Diverse stability responses of a sub-Antarctic invertebrate understorey community to experimental giant kelp removal

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ABSTRACT: Ecological stability is crucial for understanding anthropogenic biodiversity loss and its consequences, especially when disturbances affect species that influence numerous others. The giant kelp *Macrocystis pyrifera*, an iconic foundation species, supports diverse communities on temperate and subpolar coasts. While giant kelp communities in temperate regions have been extensively studied, field-based manipulative research in subpolar latitudes is still limited. We investigated the resistance, resilience, and recovery of a community subjected to experimental giant kelp removal in a sub-Antarctic ecosystem. We simulated pulsed kelp loss caused by destructive storms and monitored the macrobenthic invertebrate understorey for 12 mo. The experimental disturbance elicited varying stability responses of the understorey. Understorey community biomass was strongly resistant to the disturbance but declined gradually (i.e. low resilience), showing incomplete recovery compared to undisturbed communities. Community density (total number of individuals per sample) increased notably following the removal (i.e. weak resistance) but ultimately returned to undisturbed levels (i.e. high resilience and complete recovery). Species composition exhibited low resistance and resilience, and no recovery from the disturbance. Secondary coextinctions of several understorey species accounted for the observed low compositional stability. In contrast to giant kelp communities in temperate latitudes, the slower recovery rates of kelp and the loss of key positive interactions likely contributed to the observed stability responses in this subpolar ecosystem's invertebrate understorey. By examining the response of a sub-Antarctic understorey community to giant kelp removal, our study enhances our understanding of how foundation species sustain local biodiversity.

KEY WORDS: Instability · Perturbation · Kelp forests · Harvesting · Community dynamics · Dimensionality · Marine

1. INTRODUCTION

Stability is at the heart of ecological research (Donohue et al. 2016, Kéfi et al. 2019). The study of ecological stability gains special relevance for fundamental and applied ecology when disturbances impact species that have strong effects on the community, such as foundation species. By forming key biogenic habitats and locally stable environmental conditions, foundation species control community structure, ecosystem functioning, and the provision of ecosystem services to people (Dayton 1972, Ellison

et al. 2005, Ellison 2019). While long-lived foundation species (e.g. corals) have received considerable attention in the ecological literature (reviewed by Ellison 2019), comparatively less research has been conducted to understand the stability of communities supported by short-lived, highly dynamic foundation species (e.g. mussels or kelps; Bulleri et al. 2012, Lamy et al. 2020, Valdivia et al. 2021a, Bularz et al. 2022).

Ecological stability (hereafter simply 'stability') refers to the ability of populations, communities, and ecosystems to resist and recover from disturbances (Pimm 1984, Grimm & Wissel 1997). Stability is, therefore, a multifaceted concept encompassing several dimensions (Donohue et al. 2013, Hillebrand et al. 2018). For example, resistance represents the degree to which an aggregate or compositional community property remains unchanged after a disturbance takes place, resilience is the recovery velocity after the disturbance (Pimm's resilience or Holling's engineering resilience), and recovery is the degree to which the community achieves pre-disturbance levels (Harrison 1979, Pimm 1984, Holling 1996, Grimm & Wissel 1997). Moreover, stability dimensions can be expressed in terms of species identities and abundances, or aggregate community-level properties like community biomass, cover, and density (i.e. compositional or aggregate stability, respectively; Micheli et al. 1999). The disparate associations (positive, neutral, and negative) observed among these properties indicate that several aspects of stability should be assessed simultaneously to understand the stability of an ecosystem (Harrison 1979, Donohue et al. 2013, Hillebrand et al. 2018, Radchuk et al. 2019, Polazzo & Rico 2021).

The giant kelp *Macrocystis pyrifera* is an important foundation species in temperate and subpolar regions of both hemispheres (Mann 1973, Graham et al. 2007, Krumhansl et al. 2016, Mora-Soto et al. 2020). Giant kelp forests have a range of ecosystem and meta-ecosystem effects, encompassing promoting biodiversity, providing trophic subsidies to neighbouring ecosystems, controlling biogeochemical fluxes, and supporting fisheries (reviewed in Miller et al. 2018, see also Pardo et al. 2021). Moreover, the stability of giant kelps (measured as invariability in biomass) directly enhances understorey species richness, which cascades into positive effects on understorey invariability and asynchrony (Miller et al. 2018, Lamy et al. 2020). These effects reflect, in part, negative effects of the physical structure of the giant kelp on understorey seaweeds (interference competition via shading) along with food and habitat provision to macro-

invertebrates (Schiel & Foster 2015, Castorani et al. 2018, Miller et al. 2018). In this vein, experimental removals of *M. pyrifera* have been shown to elicit secondary coextinctions of species with similar environmental tolerances (Graham 2004, Castorani et al. 2018, Morton et al. 2022), which can trigger significant aggregate and compositional stability responses.

The habitat-forming life stage (sporophyte) of *M. pyrifera* anchors to the seafloor by means of a holdfast and extends along the water column to the sea surface thanks to a group of buoyant fronds (Fig. 1). This large vertical structure is prone to mass loss from large waves that can even dislodge the sporophyte from the seafloor (Seymour et al. 1989, Dayton et al. 1992). Accordingly, wave disturbances can lead to the formation of large cleared patches within a giant kelp forest (Byrnes et al. 2011, Castorani et al. 2022). Yet, local kelp populations can recover from these perturbations in 1 or 2 yr thanks to dispersal from neighbouring localities and rapid post-settlement growth (Castorani et al. 2017). These dynamics in the abundance of giant kelps can influence the aggregate and compositional properties of the understorey community (Detmer et al. 2021). If the associated species are adapted to these fluctuations, then they can also recover rapidly (i.e. high resilience) and reach a relatively complete recovery at a similar temporal scale (Krumhansl et al. 2017). However, most manipulative and observational research on the ecological consequences of *M. pyrifera* loss — and kelps in general — comes from temperate regions, and less research has been conducted in subpolar latitudes (Krumhansl et al. 2016). Therefore, we still do not fully understand the role of giant kelp, as a foundation species, in the stability of local communities.

Here, we analysed multiple stability dimensions of a local community exposed to the experimental removal of *M. pyrifera* in a sub-Antarctic rocky subtidal. We explored the resistance, resilience, and recovery of both aggregate (community biomass and density) and compositional properties of a species-rich assemblage of macrobenthic invertebrates developing in a perennial giant kelp forest. In a rocky reef of the Strait of Magellan, Chilean south Patagonia, we mimicked a pulsed loss of giant kelp from extreme destructive storms and monitored the invertebrate community responses for 12 mo. We focused on understorey sessile and mobile invertebrates of this site because of their high taxonomic and functional diversity that encompasses 9 phyla and several feeding types, respectively (suspension feeders, grazers, scavengers, detritivores, and predators; Friedlander

Fig. 1. A giant kelp sporophyte (vegetative, habitat-forming life stage) at the border of a relatively homogeneous kelp patch. Photo credit: Ignacio Garrido

et al. 2023). Previous studies have shed important insights into spatiotemporal patterns of variation in Patagonian kelp forests (e.g. Santelices & Ojeda 1984a, Rios et al. 2007, Beaton et al. 2020, Hüne et al. 2021, Friedlander et al. 2023). For instance, observational work hints at a high temporal persistence of giant kelp forests at annual and centennial scales in the region (Mansilla et al. 2007, Palacios 2008, Mora-Soto et al. 2021). The experimental removal of *M. pyrifera* canopies in this region can have species-specific effects on biota thriving in a 2 layer understorey: in a secondary stratum beneath the primary *M. pyrifera* floating canopy, the disturbance reduces the biomass of *Lessonia flavicans* kelps; in a tertiary and deeper stratum, the disturbance favours the turnover of rare seaweeds without affecting species richness (Santelices & Ojeda 1984a). That early study did not consider, however, the diverse assemblage of invertebrates associated with *M. pyrifera*, which is the focus of our study. In our study, 2 interrelated hypotheses were investigated:

H_1: giant kelps ameliorate the abiotic environment and enhance habitat complexity, which strongly influences the population dynamics of several other species (e.g. Castorani et al. 2018). Thus, we predict that the aggregate and compositional resistance of the understorey to canopy removal should be low.

H_2: giant kelps, which have rapid generation times and growth rates, can be disturbed by storms and swells on an intra-annual basis (Dayton et al. 1992). If most understorey species are adapted to this temporal variation, then they could exhibit a fast resilience and relatively complete recovery within 1 yr after experimental canopy removal.

2. MATERIALS AND METHODS

2.1. Study site

The study was conducted between February 2017 and February 2018 at Bahía el Águila, located at the southern tip of Brunswick Peninsula in the Strait of Magellan, Chilean south Patagonia (53.785° S, 70.973° W; Fig. 2). At Bahía el Águila, the Strait of Magellan is ca. 9.5 km wide and reaches 200 m in

depth (Fig. 2A; Medeiros & Kjerfve 1988). The giant kelp forest forms a narrow and relatively homogenous alongshore belt, which broadens towards the bay's mouth (Fig. 2B; Mora-Soto et al. 2020) and spans from 2 to ca. 15 m deep. This is a perennial kelp forest that is observed persistently over the year (Mansilla et al. 2007, Palacios 2008). Nevertheless, the forest can exhibit broad density fluctuations. Mean giant kelp densities reach 1.06 ind. m^{-2} (SEM = 0.18) and 1.92 (0.34) ind. m^{-2} in autumn and spring, respectively (Palacios 2008). The maximum height of giant kelp canopies at Bahía el Águila ranges from 5.1–6.0 m in spring to more than 7.1 m in winter (Palacios 2008). The invertebrate understorey at the study site encompasses a phylogenetically diverse community of almost 150 species (Table S1 in the Supplement at www.int-res. com/articles/suppl/m716p063_supp.pdf).

Mean seawater temperature (salinity) at 7 m depth ranged from 9.3°C (28.5 PSU) in February 2017 to 7.6°C (29.5 PSU) in June 2017. Monthly mean of wind magnitude, an important driver of winter storms in this region, varied during the experiment between 1.37 and 5.19 m s^{-2} (mean: 3.22 m s^{-1}, n = 13; Fig. S1A). This range overlapped with 10 yr wind magnitude data (min.: 0.81 m s^{-1}, mean: 3.30 m s^{-1}, max.: 5.7 m s^{-1}, n = 132; Fig. S1A). Monthly sea level (cm) means ranged between 178 and 204 cm (mean: 190 cm, n = 13; Fig. S1B). Long-term sea level data exhibited similar ranges (min.: 157 cm, mean: 187 cm, max.: 204 cm, n = 132; Fig. S1B).

2.2. Experimental design and setup

The manipulative experiment included *Macrocystis* removal as a fixed factor with 2 levels: either disturbed or control. In February 2017, 6 (20 × 20 m) patches were equally distributed in 3 blocks and marked with buoys within the kelp forest (Fig. 2B). All blocks shared the same rocky substrate, and the relatively small size of the bay allowed us to assume relatively homogenous environmental conditions among blocks.

In each block, one of the patches was haphazardly assigned to the disturbed treatment (Fig. 2B), in which all *M. pyrifera* individuals were removed by detaching the holdfast from the substratum with the aid of chisels and knives. The disturbance was applied only once at the onset of the experiment — i.e. a pulse disturbance. According to available maximum
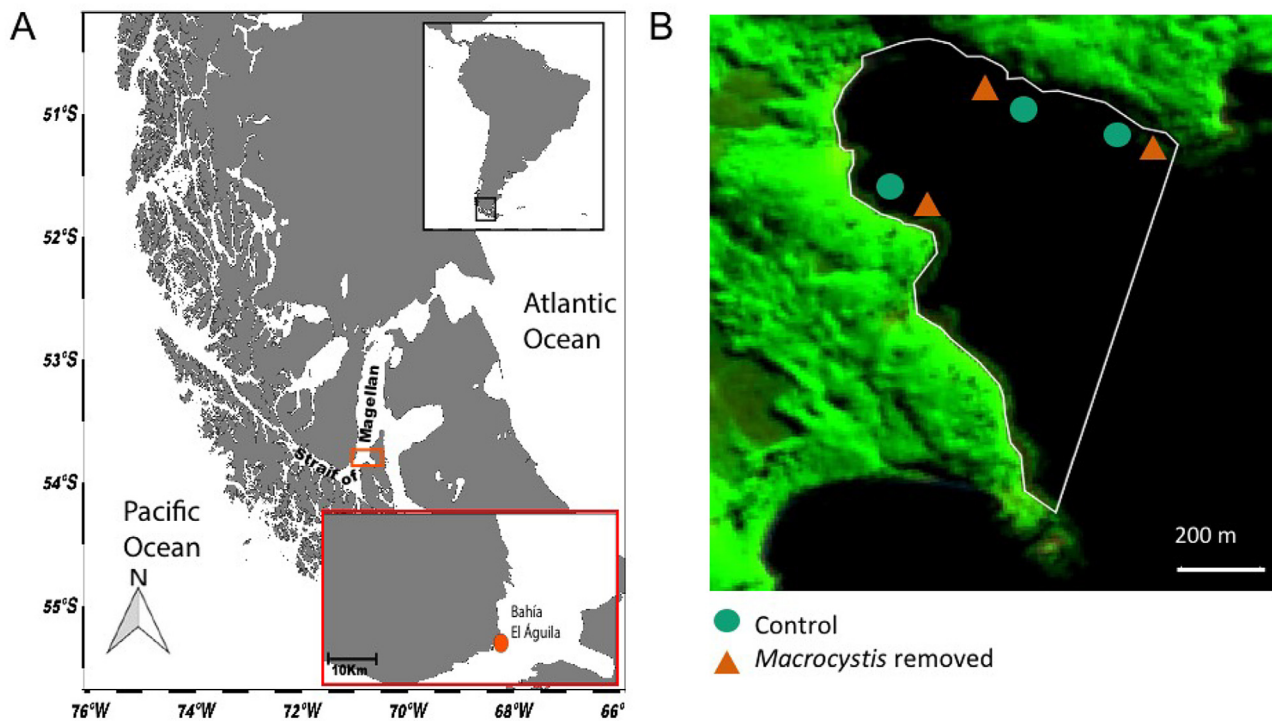

Fig. 2. Study site in Chilean south Patagonia. (A) Strait of Magellan in the southern tip of Peninsula Brunswick. (B) Bahía El Águila in March 2017. In (B), the kelp forest is denoted as a green alongshore belt and within a water mask area indicated with a white line. Copernicus Sentinel-2 (10 m pixel resolution, European Space Agency) data were retrieved for 2017 from the US Geological Survey and the colour image was based on top-of-the-atmosphere reflectance of green, near-infrared, and short wave infrared bands (Google Earth Engine)

height data for giant kelp from this site (see Section 2.1), we considered that 20 × 20 m clearings were appropriate to find the balance between representativity and the manipulation of these natural populations. The remaining patch in each block was assigned to the control group, in which *M. pyrifera* individuals were not manipulated. All manipulations and measurements were carried out by means of SCUBA diving. Preliminary analyses indicated no *a priori* statistically significant differences between *Macrocystis* removal and control plots for biomass, density, or composition (Tables S2 & S3).

2.3. Sampling procedure

Species abundances in the understorey were measured immediately before the experimental removal took place in February 2017, and then in June 2017, November 2017, and February 2018. At each sampling time and patch, we haphazardly located five 50 × 50 cm plots by means of SCUBA diving. For each plot, we used suction dredge sampling to collect all sessile and mobile macrobenthic invertebrates (>5 mm length; see also Wahle & Steneck 1991). We used a portable underwater venture-suction sampler that consisted of an auxiliary SCUBA cylinder connected to a 1.8 m long, 10 cm diameter PVC pipe. The surface of the plot was dredged with one of the ends of the pipe, and the collected material was accumulated in a 5 mm pore mesh mounted at the other end of the pipe. While this method limited our ability to representatively quantify the abundance of larger sessile organisms, such as seaweeds, it allowed us to quantify a large number of invertebrate species (ca. 150 species; Table S1).

After suction dredging, samples were placed into separated and labelled plastic bags on the boat and then transported within a few hours to a temporary field station nearby for pre-processing. In the laboratory, organisms were sorted and identified to the lowest taxonomic level possible, usually to species level (Table S1), with the aid of field guides and textbooks (e.g. Forcelli 2000, Häussermann & Försterra 2009, Turon et al. 2016). Species abundance was expressed as density (ind. per 0.25 m^2). We estimated community biomass as the wet mass (g per 0.25 m^2, 0.01 g accuracy) of all individuals in each quadrat.

Due to harsh weather and swells, some patches or plots were not sampled according to the original design: 4 out of 5 plots were sampled in each of 2 of the disturbed patches in February 2017, 2 out of 3 control patches were sampled in June 2017, 3 out of

5 plots were sampled in one of the control patches in June 2017, and 2 out of 3 control patches were sampled in February 2018 (Table S4). Due to the resulting imbalanced design, data were resampled to estimate each stability dimension: the individual observations within each treatment by time combination were randomly sampled with replacement. All other analyses were carried out on raw data.

2.4. Dimensions of aggregate and compositional stability

We focused on 3 stability dimensions: resistance, resilience, and recovery. We analysed community biomass and density—i.e. the sum of biomass or density across all species in each plot, respectively—as part of the aggregate domain. For simplicity, both community properties are hereafter referred to as 'biomass' and 'density'. Bray-Curtis (BC) dissimilarities were used to represent the compositional domain.

The stability metrics for biomass and density were obtained from ln-response ratios (lRRs) calculated for every sampling time as $lRR = \ln(F_{dist}/F_{con})$, where F_{dist} and F_{con} are the biomass or density of disturbed and the control conditions, respectively. For species composition, we used pairwise BC dissimilarities between the disturbed and control conditions (Odum 1950, Legendre & Legendre 1998): $BC = dis(C_{dist}/C_{con})$, where C_{dist} and C_{con} are the species abundance matrices in the disturbed and control conditions, respectively (Hillebrand et al. 2018). The range of BC is [0, 1], where 0 implies that both samples share the same species and abundances and 1 indicates that the samples share no species.

Resistance (*a*) was calculated as the lRR and BC of the second sampling time, i.e. June 2017. For aggregate properties, $a = 0$ denotes maximum resistance, $a < 0$ indicates low resistance due to underperformance relative to controls, and $a > 0$ implies low resistance due to overperformance with respect to the control. For composition, $a = 0$ and $a > 0$ denote maximum and low resistance, respectively.

Resilience (*b*) was calculated as the slope of a linear regression of lRR or BC over time (Hillebrand et al. 2018): lRR or $BC = m + b \times t$, where m, b, and t are the intercept, slope, and time, respectively. For aggregate properties and composition, $b = 0$ indicates no change over time. If resistance were positive ($a > 0$, overperformance of disturbed plots relative to controls), $b < 0$ would indicate that the communities in the disturbed plots are returning to the control levels,

and $b > 0$ would suggest that the disturbed communities are further departing from controls; if resistance were negative ($a < 0$, disturbed plots underperform with respect to controls), $b > 0$ would denote that the disturbed communities are converging to control levels, and $b < 0$ would indicate a further departure from controls (Hillebrand et al. 2018). In the case of $a = 0$, either positive or negative b values denote that the disturbed plots depart from controls.

Recovery (c) was represented by the lRR or BC calculated at the end of the experiment (February 2018). For aggregate properties, $c = 0$ denotes maximum recovery, $c < 0$ indicates incomplete recovery, and $c > 0$ represents overcompensation with respect to the control. For composition, $c = 0$ and $c > 0$ denote maximum and incomplete recovery, respectively (Hillebrand et al. 2018, Radchuk et al. 2019).

2.5. Statistical analyses

An overall model was used to separately analyse the temporal patterns in biomass, density, and composition: $\beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_{1,2} (X_1 \times X_2)$, where X_1 is canopy removal and X_2 is sampling time. The model analysed both independent (β_1 and β_2) and interactive ($\beta_{1,2}$) effects on univariate and multivariate responses. General linear models were used for biomass and density as response variables; a generalised negative-binomial linear model, in which parameter p-values were obtained after 999 resampling iterations, was used for composition (Wang et al. 2012). Visual exploration of residual and quantile–quantile plots indicated that a ln transformation of density was needed to improve model fit. No transformations were applied to biomass or species densities. We used a likelihood ratio-based coefficient of determination (R^2) to assess the goodness-of-fit of each model.

Patch was included as a random effect on the intercept of each univariate model (biomass and density). We used a likelihood ratio test to assess the statistical significance of patch. Both tests suggested that patch had no statistically significant effects on biomass and density (likelihood ratio $<$ 0.001, p = 0.9997 for biomass; likelihood ratio = 0.135, p = 0.7125 for density). Therefore, the random effects were removed and the models were refit to data.

We used a distance-based redundancy analysis ordination based on BC dissimilarities to depict the spatiotemporal patterns in composition (db-RDA; Legendre & Anderson 1999). In the db-RDA, we used the model of separate and interactive effects of canopy removal and sampling time, as described above. Separate t-tests were used to compare each of the metrics of resistance, resilience, and recovery against the reference values ($\mu = 0$).

The species that had the largest contribution to the effect of *Macrocystis* removal on species composition were identified. To this aim, we analysed the contribution of each species to the between-treatment BC dissimilarities in similarity percentage routines (SIMPER; Clarke 1993). SIMPERs were conducted separately for each sampling time. We used 999 permutations of data to determine the statistical significance of each species' mean contribution to the between-treatment dissimilarity.

Finally, we assessed the degree of association among the observed stability dimensions. Pearson product-moment correlations (r) were calculated among stability dimensions, separately for biomass, density, and composition. In addition, we calculated the correlations between aggregate and compositional stabilities separately for resistance, resilience, and recovery.

All calculations and analyses were conducted in the R programming environment (R Core Team 2021). The base, 'cowplot', 'ggrepel', 'ggpubr', 'readxl', 'sjPlot', 'tidyverse', and 'vegan' packages were used for data reading, manipulation, and plotting; 'mvabund' and 'nlme' for linear models; and 'ggcorrplot' for correlations (Wickham et al. 2019, Kassambara 2020, Oksanen et al. 2020, Wilke 2020, Lüdecke 2021, Pinheiro et al. 2021, Slowikowski 2021, Alboukadel 2022, Wang et al. 2022, Wickham & Bryan 2022).

3. RESULTS

3.1. Community-level dynamics in the understorey

A total of 149 species of invertebrates and 2 species of fishes were identified in the experimental plots (Table S1). Across time and plots, 102 species were identified in control plots and 100 in disturbed plots. These species were distributed among 9 phyla. Mollusca was the most diverse phylum, followed by Arthropoda and Echinodermata (61, 50, and 18 species, respectively). Porifera, Cnidaria, and Brachiopoda were each represented by a single species (Table S1). Species count data are publicly available at https://doi.org/10.6084/m9.figshare.23524032.v2.

In the control plots, biomass increased over time (Fig. 3A). In the disturbed plots, however, biomass increased between February and June 2017 and then decreased until the end of the experiment (Fig. 3A). Accordingly, we observed a statistically significant

interaction between removal and time, as biomass was lower in removal than control plots during November 2017 and February 2018 (Table S2). The model accounted for 39% of the variation in biomass ($R^2 = 0.39$).

Density exhibited an overall decrease over time but increased in the disturbed plots in June 2017 (Fig. 3B). In this respect, the statistical model suggested a significant interaction between removal and time: mean density was greater in disturbed than control plots only during June 2017 (Table S2). The model accounted for 32.5% of the variation in density ($R^2 = 0.325$).

The differences in composition between controls and disturbed plots increased over time and were particularly large in November 2017 (time 2 in Fig. 3C, Table S3). The compositions of control and disturbed communities tended to converge towards the end of the experiment in February 2018 (time 3 in Fig. 3C, Table S3).

In total, 3, 10, and 2 species contributed significantly to the between-group dissimilarity in June 2017, November 2017, and February 2018 (Table 1). In June 2017, the mean density of *Dendropoma* sp. and *Lumbrineris* sp. increased, and that of *Pareuthria atrata* diminished between control and disturbed

plots (Table 1). In November 2017, the density of all species — except *Dendropoma* sp. — that significantly contributed to between-group dissimilarities decreased between control and disturbed plots (Table 1). During this sampling time, 8 species exhibited mean densities of 0 ind. m^{-2} in the *Macrocystis* removal plots (Table 1). In February 2018, canopy removal resulted in a decrement (increment) in the density of *Chiridota pisanii* (*Fissurella picta*) (Table 1).

3.2. Stability dimensions of the understorey

Biomass of invertebrates was strongly resistant to canopy removal, as we did not detect a statistically significant difference between *a* and zero (Fig. 4A, Table 2). However, biomass resilience was negative and differed from zero (Fig. 4B, Table 2), which reflected the decrease in biomass of the disturbed plots relative to controls (Fig. 3A). Recovery of biomass was incomplete 12 mo following the disturbance, as the negative difference between *c* and zero was statistically significant (Fig. 4C, Table 2).

Density exhibited low resistance due to overcompensation in disturbed plots compared to controls (i.e. the positive difference between *a* and zero was statistically
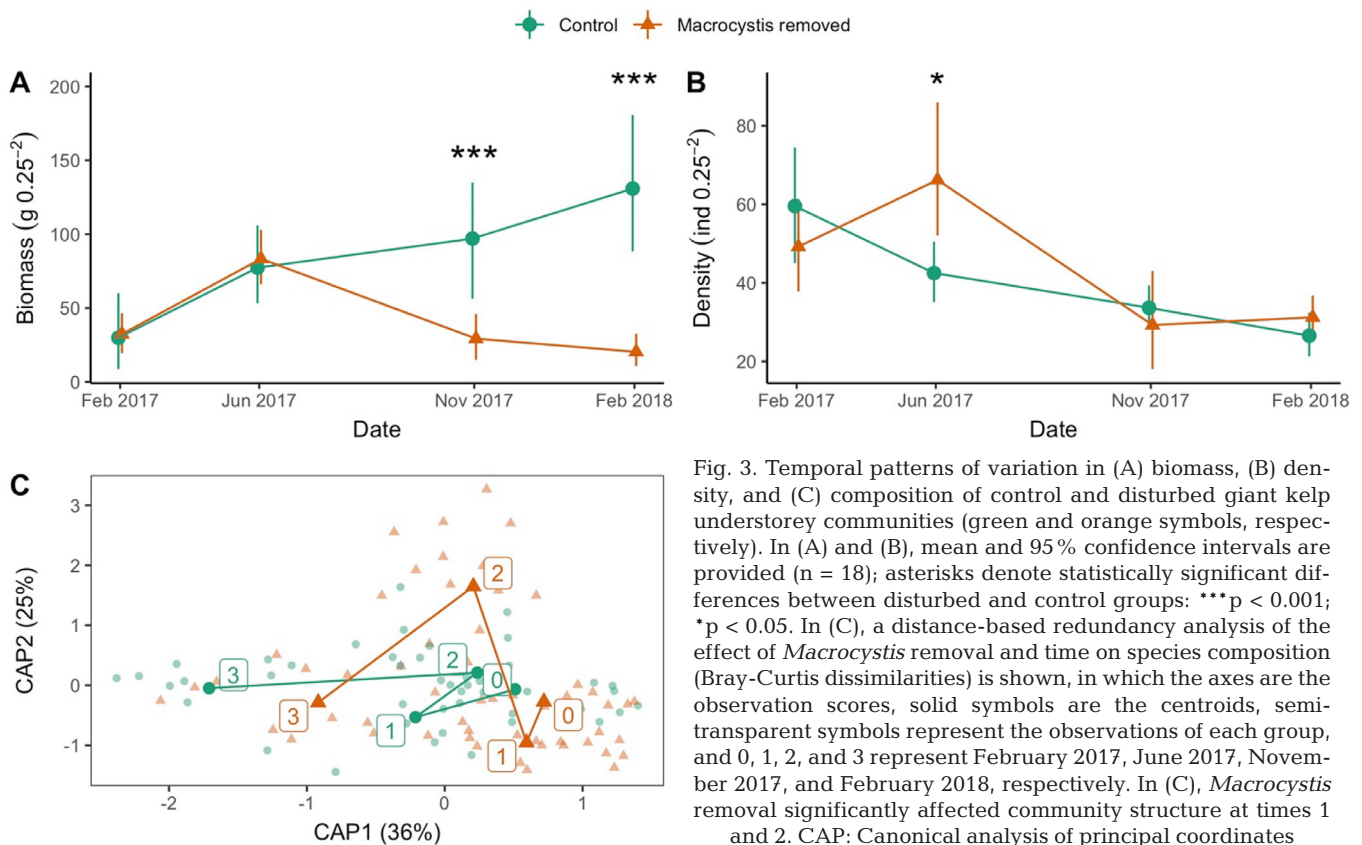

Fig. 3. Temporal patterns of variation in (A) biomass, (B) density, and (C) composition of control and disturbed giant kelp understorey communities (green and orange symbols, respectively). In (A) and (B), mean and 95% confidence intervals are provided (n = 18); asterisks denote statistically significant differences between disturbed and control groups: ***p < 0.001; *p < 0.05. In (C), a distance-based redundancy analysis of the effect of *Macrocystis* removal and time on species composition (Bray-Curtis dissimilarities) is shown, in which the axes are the observation scores, solid symbols are the centroids, semi-transparent symbols represent the observations of each group, and 0, 1, 2, and 3 represent February 2017, June 2017, November 2017, and February 2018, respectively. In (C), *Macrocystis* removal significantly affected community structure at times 1 and 2. CAP: Canonical analysis of principal coordinates

Table 1. Density (ind. per 0.25 m^2) of species with statistically significant (p < 0.05) contributions from SIMPER routines to the Bray-Curtis dissimilarities between *Macrocystis* removal and control plots at each sampling time. Species that increased (decreased) in density as a response to *Macrocystis* removal are marked with a ↑ (↓)

Sampling date	Species	Control Mean	SD	*Macrocystis* removal Mean	SD	Response
June 2017	*Dendropoma* sp.	0.00	0.00	1.00	0.00	↑
	Lumbrineris sp.	0.13	0.35	2.07	1.71	↑
	Pareuthria atrata	1.13	1.55	0.00	0.00	↓
November 2017	*Campylonotus vagans*	0.40	0.63	0.07	0.26	↓
	Dendropoma sp.	0.80	0.41	1.00	0.00	↑
	Harmothoe ernesti	0.13	0.35	0.00	0.00	↓
	Nucula pisum	1.93	3.67	0.00	0.00	↓
	Odontaster penicillatus	0.20	0.41	0.00	0.00	↓
	Ophiophragmus sp.	2.07	5.90	0.00	0.00	↓
	Paralomis granulosa	0.20	0.41	0.00	0.00	↓
	Plaxiphora aurata	0.33	0.82	0.00	0.00	↓
	Trophon geversianus	0.07	0.26	0.00	0.00	↓
	Tryphosites chevreuxi	0.60	1.12	0.00	0.00	↓
February 2018	*Chiridota pisanii*	4.50	3.50	1.40	2.29	↓
	Fissurella picta	0.40	0.52	1.27	1.03	↑

significant; Fig. 4D, Table 1). Resilience of density was represented by a small and statistically non-significant negative slope of the recovery trajectory (Fig. 4E, Table 2). Despite the slow recovery rate, density reached control values after 12 mo (i.e. *c* = 0; Fig. 4F, Table 2).

Compositional resistance was very low, as BC dissimilarity between disturbed and control communities averaged 0.68 and was statistically different from zero (Fig. 4G, Table 1). Moreover, the slope of the recovery trajectory of composition approached zero (i.e. no resilience; Fig. 4H, Table 1). As a result, compositional recovery was incomplete at the end of the experiment (i.e. the difference between *c* and zero was statistically significant; Fig. 4I, Table 1).
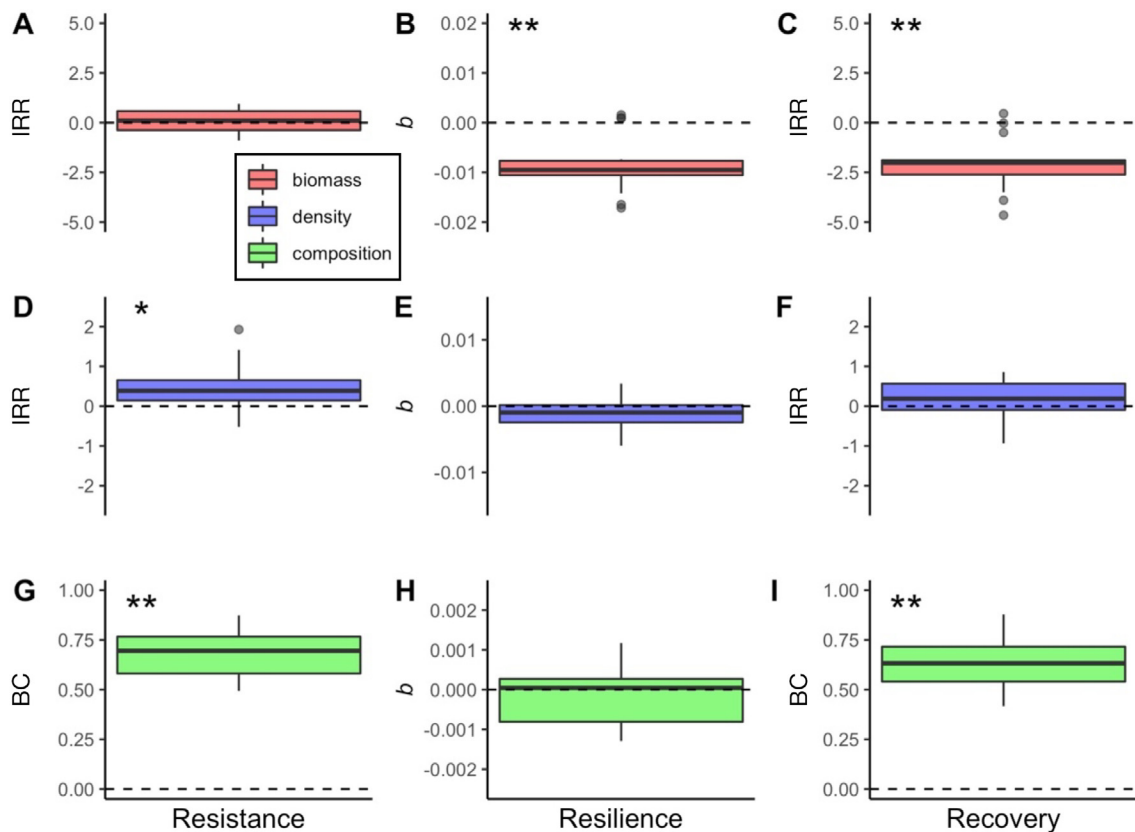

Fig. 4. Stability responses of understorey communities to the experimental removal of giant kelp, *Macrocystis pyrifera*. Aggregate (biomass and density) and compositional (the combination of species incidences and abundances) stabilities were analysed. lRR and BC: ln response ratio and Bray-Curtis dissimilarity, respectively, calculated between disturbed and control communities; *b*: slope of lRR or BC against time. Bar: median; box: 25th–75th percentiles (IQR), whiskers: upper/lower limits of 1.5 × IQR; dots: outliers. Asterisks identify statistically significant differences against reference values (dashed lines): **p < 0.01; *p < 0.05 (n = 18)

Table 2. Summary of *t*-tests on stability dimensions of understorey communities disturbed by the experimental removal of the giant kelp *Macrocystis pyrifera*. Each dimension was compared with its reference value ($\mu = 0$). For biomass and density, resistance and recovery were measured as ln response ratios (lRR) between disturbed and control communities, and resilience as the slope of lRR over time. For composition, resistance and resilience were expressed as Bray-Curtis (BC) dissimilarities between disturbed and control communities, and resilience as the temporal slope of BC

Response	Dimension	Mean	Lower CI	Upper CI	t	p
Biomass	Resistance (*a*)	0.07	−0.23	0.37	0.50	0.62
	Resilience (*b*)	−0.01	−0.01	−0.01	−6.92	<0.01
	Recovery (*c*)	−2.12	−2.74	−1.49	−7.17	<0.01
Density	*a*	0.44	0.13	0.75	3.00	0.01
	b	−0.01	−0.01	0.01	−1.95	0.07
	c	0.17	−0.09	0.44	1.37	0.19
Composition	*a*	0.68	0.62	0.74	23.31	<0.01
	b	~0.00	~0.00	~0.00	−0.92	0.37
	c	0.63	0.57	0.69	21.79	<0.01

3.3. Associations among stability dimensions

For biomass, resilience and recovery were positively correlated (Fig. S2) and no other statistically significant correlation was observed (Fig. S2). For density and composition, resilience and recovery also correlated positively (Fig. S2), and resistance and resilience were negatively correlated (Fig. S2). On the other hand, we observed no statistically significant correlation between the aggregate and compositional proxies for resistance, resilience, or recovery (p > 0.05 for all correlations).

4. DISCUSSION

In this study, the experimental removal of a foundation habitat-forming species, *Macrocystis pyrifera*, triggered mixed stability responses of the understorey macrobenthic invertebrates in a sub-Antarctic community. We first hypothesised low resistance of the understorey to canopy removal (H_1). While the number of all individuals per plot (hereafter density) and species composition supported this prediction, understorey community biomass (hereafter biomass) exhibited no detectable immediate response to the disturbance. Secondly, we predicted high resilience and complete recovery of the understorey within 1 yr after *Macrocystis* removal (H_2). In this case, density supported the prediction, but biomass decreased over time and species composition exhibited no resilience and no recovery. The strong compositional responses to *Macro-*cystis removal stemmed mostly from local coextinctions of several species in the understorey. Along the following lines, we discuss the relevance of abiotic environmental conditions, kelp recovery rates, and the loss of positive biotic interactions as potential mechanisms underpinning the observed stability community responses in context with previous work on foundation species from temperate and subpolar regions.

4.1. H_1: low aggregate and compositional resistance of the understorey to *Macrocystis* removal

The low resistance of density (due to overshooting compared to controls) and species composition to the experimental disturbance could reflect initial dispersal of invertebrates from neighbouring kelps. These individuals, in turn, could have compensated for the loss of biomass in the disturbed communities. The relationship between functional traits of the species accounting for this effect and the environmental impacts of *Macrocystis* removal could help to explain this result. Among the species that contributed significantly to the between-treatment compositional differences, the species that increased in abundance upon *Macrocystis* removal during June 2017 are either deposit or suspension feeders (*Lumbrineris* sp. and *Dendropoma* sp., respectively, see Table 1; Vizzini et al. 2012, Checon et al. 2017). The removal of giant kelps could have enhanced the velocity of currents that supply nutrients and planktonic food to suspension feeders, as *Macrocystis* canopies can attenuate current velocities (Jackson & Winant 1983, Elsmore et al. 2022). In addition, the physical structure of kelps promotes turbulent hydrodynamics (Rosman et al. 2010); thus, canopy removal could have benefited the larval transport of some invertebrates (Morton & Anderson 2013) and the delivery of suspended food for deposit and suspension feeders (Miller et al. 2018). Finally, canopy removal could have boosted the growth of epiphytic organisms, as shown for other kelps elsewhere (Bennett et al. 2015). In this way, our experimental removal of giant kelps could have initially improved the supply of nutrients, larvae, and food, which could account for the observed density peak of *Lumbrineris* sp. and *Dendropoma* sp. in June 2017.

4.2. H_2: fast resilience and complete recovery within 1 yr after experimental canopy removal

Following the initial peak upon *Macrocystis* removal, understorey density converged toward control levels and achieved complete recovery 5 mo later, supporting our prediction of fast resilience and complete recovery. However, biomass and species composition exhibited very low resilience and no recovery. Along with the dominance of small-sized organisms, these stability responses probably reflect secondary coextinctions of understorey species in the disturbed community. Indeed, the density of several species decreased to 0 ind. m^{-2} during November 2018 as a response to canopy removal (Table 1). Contrary to temperate regions (Dayton et al. 1992, Miller et al. 2018), giant kelp in our study region facilitates the populations of subordinate habitat-forming seaweeds such as *Lessonia flavicans* (Santelices & Ojeda 1984a). This species, in turn, facilitates the development of a species-rich community of invertebrates (Velasco-Charpentier et al. 2021). Such a facilitation cascade — i.e. when a habitat-former facilitates another habitat-former — can have greater positive effects on local diversity than the separate effects of each foundation species, especially in harsh environments (Thomsen et al. 2010, Gribben et al. 2019). Therefore, it is possible that the loss of a facilitation cascade upon *Macrocystis* removal underpinned the significant stability responses of biomass and composition, along with the observed loss of several understorey invertebrate species.

In general, our results provided mixed support for the hypothesis of fast and complete recovery of the understorey community. Our premise was that giant kelp populations recover quickly from disturbances due to rapid generation, colonisation, and growth rates, as observed in temperate shores (Castorani et al. 2017, 2018). However, growth and productivity rates of giant kelps and some understorey seaweeds in subpolar zones are substantially lower than in temperate zones (e.g. southeast Alaska; Bell & Kroeker 2022). Upon the experimental removal of *M. pyrifera* canopies in Chilean Patagonia, in addition, recruitment of this species can be very low at the depth range of our experiment (above 25 m; Santelices & Ojeda 1984b). Although we did not quantify kelp recruitment, anecdotal observations indicated that there was almost no kelp recruitment in the disturbed patches during the experiment (I. Garrido pers. obs.). Since giant kelp population dynamics can directly influence the dynamics of the populations in the understorey community (Detmer et al. 2021), rel-

atively slow giant kelp population dynamics could have delayed the recovery of invertebrate understorey biomass and composition in our study.

4.3. Associations among stability dimensions

We observed positive, negative, and neutral correlations among the understorey stability responses to *Macrocystis* removal. Resilience and recovery were positively correlated for density, biomass, and composition, but resistance and resilience were negatively correlated for density (Fig. S2). These correlations agree with early theoretical models (Harrison 1979) and manipulative studies on other foundation species, latitudes, and ecosystem types (Hillebrand et al. 2018, Valdivia et al. 2021a). How do we explain these (seemly) common correlation patterns? On the one hand, the positive resilience–recovery correlation would be expected, as faster community trajectories should allow for more complete recovery or even overshooting relative to reference values (e.g. Hillebrand et al. 2018). On the other hand, the negative resistance–resilience correlation may have multiple causes. In our study, the initial increase and further decay in density led to the negative resistance–resilience correlation. Yet, stronger negative impacts would allow for more chances for colonisation and population growth, leading to the same negative correlation (Harrison 1979). In addition, even very small disturbances (strong resistance) can be followed by very large effects over time (fast community trajectories and no recovery) in ecosystems characterised by chaotic dynamics (Benincà et al. 2015, Medeiros et al. 2023). Such non-equilibrium dynamics would also account for the observed lagged response of biomass to *Macrocystis* removal, as the strong initial resistance was followed by a significant departure from controls and no final recovery. In this way, our study and previous work may suggest the emergence of a common pattern of stability dimensionality.

The aggregate and compositional community responses remained uncorrelated for the 3 stability dimensions, similar to previous studies on other foundation species elsewhere (Hillebrand & Kunze 2020, White et al. 2020, Valdivia et al. 2021a). This lack of correlation implies that different communities may be able to support similar levels of community-level properties, which is possible when competitive release and/or differential environmental responses allow for asynchronous species fluctuations (Micheli et al. 1999, Guelzow et al. 2017, Lamy et al. 2021). Although species asynchrony tends to decrease from

low to high latitudes (Bulleri et al. 2012), it is still common across spatial scales and ecosystem types worldwide (Gonzalez & Loreau 2009, Lamy et al. 2020, Valencia et al. 2020, Valdivia et al. 2021b) and could well have a role in the stability of this subpolar ecosystem.

5. CONCLUSIONS

The experimental removal of the giant kelp *Macrocystis pyrifera* elicited sometimes disparate stability responses of the understorey invertebrate community in a subpolar ecosystem. The understorey fauna was strongly resistant in terms of biomass, but weakly resistant in terms of density and composition. Subsequently, understorey biomass decreased over time (low resilience and recovery), density fully recovered (high resilience and recovery), and composition departed significantly from reference conditions (low resilience and recovery). The large compositional responses to *Macrocystis* removal were accounted for by local coextinctions of species with likely similar environmental tolerances. These complex community impacts of *Macrocystis* removal led to positive, negative, and neutral correlations among stability dimensions. In contrast with evidence coming from temperate regions, slower kelp population recovery, loss of facilitation cascades, and local coextinctions could account for the observed understorey stability responses in this subpolar ecosystem. With this study, we hope to stimulate further comparative experimental research on giant kelp communities along latitudinal gradients, with an eye on improving our mechanistic understanding of the stability of foundation-species-dependent ecosystems.

Data availability. Data are available at https://doi.org/10.6084/m9.figshare.23524032.v2.

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