdfast and understory reef), ~55,000 individuals representing 183 taxa were recorded. Faunal assemblages associated with *E. cokeri* holdfasts were typically diverse and abundant (Fig. 2). The abundance of individuals and number of taxa per holdfast ranged from 28 to 792, and from 7 to 52, respectively. Holdfast assemblages were dominated by arthropods (45% of individuals), annelids (31%) and echinoderms (14%) (Fig. 3). Understory reef-associated assemblages were less diverse, with taxon richness ranging from 0 to 24 per quadrat, while the total abundance of individuals was highly variable and ranged from 0 to 1646. Reef-associated assemblages were dominated by molluscs (66% of individuals), annelids (17%) and arthropods (14%) (Fig. 3).

Univariate PERMANOVA detected a significant interaction between habitat and sampling event (Table 2), suggesting that variation between habitat types was not consistent

Table 1 Summary of biological and physical conditions at each site and sampling event

Site	Sampling event	Physical				Biological			
		Depth (m)	SST (°C)	Upwelling (m s ⁻¹)	(log)Wave fetch (km)	Urchin density (mean ind. m ⁻¹ ± se)	Gastropod density (mean ind. m ⁻¹ ± se)	Holdfast weight (mean g ± se)	Holdfast volume (mean g ± se)
El Huaro	Mar-18	8.3	18.49	7.12 × 10 ⁻⁶	4.27	10.33 ± 2.72	48.44 ± 27.89	174.79 ± 32.98	154.11 ± 29.00
	Aug-18	7.7	17.64	9.56 × 10 ⁻⁶	4.27	13.78 ± 4.08	158.22 ± 34.16	178.49 ± 31.72	156.89 ± 27.81
	Feb-19	7.8	21.52	4.82 × 10 ⁻⁶	4.27	18.22 ± 2.90	315.11 ± 78.84	208.74 ± 30.65	182.67 ± 26.10
	Jul-19	8.3	18.42	1.28 × 10 ⁻⁵	4.27	9.89 ± 5.50	45.67 ± 37.53	174.40 ± 20.59	150.22 ± 17.34
	Feb-20	7.6	19.51	1.78 × 10 ⁻⁶	4.27	15.6 ± 10.63	37.40 ± 15.35	164.77 ± 19.85	137.78 ± 15.95
La Gramita	Nov-16	6.9	17.50	8.66 × 10 ⁻⁶	4.44	1.56 ± 0.56	0.00 ± 0.00	102.14 ± 16.43	93.64 ± 13.74
	Mar-18	6.8	18.49	7.12 × 10 ⁻⁶	4.44	2.33 ± 0.80	73.78 ± 38.68	126.73 ± 5.29	95.67 ± 9.08
	Aug-18	7.0	17.64	9.56 × 10 ⁻⁶	4.44	7.56 ± 3.32	125.67 ± 77.43	203.55 ± 23.22	169.00 ± 14.27
	Feb-19	6.6	21.52	4.82 × 10 ⁻⁶	4.44	1.78 ± 0.62	7.44 ± 3.02	181.05 ± 35.66	155.22 ± 29.56
	Jul-19	6.3	18.42	1.28 × 10 ⁻⁵	4.44	2.00 ± 0.65	7.44 ± 3.73	142.82 ± 19.49	119.67 ± 16.23
Rio Seco	Nov-16	5.3	19.24	5.18 × 10 ⁻⁶	4.31	29.67 ± 5.63	64.78 ± 28.69	153.83 ± 31.42	130.00 ± 21.70
	Mar-18	5.3	17.85	9.86 × 10 ⁻⁶	4.31	22.78 ± 8.79	268.11 ± 126.14	228.60 ± 21.19	194.78 ± 17.59
	Aug-18	7.8	18.96	1.15 × 10 ⁻⁵	4.31	6.33 ± 1.96	84.89 ± 42.10	134.38 ± 20.10	115.00 ± 19.19
	Feb-19	7.9	17.82	3.08 × 10 ⁻⁶	4.31	6.22 ± 0.90	3.33 ± 1.70	163.73 ± 23.66	136.89 ± 19.53
	Jul-19	6.9	21.75	1.09 × 10 ⁻⁵	4.31	9.89 ± 1.39	14.22 ± 7.60	149.77 ± 19.83	121.33 ± 16.15
	Feb-20	7.2	18.86	2.12 × 10 ⁻⁶	4.31	22.60 ± 8.60	278.40 ± 117.80	126.93 ± 23.58	105.78 ± 22.19
Tuquillo	Nov-16	7.0	17.72	4.37 × 10 ⁻⁶	4.28	1.22 ± 0.88	40.89 ± 24.94	92.30 ± 12.90	85.56 ± 11.76
	Mar-18	7.7	19.01	9.18 × 10 ⁻⁶	4.28	4.67 ± 1.20	54.67 ± 13.94	111.56 ± 12.93	93.89 ± 10.87
	Aug-18	8.3	17.68	1.26 × 10 ⁻⁵	4.28	1.22 ± 0.72	26.00 ± 17.38	170.35 ± 21.16	120.44 ± 9.17
	Feb-19	7.8	21.24	2.84 × 10 ⁻⁶	4.28	5.33 ± 0.90	160.78 ± 71.83	149.85 ± 24.08	128.56 ± 19.64
	Jul-19	6.7	18.73	1.17 × 10 ⁻⁵	4.28	1.44 ± 0.60	61.33 ± 17.25	303.38 ± 21.10	252.33 ± 19.90

across sampling events. Significant main effects of habitat and event were also detected, with higher overall abundances associated with holdfast rather than reef assemblages, and pronounced variability amongst sampling periods (Table 2, Fig. 2). For holdfast assemblages, abundances ranged from 89.3 ± 14.2 (La Gramita, July-2019) to 510.9 ± 57.5 (El Huaro, February-2019) and was markedly more variable over time at El Huaro and La Gramita compared with Rio Seco and Tuquillo (Fig. 2). For reef assemblages, mean total abundance ranged from 6.5 ± 1.4 (Tuquillo, August-2018) to 457.6 ± 215.8 (Rio Seco, March-2018), with much greater variability between sampling events (e.g., at Rio Seco).

For total biomass, univariate PERMANOVA detected significant main effects of habitat, site and event (Table 2). Post hoc tests indicated that total biomass was greater at El Huaro and Rio Seco compared with La Gramita, and higher in holdfasts than on reef surfaces. The mean total biomass of holdfast assemblages ranged from 3.4 ± 1.5 g (Tuquillo, March-2018) to 26.4 ± 4.3 g (Rio Seco, March-2018) and was generally consistent between sampling events, while total biomass of reef assemblages ranged from 1.5 ± 0.3 g (Tuquillo, November-2016) to 42.3 ± 19.5 g (Rio Seco, March 2018) and exhibited greater variability (Fig. 2).

For mean richness, significant main effects of habitat and event were detected (Table 2), with consistently higher values associated with holdfast compared to reef assemblages. The mean number of taxa per holdfast ranged from 17.0 ± 1.6 (El Huaro, July-2019) to 30.7 ± 3.5 (La Gramita, February-2019), with richness values remaining relatively consistent across sites and over sampling events (Fig. 2, Table 2). Mean richness of reef assemblages ranged from 4.1 ± 0.7 (El Huaro, August-2018) to 12.0 ± 2.1 (La Gramita, March-2018) and were broadly comparable across sites and events. Overall, holdfast assemblages exhibited higher richness than reef assemblages, and the magnitude of variation between sampling events was not entirely consistent across sites (Fig. 2).

Overall composition of assemblages differed markedly between habitat types, with a greater relative abundance of arthropods, annelids and echinoderms in holdfast assemblages and a higher proportion of molluscs in understory reef assemblages (Fig. 3). For holdfast assemblages, the relative abundance of major taxonomic groups was relatively consistent across sites and events, whereas broad taxonomic composition was markedly more variable for reef-associated assemblages (Fig. 3). At a fine taxonomic level, the

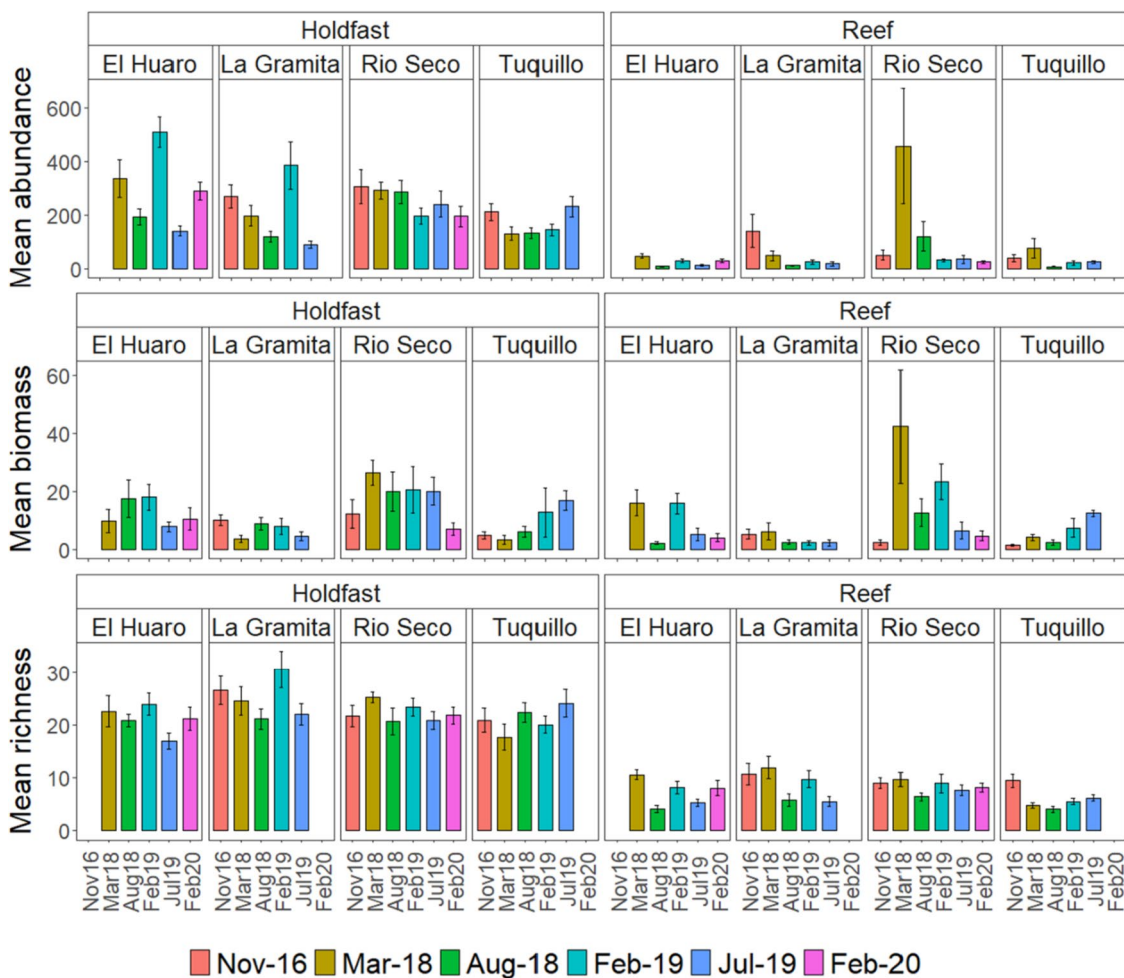


Fig. 2 Mean abundance, biomass (in g) and taxon richness per holdfast and understory reef sample for each site and sampling event. Values are means \pm standard error (SE). N.B. El Huardo was not sampled

in November 2016 and neither La Gramita nor Tuquillo were sampled in February 2020

ten most-commonly recorded taxa across each habitat type exhibited contrasting variability patterns (Fig. 4). In general, the abundances of common taxa within holdfast assemblages were more consistent across sites and events compared with those in reef-associated assemblages (Fig. 4). For example, the abundances of two of the most commonly recorded taxa in the holdfast assemblages, the polychaete *Ehlersia* sp. and the amphipod *Aora typica*, were largely consistent across sites and events (Fig. 4). In contrast, the gastropod *Caecum chilense* and *Hydroides* sp1, which were both abundant in reef-associated assemblages, exhibited markedly greater spatiotemporal variability. The abundance of the bivalve *Semimytilus algosus* was notably variable in both habitats, with very high abundances at Rio Seco in March and August 2018 (Fig. 4).

The relative abundance of different trophic groups also differed between assemblage types, with greater representation of carnivores in holdfasts and higher relative

abundances of filter and deposit feeders within reef assemblages (Fig. 5). Trophic group composition within holdfast assemblages was broadly comparable between sites and varied somewhat between sampling events, but inconsistently (Fig. 5). The relative abundance of trophic groups within reef-associated assemblages was generally more variable across sites and events (Fig. 5).

Multivariate assemblage structure (based on absolute abundances) varied significantly across all main effects and interaction terms (Table 2). MDS ordination of the entire dataset showed clear partitioning between holdfast and reef assemblages, with much greater within-group variability and dispersion for reef compared with holdfast assemblages (Fig. 2). Each assemblage type was then analyzed separately to examine variability between sites and events (Fig. 6). In both cases, assemblage structure was highly variable and did not clearly partition between sites and events (Fig. 6). Even so, once samples were averaged to each site/event

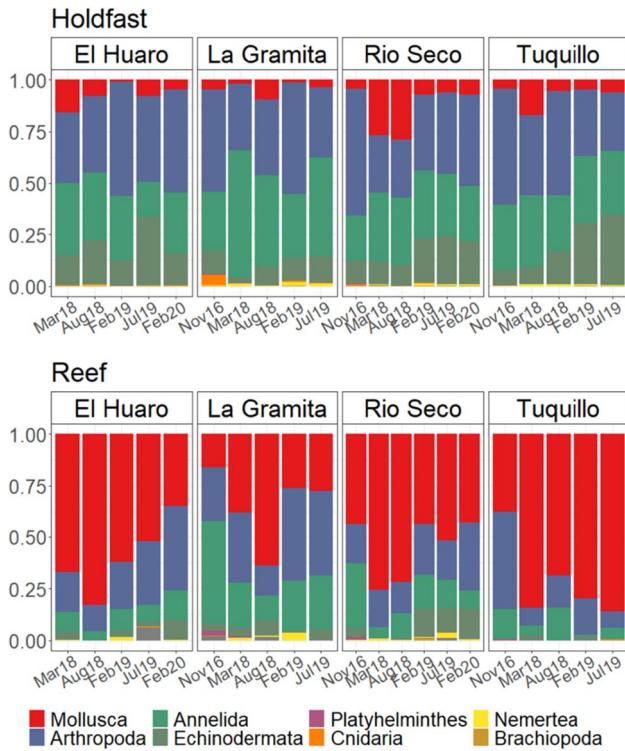


Fig. 3 Relative abundance of major taxonomic groups for both holdfast and understory reef assemblages for each site and sampling event. N.B. El Huaro was not sampled in November 2016 and neither La Gramita nor Tuquillo were sampled in February 2020

combination, some structuring was evident, particularly between Rio Seco and Tuquillo, for both assemblage types (Fig. 6).

Discussion

Our study is the first to examine spatiotemporal variability in the structure and diversity of faunal assemblages associated with the kelp *Eisenia cokeri*. These kelp forest communities are notably rich, with > 180 distinct taxa recorded across four sites, and comprised a diversity of taxonomic and trophic groups. As such, kelp forests underpinned by *E. cokeri* are likely to play an important role in the wider coastal ecosystem of the Northern Humboldt Current System (NHCS) region. Overall, holdfast assemblages exhibited greater abundance, biomass and richness compared with understory assemblages on reef surfaces, while coarse taxonomic and functional composition differed between the two habitat types. Our study suggests that *E. cokeri* serves as an important foundation species in Peru, by structuring associated communities and maintaining local diversity.

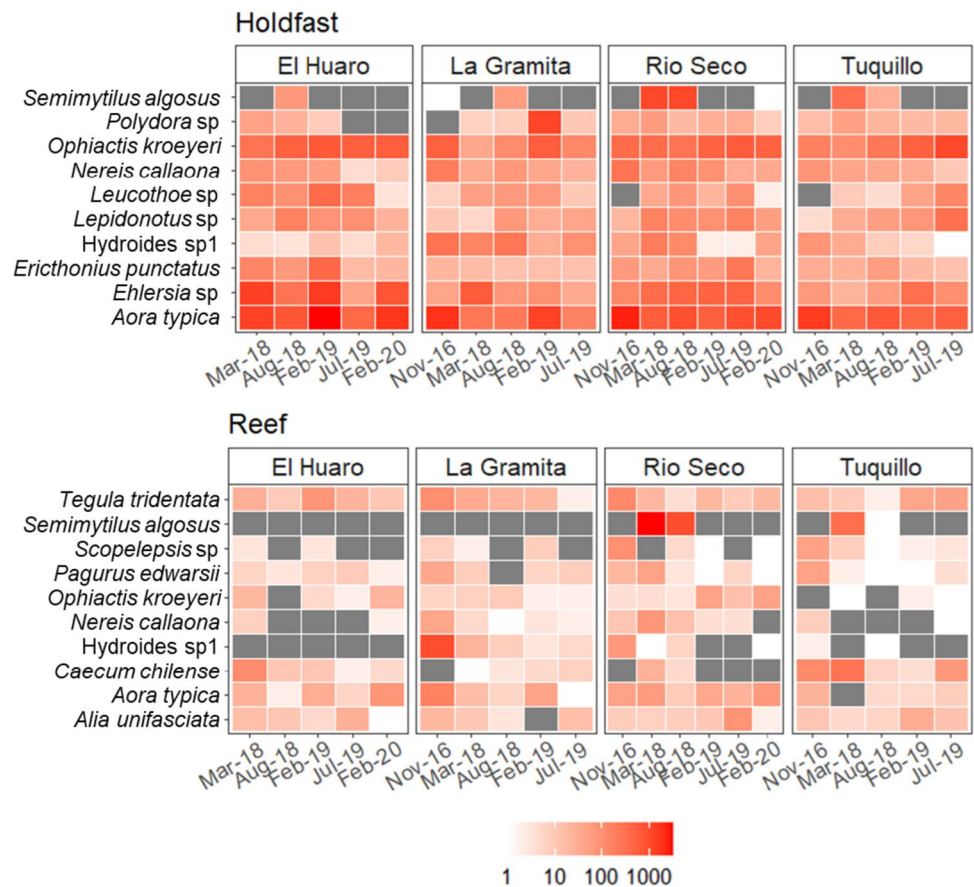
It is well established that kelp holdfasts serve as favorable habitat for macroinvertebrates, by providing complex biogenic living space that offers protection from predators and physical disturbance, as well as increased food supply (reviewed by Teagle et al. 2017). In comparison, reef surfaces generally offer less complexity and protection, although understory macroalgal assemblages can be functionally and morphologically diverse and support rich faunal assemblages (Bué et al. 2020; Smale et al. 2020). It is evident that the structurally complex and intricate holdfasts of *E. cokeri*, as with other kelp species globally (Teagle et al. 2017), form favourable habitat and support higher levels of diversity than adjacent denuded reef surfaces. A

Table 2 Results of PERMANOVA tests to examine variability between habitats, sites and sampling events, for (a) total abundance, (b) total biomass, (c) total richness and (d) multivariate assemblage structure

(a) Abundance				(b) Biomass			
Source	df	F	P	Source	df	F	P
Habitat	1	30.1	0.012	Habitat	1	11.4	0.043
Site	3	1.2	0.311	Site	3	3.9	0.023
Event (site)	17	5.4	0.001	Event (site)	17	3.4	0.001
Habitat × site	3	1.5	0.270	Habitat × site	3	0.2	0.921
Habitat × event (site)	17	3.5	0.001	Habitat × event (site)	17	0.9	0.598
(c) Richness				(d) Multivariate structure			
Source	df	F	P	Source	df	F	P
Habitat	1	683	0.001	Habitat	1	27.4	0.001
Site	3	2.2	0.117	Site	3	1.8	0.001
Event (site)	17	3.0	0.001	Event (site)	17	3.3	0.001
Habitat × site	3	1.2	0.351	Habitat × site	3	1.6	0.017
Habitat × event (site)	17	0.8	0.581	Habitat × event (site)	17	1.8	0.001

Significant *P*-values are shown in bold

Fig. 4 Heat map of the abundance of the top ten most common taxa recorded across the study, for each site and sampling event. Grey shading indicates absence. N.B. El Huaro was not sampled in November 2016 and neither La Gramita nor Tuquillo were sampled in February 2020



previous study by Carbajal et al. (2022), conducted at a single site, also reported higher richness associated with *E. cokeri* holdfasts compared with adjacent understory reef surfaces. Our study corroborates this finding and indicates that this is a general, consistent feature of this ecosystem. As well as higher richness, holdfast structures generally supported higher abundance and biomass than understory reef assemblages, although differences were less consistent. This likely relates to a greater total habitat volume (i.e., living space) within intricate kelp holdfasts compared to the more homogenous and less complex reef surface. Given that holdfast structures offer protection from predators (Feehan et al. 2014) and increased food supply through accumulation of allochthonous organic matter (Schaal et al. 2012), it is perhaps not surprising that they often support greater faunal abundances than less structured microhabitats.

Holdfast assemblages exhibited dissimilar multivariate structure and taxonomic and trophic composition compared to reef assemblages. In general, holdfast assemblages supported greater relative abundances of arthropods, annelids, echinoderms, and carnivorous taxa, whereas reef assemblages comprised a higher proportion of molluscs and deposit/filter feeders. Elevated abundances of small predators (e.g., crabs, echinoderms) within kelp holdfasts have

been reported from other systems (Ojeda and Santelices 1984; Leclerc et al. 2015), as internal living spaces within holdfasts offer shelter from hydrodynamic disturbances and refuge from larger predators, particularly during periods of inactivity. The higher relative abundances of filter feeders (e.g., bivalves, molluscs) on reef surfaces likely relate to stochastic recruitment events and the sensitivity of delicate filter-feeding sessile organisms to increased sedimentation rates within holdfasts (Teagle et al. 2018). The differing taxonomic and trophic structure between holdfast and reef assemblages suggest that these assemblages also differ in their ecological functioning (Schaal et al. 2012). More generally, previous examinations of holdfast assemblages from other host kelp species and regions have often revealed a dominance of arthropods and polychaetes (Ríos et al. 2007; Tuya et al. 2011; Teagle et al. 2018), as reported here, which emerges as a general feature of these communities.

Perhaps most importantly, reef assemblages exhibited far greater spatial and temporal variability compared with holdfast assemblages, which were markedly more similar between sites and sampling events. Spatially, holdfast assemblages exhibited greater similarity both between and within sites, compared with reef assemblages which were far more heterogenous. Similarly, reef assemblages were less consistent through time, with abundances of key taxa highly

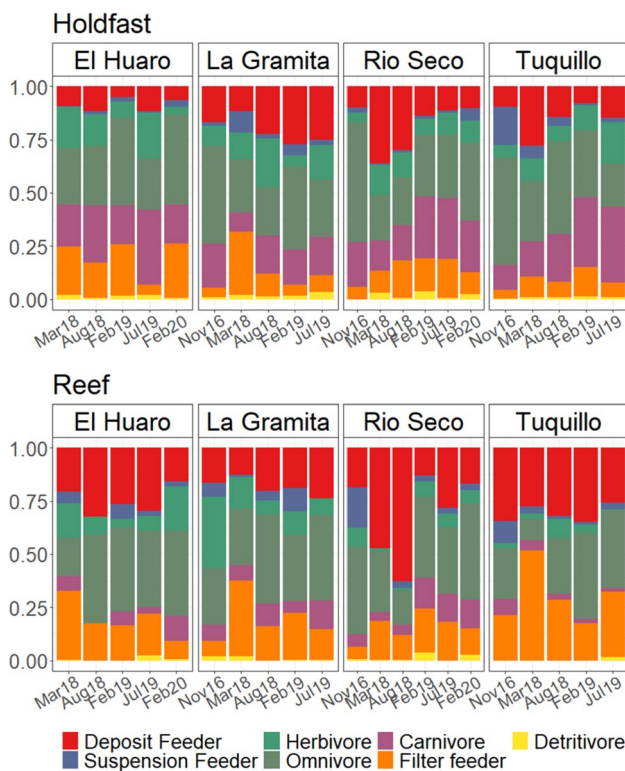


Fig. 5 Relative abundance of trophic groups for both holdfast and understory reef assemblages for each site and sampling event. N.B. El Huario was not sampled in November 2016 and neither La Gramita nor Tuquillo were sampled in February 2020

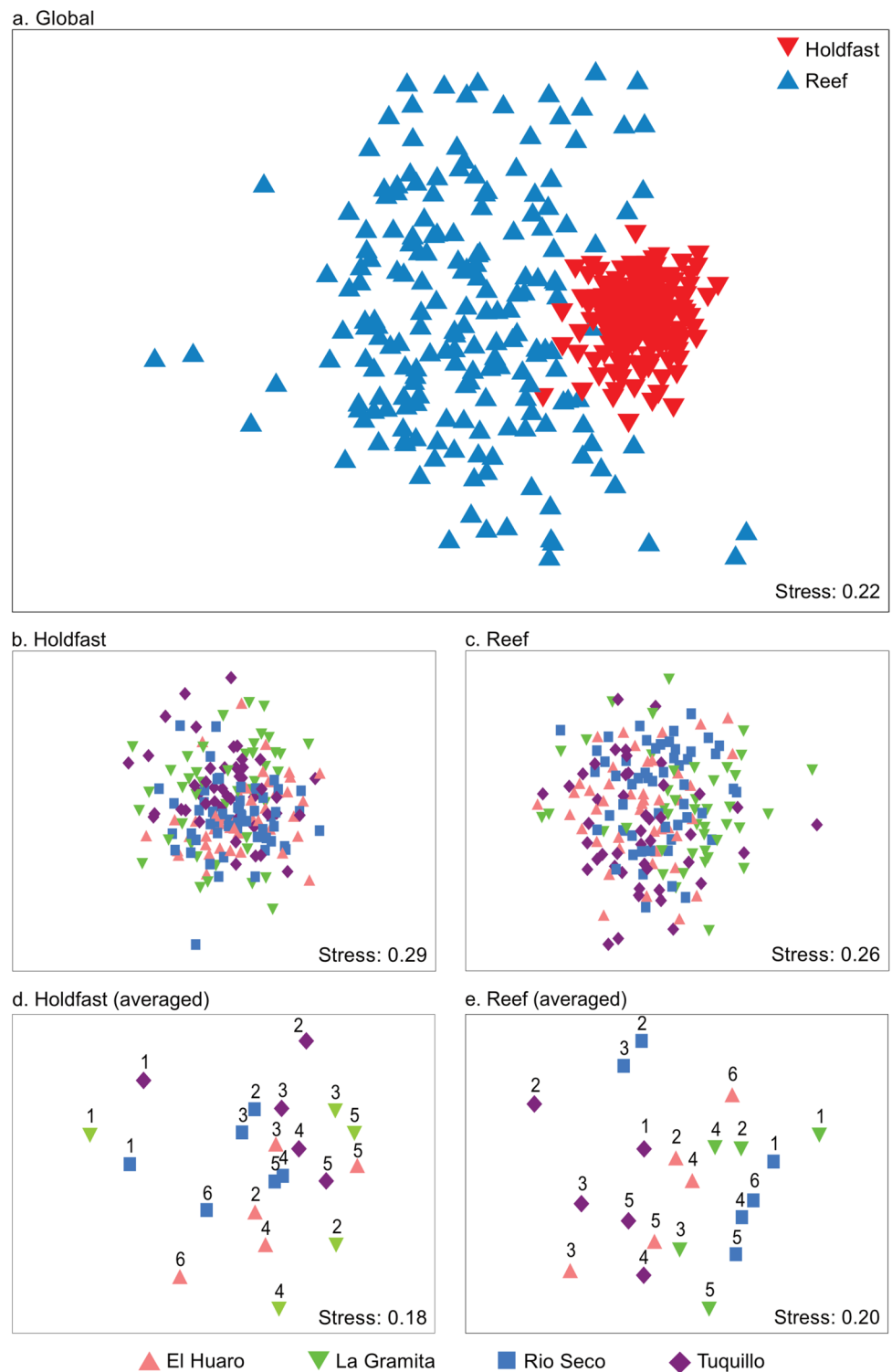
variable between sampling events. This suggests that kelp holdfasts are perhaps less influenced by environmental variability, stochastic events, and disturbances, offering more stable habitats, and facilitating the development and persistence of populations and assemblages through time. A similar pattern has been observed in *Laminaria* forests in the northeast Atlantic (Leclerc et al. 2016). Even so, we did record some temporal variability in holdfast assemblage structure, likely relating to seasonal differences in recruitment and population dynamics (Ríos et al. 2007; Winkler et al. 2017; Akita et al. 2019), intra- and interannual variability in environmental factors such as upwelling strength, storm disturbances that affect kelp population structure and associated species

abundances (Christie et al. 2009; Castorani et al. 2018), and sporadic or stochastic recruitment events (Watanabe 1984; Pearse and Hines 1987). For example, in both habitat types we observed intense sporadic recruitment of the bivalve *Semimytilus algosus* at Rio Seco in 2018, likely driven by variability in ocean currents and connectivity that caused overall shifts in assemblage structure.

We observed significant site-level variability for most assemblage metrics. While the processes driving spatial variability at the scale of kilometers remain unclear and warrant further investigation, a number of environmental factors varying at this spatial scale could underpin the observed differences in ecological pattern. Here, depth, upwelling strength, wave fetch and temperature were broadly comparable across the study sites, whereas variability in grazer density was more pronounced, with typically greater abundances recorded at El Huario and Rio Seco. Differences in grazing pressure may influence both kelp population structure and understory macroalgal assemblages, which in turn could affect faunal assemblages. Between-site variability in grazing pressure is known to be a key factor driving variability in kelp associated communities at that spatial scale (Leli-aert et al. 2000; Pérez-Matus et al. 2017), and may also be important in the HCS. Other factors, such as ocean currents and connectivity, predation pressure, food supply, sedimentation rates and habitat complexity and structure may also be important drivers of pattern and necessitate further research.

In conclusion, the understudied kelp *E. cokeri* functions as an important foundation organism in the HCS in Peru, by offering favourable habitat for a wide range of faunal species, elevating local biodiversity, and supporting wider ecosystem functioning. At higher latitudes, the distribution of *E. cokeri* overlaps with other habitat-forming kelp species (i.e., *Macrocystis pyrifera*, *Lessonia trabeculata*), where it supports distinct faunal assemblages (Carbajal et al. 2022). However, within the current study region there is limited functional redundancy, as no other warm-tolerant, habitat-forming macroalgae persist at such low latitudes (Uribe et al. 2022). It is imperative, therefore, that *E. cokeri* populations are effectively managed, conserved, and protected from stressors (e.g., direct harvesting, decreased water quality) to maintain biodiversity and overall ecosystem functioning.

Fig. 6 MDS plots depicting multivariate structure of faunal assemblages based on absolute abundances; **a** all holdfast and reef samples collected across the study, **b** holdfast and **c** reef associated assemblages analyzed separately, and **d** holdfast and **e** reef associated assemblages with centroids as averages for each site/event combination (numbers indicate sampling event with 1 being the first event and 6 being the final event)



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Data availability All data is available on request.

Declarations

Conflict of interest The authors declare no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed during sample and data acquisition in this study, including Animal Care and Use Protocols in place at IMARPE.

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