

RECONCILING RESILIENCE ACROSS
ECOLOGICAL SYSTEMS, SPECIES AND SUBDISCIPLINES

Research Article

Latitudinal variation in long-term stability of North American rocky intertidal communities

C. Melissa Miner¹  | Jennifer L. Burnaford²  | Karah Ammann¹  | Benjamin H. Becker³ | Steven C. Fradkin⁴  | Stacey Ostermann-Kelm⁵ | Jayson R. Smith⁶ | Stephen G. Whitaker⁷ | Peter T. Raimondi¹ 

¹Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, CA, USA; ²Department of Biological Science, California State University, Fullerton, CA, USA; ³U.S. National Park Service, Point Reyes National Seashore, Point Reyes Station, CA, USA; ⁴U.S. National Park Service, Olympic National Park, Port Angeles, WA, USA; ⁵U.S. National Park Service, Inventory and Monitoring Division, Thousand Oaks, CA, USA; ⁶Department of Biological Sciences, California State Polytechnic University, Pomona, CA, USA and ⁷U.S. National Park Service, Channel Islands National Park, Ventura, CA, USA

Correspondence

C. Melissa Miner
Email: cmminer@ucsc.edu

Funding information

David and Lucille Packard Foundation; U.S. Department of the Interior Bureau of Ocean Energy Management; National Park Service; California Ocean Protection Council

Handling Editor: Pol Capdevila

Abstract

1. Although long-term ecological stability is often discussed as a community attribute, it is typically investigated at the species level (e.g. density, biomass), or as a univariate metric (e.g. species diversity). To provide a more comprehensive assessment of long-term community stability, we used a multivariate similarity approach that included all species and their relative abundances.
2. We used data from 74 sites sampled annually from 2006 to 2017 to examine broad temporal and spatial patterns of change within rocky intertidal communities along the west coast of North America. We explored relationships between community change (inverse of stability) and the following potential drivers of change/stability: (a) marine heatwave events; (b) three attributes of biodiversity: richness, diversity and evenness and (c) presence of the mussel, *Mytilus californianus*, a dominant space holder and foundation species in this system.
3. At a broad scale, we found an inverse relationship between community stability and elevated water temperatures. In addition, we found substantial differences in stability among regions, with lower stability in the south, which may provide a glimpse into the patterns expected with a changing climate. At the site level, community stability was linked to high species richness and, perhaps counterintuitively, to low evenness, which could be a consequence of the dominance of mussels in this system.
4. *Synthesis.* Assessments of long-term stability at the whole-community level are rarely done but are key to a comprehensive understanding of the impacts of climate change. In communities structured around a spatially dominant species, long-term stability can be linked to the stability of this 'foundation species', as well as to traditional predictors, such as species richness.

This is an open access article under the terms of the Creative Commons Attribution-NonCommercial-NoDerivs License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

© 2021 The Authors. *Journal of Animal Ecology* published by John Wiley & Sons Ltd on behalf of British Ecological Society

KEYWORDS

community stability, foundation species, global change ecology, long-term monitoring, mussels, *Mytilus californianus*, temperate rocky intertidal

1 | INTRODUCTION

Coastal marine ecosystems are experiencing major alterations in oceanic conditions associated with climate change, including warming, acidification, sea-level rise, increased stratification and subsequent decline in dissolved oxygen, increased wave power, and changes in local and regional ocean circulation patterns (Alheit & Bakun, 2010; Bindoff et al., 2019; Brierley & Kingsford, 2009; Doney et al., 2012; Keeling et al., 2010; Narayan et al., 2010; Reguero et al., 2019). Furthermore, extreme events resulting in rapid changes in environmental conditions, such as El Niño Southern Oscillation (ENSO) events and marine heatwaves, are becoming more frequent and intense (Freund et al., 2019; Frölicher & Laufkötter, 2018; Oliver et al., 2018). These large-scale agents of disturbance can result in short- and long-term modifications of community structure and can be particularly disruptive when multiple ecological factors are affected. For example, elevated ocean temperature can result in local extirpations, species range shifts, altered ecosystem functioning and changes in biotic interactions (Harley et al., 2006; Sanford et al., 2019). These impacts can be compounded by other factors associated with marine heatwaves, such as harmful algal blooms or disruption of upwelling intensity and duration (Bograd et al., 2009; Harley et al., 2006).

Assessing and mitigating change in ecological communities resulting from a rapidly changing climate necessitates a broadly applicable and mechanistically sound understanding of the factors influencing ecological stability. Recent studies investigating the mechanistic drivers of ecological stability have greatly advanced the field and clarified the terminology used to describe the components of stability (Donohue et al., 2013, 2016; Grimm & Wissel, 1997; Hodgson et al., 2015; Ingirsch & Bahn, 2018; Ives & Carpenter, 2007). However, due to the logistical constraints of carrying out large-scale, long-term experimental efforts, these studies tend to be limited in spatial and/or temporal scale (e.g. Donohue et al., 2013; Grman et al., 2010; Hillebrand et al., 2018), simplistic in terms of community complexity (Hillebrand et al., 2018; Wittebolle et al., 2009), or are primarily theoretical in nature (Arnoldi et al., 2016). Because investigation of a single component in isolation can result in an underestimation of the potential for perturbation to alter ecological stability, and because there is evidence of strong correlation among many components of ecological stability, a more integrated approach is required (Donohue et al., 2013; Hillebrand et al., 2018; Kéfi et al., 2019). To achieve a more complete understanding of the key drivers of ecological stability, particularly those operating at large scales, patterns of association between identified mechanisms and community change must be examined broadly, through temporally

and geographically expansive surveys (Hawkins et al., 2009; Underwood et al., 2000; Witman et al., 2015). Geographically broad, long-term ecological community monitoring surveys can provide important 'natural experiment' data that can be used to link variation in environmental conditions or natural or anthropogenic disturbance to community change (e.g. Croll et al., 2005; Rogers et al., 2012).

Understanding how disturbance impacts long-term stability of a system at the community composition level, utilizing data that include both species' diversity and relative abundance/evenness, has long been a goal of ecological stability research (e.g. Grman et al., 2010; Hillebrand et al., 2008). However, achieving this goal can be challenging for both logistical and analytical reasons. Assessing community composition (as opposed to tracking changes in a single species) requires researchers to have a high level of taxonomic expertise, consistency in species identification across space and time, and resources to support long-term studies. The Multi-Agency Rocky Intertidal Network (MARINe) was formed in 1997 to support the collection of taxonomically complex, long-term, quantitative community monitoring data from temperate rocky intertidal shores spanning the west coast of North America. Previous work using this broad-scale dataset has examined possible links between marine heatwave events and disease events affecting population trends for single species (sea stars, Miner et al., 2018; abalone, Raimondi et al., 2002). These efforts revealed mixed results in terms of linking water temperature to impact of disease on populations (temperature and disease impact were highly correlated for black abalone, but not for ochre sea stars). However, considerable spatial structure was observed in the patterns of impact, with more extreme declines in species' abundance in southern than in northern regions. Because temperate rocky intertidal communities are both highly diverse and at high risk of disruption from climate change, particularly at lower latitudes (Doney et al., 2012; Hawkins et al., 2008; Hobday & Pecl, 2014; Howard et al., 2013), we were interested in broadening our investigation to explore whether change at the whole-community level was correlated with marine heat events. The broad geographical and temporal scope of the MARINe study—spanning two ENSO events (2009–2010 and 2015–2016) and an unprecedented marine heatwave event that stretched from Alaska, USA to Baja California, Mexico from 2014 to 2016 (Cavole et al., 2016)—provided an excellent opportunity to examine spatial patterns of change and stability. In this study, we specifically examined long-term patterns of ecological stability (defined as the absence of change over time in a composite metric incorporating species diversity and relative abundance) at the community level, hereafter referred to as 'community stability'.

Here, we use an approach based on a multivariate assessment of similarity to achieve a comprehensive, long-term assessment of

community stability. We used the results from this analysis to examine local (site) and regional scale patterns of community stability and identify potential drivers of community change. Specifically, we asked the following questions: (a) Is there an association between community stability and water temperature, and if so, do these associations exhibit regional patterns? and (b) Is there a positive relationship between stability and three general attributes of biodiversity commonly identified as important for community stability: species richness, diversity and evenness? The results of these initial analyses prompted an investigation of a less well-studied component of community stability: species dominance. Numerous studies have demonstrated a link between evenness of species abundances and community stability, concluding that higher evenness allows for functional redundancy and thus a more stable community. However, a handful of investigations have shown either no association between community stability and evenness (Isbell et al., 2009) or a link between increased stability and low evenness values, driven by the presence of one or a handful of dominant species (e.g. Grman et al., 2010; Valdivia et al., 2013). Our results suggested a similar pattern, and thus motivated a final question: Is there a relationship between community stability and persistence in cover of the mussel, *Mytilus californianus*, a spatially dominant foundation species within the community (Dayton, 1972; Seed & Suchanek, 1992; Suchanek, 1992)?

2 | MATERIALS AND METHODS

2.1 | Site locations

Along the Pacific coast of North America, the Multi-Agency Rocky Intertidal Network (MARINE; see www.pacificrockyintertidal.org) monitoring programme coordinates the collection of long-term, biological community-level data through a consortium of federal, state, university and private organizations. MARINE sites stretch from the Olympic Peninsula, Washington to San Diego, California (including sites on the Channel Islands in southern California), spanning 16 degrees of latitude. Only sites with at least 10 years of data were included in the analyses presented here (74 sites, Figure 1, Table S1). There is a general sea surface temperature gradient across this study region, with cooler temperatures in the north and warmer temperatures in the south. However, this general pattern masks considerable spatial/temporal variability in oceanographic conditions, driven primarily by spatially constrained areas of upwelling that occur seasonally (Bograd et al., 2009). Most of the sites included in the analyses are wave-exposed, outer-coast locations with gently sloping rocky intertidal benches at least 30 m wide (contiguous along-shore reef), containing macrophyte and macroinvertebrate communities representative of the region. Collectively, these sites span a range of regulatory protection categories (e.g. limited-take Marine-Protected Areas, no-take MPAs and non-MPA sites) and proximity to known biogeographical boundaries. Sites are not evenly spaced along the coast due to geographical gaps resulting from long stretches of beach, mud flat, cobble/boulder fields and/or sheer cliffs. The level

of public access varies among sites and encompasses a wide spectrum of human impact, from sites that receive well over 75,000 visitors each year (Ambrose & Smith, 2005; Ware, 2009) to those adjacent to private land with almost no human visitation. Detailed descriptions of each site can be found on the MARINE website.

To assess potential differences in patterns of community stability at a coast-wide scale (see Section 2.4), we grouped sites into three regions aligned with biogeographical provinces as described by Blanchette et al. (2008): (1) 'North' (Washington, Oregon, northern California: 19 sites), (2) 'Central' (San Francisco to Point Conception, CA: 20 sites) and (3) 'South' (Point Conception to San Diego, CA: 16 sites). We added a fourth region, (4) the northern 'Channel Islands' (19 sites), as these sites experience an oceanographic climate distinct from the neighbouring southern California mainland (Harms & Winant, 1998; Kapsenberg & Hofmann, 2016; Figure 1; Table S1).

2.2 | Sampling approach

At each site, long-term fixed plots (50 cm × 75 cm) were located within common, conspicuous and ecologically important focal species assemblages, which generally formed distinct bands within the intertidal zone. Focal assemblages included mussels (*Mytilus californianus*), barnacles (*Chthamalus dalli/fissus*, *Balanus glandula*, *Semibalanus cariosus*, *Tetraclita rubescens*), gooseneck barnacles (*Pollicipes polymerus*), anemones (*Anthopleura* spp.), rockweeds (*Pelvetiopsis californica*, *Pelvetiopsis limitata*, *Silvetia compressa*, *Fucus distichus*) and red algae (*Endocladia muricata*, *Mastocarpus* spp.). Not all focal assemblages were present at every site, a typical site contained 3–5 assemblages. Five replicate plots were established in each focal species assemblage, resulting in 15–25 plots at a typical site. Each plot was initially placed in an area with maximal abundance of a given focal species, but over time, species composition within plots might change substantially.

During each survey (conducted either annually or semi-annually), plots were photographed to create a permanent visual archive of species present. Percent cover of all sessile species was quantified using a rectangular grid of 100 uniformly spaced points placed on top of each plot. For a small subset of data (two central CA sites between 2006 and 2011), 50 points were used to record species' percent cover. When possible, this data collection was completed in the field. When this was not possible (e.g. due to poor working conditions or limited staff), percent cover was estimated in the laboratory by overlaying a grid of 100 points onto the archival plot photos. In either case, the taxon or substratum occurring directly under each point was recorded and percent cover was calculated by dividing the total number of hits out of the total number of possible points. A comparison of data collected in the field versus the laboratory from photographs found no significant effect of method (Ambrose et al., 1995). To ensure consistency between laboratory and field data, we lumped organisms that were difficult to identify to the species level from photos into higher taxonomic classifications and treated them as a single taxon in our analyses (see Table S2 for list of taxa scored).

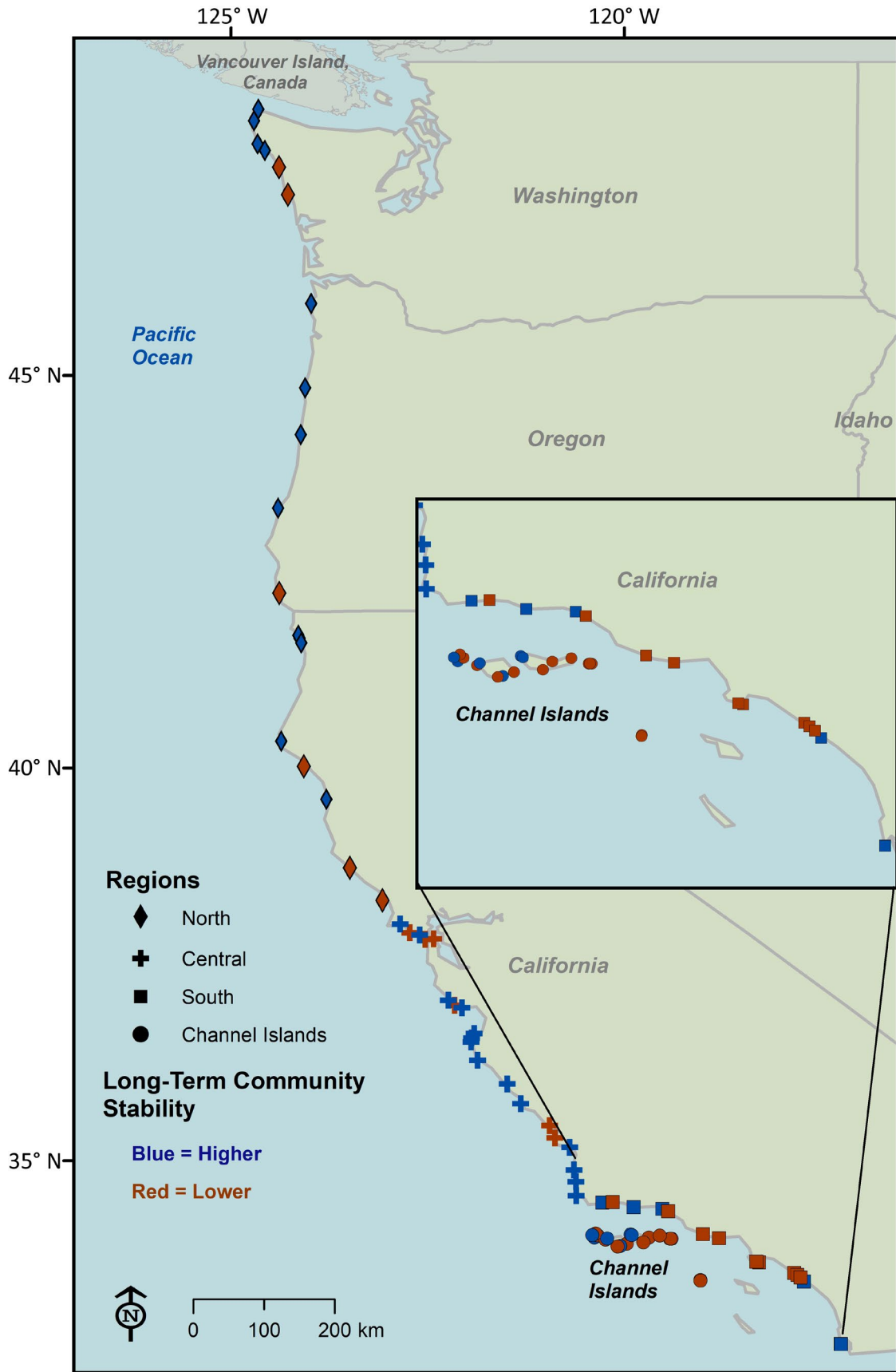


FIGURE 1 MARine long-term monitoring sites utilized in this study (see Appendix S1: Table S1 for site names), with inset for southern California. Sites were grouped into one of four regions, indicated by a symbol, and categorized as having 'higher' or 'lower' long-term community stability (see Section 2.4.4) as indicated by colour [Colour figure can be viewed at wileyonlinelibrary.com]

Fixed plots provide high statistical power to detect changes in species dynamics over time with reasonable sampling effort and allow for robust segregation of variance in community structure into temporal and spatial components (Raimondi et al., 2018). One limitation of a non-random approach is that patterns and trends observed within plots cannot readily be extrapolated to the site as a whole. However, by targeting the key intertidal assemblages listed above, our permanent plots tend to be distributed widely throughout each site. Furthermore, focal species typically occur in plots outside of those established to capture them, as can be seen by the proportion of plots at each site containing mussels (Figure S1). Thus, using the combination of all plot types to calculate mean percent cover values for each taxon at a given site should represent the general community, and importantly, allows the calculation of a representative community similarity metric (see Section 2.4), which is used here to assess temporal stability in the community.

2.3 | Water temperature

Intertidal temperature data were continuously recorded for the entire study period, typically at 15- or 30-min intervals, at 69 locations in the North and Central regions from 2006 to 2017, and at 8 locations in the Channel Islands from 2009 to 2017. Temperature data locations generally overlapped with biological data sites (18 of 19 North sites, 15 of 20 Central sites and 8 of 19 Channel Islands sites), and data from 'temperature only' locations (19 North, 17 Central) were also included to maximize spatial coverage within each region. Three different data logger models (all from Onset[®] Computer Corporation) have been used over time and across sites, due to changes in logger technology: HOBO[®] pendant UA-002-64, HOBO[®] UTBI-001 TidbiT[®] and HOBO[®] UTBI-001 TidbiT[®] v2. Loggers at most sites were housed in stainless steel wire mesh cages bolted to the substratum. At Washington and Channel Islands sites, loggers were either encased in epoxy for protection and then bolted and epoxied to the bedrock or housed in flow-through PVC containers that were bolted to the substrate. Temperature loggers were installed in the mid-low intertidal zone, in areas that would afford some protection from waves and theft. No attempt was made to standardize factors that could affect temperature during emersion, such as shading, angle of incidence to sun, etc. Therefore, we used temperature data only from periods when loggers were fully submerged and recording seawater temperature. For the South region, we used temperature data from four piers available through the Southern California Coastal Ocean Observing System (SCOOS, <http://www.sccoos.org>, Miner et al., 2018).

We also obtained longer-term water temperature records (1990–2017) from three locations along the west coast to provide broader temporal context for our findings. These locations were Scripps Pier, near San Diego in southern California, Hopkins Marine Station, near Monterey in central California, and

Amphitrite Station, on the outer coast of Vancouver Island in British Columbia. These locations span the range of sites assessed in this project.

2.4 | Analyses

2.4.1 | Quantifying community change and stability

We explored long-term stability of intertidal communities using annual percent cover data from our fixed plots to examine how community composition within sites changed over time. Our goal was to assess the longest period of sampling across the maximum number of sites. Although sampling began as early as 1980 in some regions, and as late as 2008 at six sites, we used 2006 as our start year to maximize temporal replication across the broadest geographical area; a later start year would have truncated our time series and, as described below, would have placed our initial, 'benchmark' year in a cooler than average period. Data from all assemblage types sampled at a given site were used; because only within-site comparisons were used to derive the similarity values described below, it did not matter that the number or types of assemblages surveyed differed among sites. For each site, we used percent cover of each recorded species, averaged across all plots, to calculate community-level Bray-Curtis similarity values (Clarke et al., 2006, PRIMER 7) for all pairs of years between 2006 and 2017, except for Washington sites, which were paired for all years between 2007 or 2008 and 2017 (for reasons described above). The resulting 'base matrix' was subsampled to extract the similarity values representing the initial year sampled relative to each of the other years (e.g. 2006–2007, 2006–2008, ..., 2006–2017). We calculated the mean community similarity value for a given site as the mean of these 11 (or for Washington sites, 9 or 10) values. We equated a higher mean similarity value with greater long-term community stability.

We validated our decision to use 2006 data as our 'benchmark' (rather than another metric, such as a long-term mean) using two metrics: (a) by comparing results using three different start years (2004, 2005 and 2006 for the subset of sites sampled across this longer period), and (b) by examining long-term water temperature anomalies to determine whether our 'benchmark' year fell within a 'normal' or anomalous period. Start year did not affect the results and mean annual water temperatures in 2004–2006 were neither anomalously high nor low (Figures S2 and S3). As noted above, we selected 2006 as the benchmark year because it allowed us to incorporate the maximum number of sites over the broadest geographical and temporal scale.

2.4.2 | Regional patterns of community stability

To determine whether long-term community stability varied among regions, we used a mixed-model analysis with community similarity (relative to the start year) as the response variable, region and year

as fixed effects, and sites as random effects nested within regions (JMP15.1).

2.4.3 | Sea water temperature and community stability

One of the key findings from the regional analysis was that periods of greatest community change appeared to be aligned with periods of elevated water temperature. To directly test this association across our entire study region, we assembled data from onsite temperature loggers where available, and pier data in the South region (see Section 2.3). Differences in spatial coverage and alignment of temperature data with sites meant that we were not able to assess the relationship between community stability and temperature at the site level. Instead, we assessed the relationship at the regional level, and used only the period between 2009 and 2017 to ensure that the temporal period of temperature records was identical for all regions.

Daily water temperature data capture a portion of the environmental variability that intertidal organisms are exposed to, including extreme high and low temperatures that might be lost when data are distilled down to longer-term means. Because we were interested in identifying the component(s) of water temperature that most closely aligned with the observed patterns of community change, we examined the relationship between annual regional community similarity and five different water temperature metrics (predictor variables): (a) mean annual temperature, (b) median annual temperature, (c) 90th percentile of annual temperature (warmest 10% of temperature records), (d) 10th percentile of annual temperature (coldest 10% of temperature records) and (e) the principal component score derived from the four preceding variables. The 10th and 90th percentile metrics were selected based on the idea that elevation of temperatures on either end of the spectrum might affect community stability in different ways than either the mean or median annual temperature. The principal component score was included because the temperature variables were co-linear. Each model contained the categorical factor 'region' and one of the temperature metrics or the composite of the four temperature variables (the principal component). The best fit model was assigned based on the corrected Akaike information criterion (AICc) selection.

2.4.4 | Community stability at the site level, and possible driving factors

The results of the comparison of community stability among regions indicated that a considerable amount of variance associated with random effects (using restricted maximum likelihood estimation) could be attributed to differences among sites (within regions). Hence, we investigated patterns of association between community stability within individual sites and common univariate metrics of diversity. To do this, we calculated the mean community

similarity values for each site over time. Sites were then divided into two categories—'higher' and 'lower' long-term stability—based on the median of the means (described above). For this analysis, we used only those sites that had observations for the period 2007–2017 ($n = 64$ sites) so that the mean similarity value represented the entire sample period. Sites with mean community similarity values greater than the median were categorized as having 'higher' long-term community stability and those with values below the median were categorized as having 'lower' stability. This approach (50% higher stability and 50% lower stability) removes bias that might be introduced by assigning stability status using criteria based on our perception of 'stability'. We then created a logistic model (with stability category as the response variable) that incorporated latitude and five common diversity indices as predictor variables. These were raw number of species (S); Pielou's evenness (J'), which is a measure of the evenness of species abundances in a community; Margalef's richness (d), which calibrates raw species richness by the total number of individuals sampled; Simpson's $1 - \lambda'$, which is an estimate of the pairwise encounter probability for different species (interspecific encounter); and the Shannon–Weiner diversity index (H'), which is based on both the number and evenness of species in a community. Latitude was included to account for the geographical pattern of community stability that emerged from the regional analysis (see Sections 2.4.2. and 3.1). Model selection was performed using stepwise regression with AICc ranking.

2.4.5 | Community stability and mussel cover

Results from the logistic model revealed that H' , an index that incorporates both species diversity and evenness, was included in the best fit model, and that it was inversely related to community stability. This result was counter to the prediction that community stability values would be positively associated with H' values. However, this finding was consistent with a handful of studies linking community stability to dominance by one or a few stable, long-lived species. On the west coast of North America, only one species occurs at high abundance across the broad region of coastline examined in this study: the mussel, *Mytilus californianus*. To investigate whether *M. californianus* abundance could be driving the pattern of association between H' and community stability, we re-ran the model substituting mussel cover from a representative year (2008) for H' . Because we were interested in examining how mussel cover might affect subsequent long-term community stability, we used data from 2008, an early year in the time series, to allow for comparison to subsequent years.

3 | RESULTS

3.1 | Regional patterns of community stability

The structure of rocky intertidal communities in all four regions has drifted over time such that samples became increasingly less similar

to the 'benchmark' (2006–2007–2008) state (Figures 2 and 3a). A gradual drifting of community structure over many years is not surprising, given that natural communities are not static. However, the pattern of change over time differed among regions (Figure 2; Table 1; year \times region). In general, the data show a pattern of higher long-term community stability (more similar to benchmark state) at high latitudes than at low latitudes, with northern (North and Central region) sites experiencing less community change than southern (South and Channel Islands) sites (Figures 2 and 3a).

Two periods of community change stand out for low-latitude regions. The moderate 2009–2010 ENSO event coincided with a substantial level of community change in the Channel Islands sites while changes in the three other regions were less drastic (Figure 2). Community change in the Channel Islands region began in 2008, preceding the 2009–2010 warm water event, so it is possible that factors other than water temperature were driving change during this period. Unfortunately, we do not have onshore water temperature data for this region in 2007–2008 (Figure 4). During the longer 2014–2016 warm water event, in which an ENSO event was coupled with a massive and persistent warm water 'blob' (Cavole et al., 2016; Sanford et al., 2019), substantial declines in temporal within-site similarity were observed in southern California communities on both the mainland and Channel Islands. This decline in community similarity in the southern regions was associated with a decline in cover of the mussel, *Mytilus californianus*, and a shift towards greater abundance of bare rock and warm-water-tolerant species such as the pink volcano barnacle, *Tetraclita rubescens*, the red alga *Chondracanthus canaliculatus* and coralline algae (Figure 3a,b).

3.2 | Sea water temperature and community stability

We examined the potential for specific aspects of water temperature to affect community similarity relative to the benchmark year and assessed whether those effects varied regionally using five separate models, each including region, one temperature metric (see Section 2.4.3) and the interaction (region \times temperature metric). The temperature metric and region, but not the interaction, were significant in each of the five models. The most strongly supported model (based on AICc score), with an r^2 value of 0.72, included the 10th percentile of annual temperatures, indicating that elevated temperature in the cooler part of the year was strongly associated with increased drift in community similarity values in all regions (Table 2; Figure 5). The next most supported model, the principal component for the four temperature variables, had an AICc score 18 points higher and an r^2 value of 0.53. Importantly, declines in community similarity values were associated with elevated water temperatures across all regions, including those in the north where changes were less extreme (Figure 5).

3.3 | Community stability at the site level and possible driving factors

Within each region, we found sites categorized as having 'higher' long-term community stability (defined as having a mean community similarity value greater than the median across all sites over the period of study) and sites categorized as having 'lower' stability

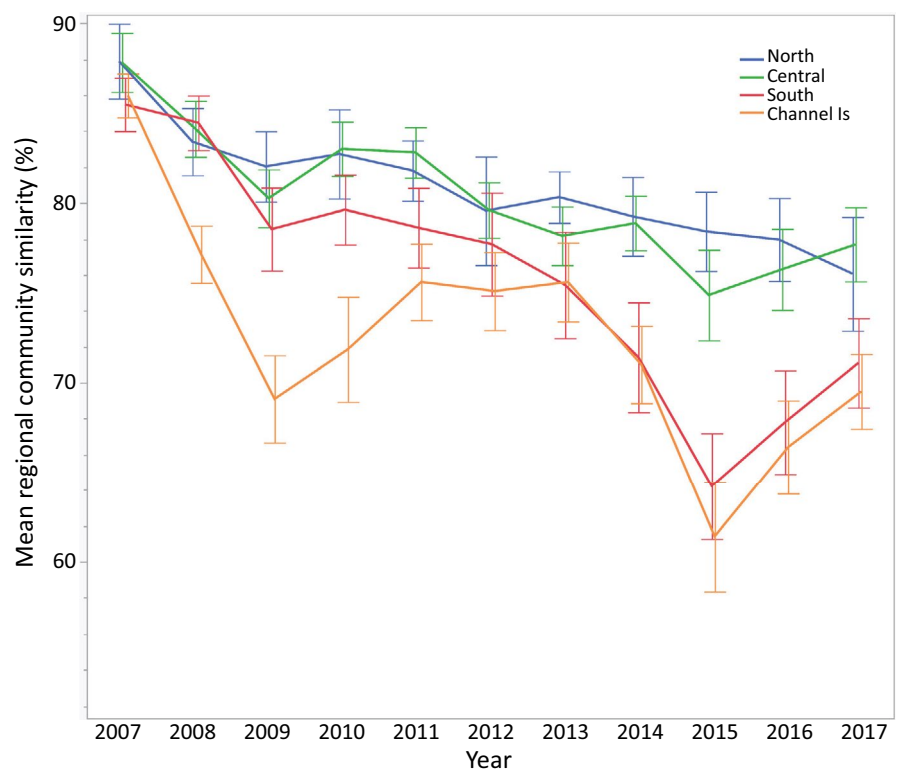


FIGURE 2 Patterns of community stability over time, as represented by annual mean similarity values relative to the start year (± 1 SE) across sites within each of four regions, represented by colour [Colour figure can be viewed at wileyonlinelibrary.com]

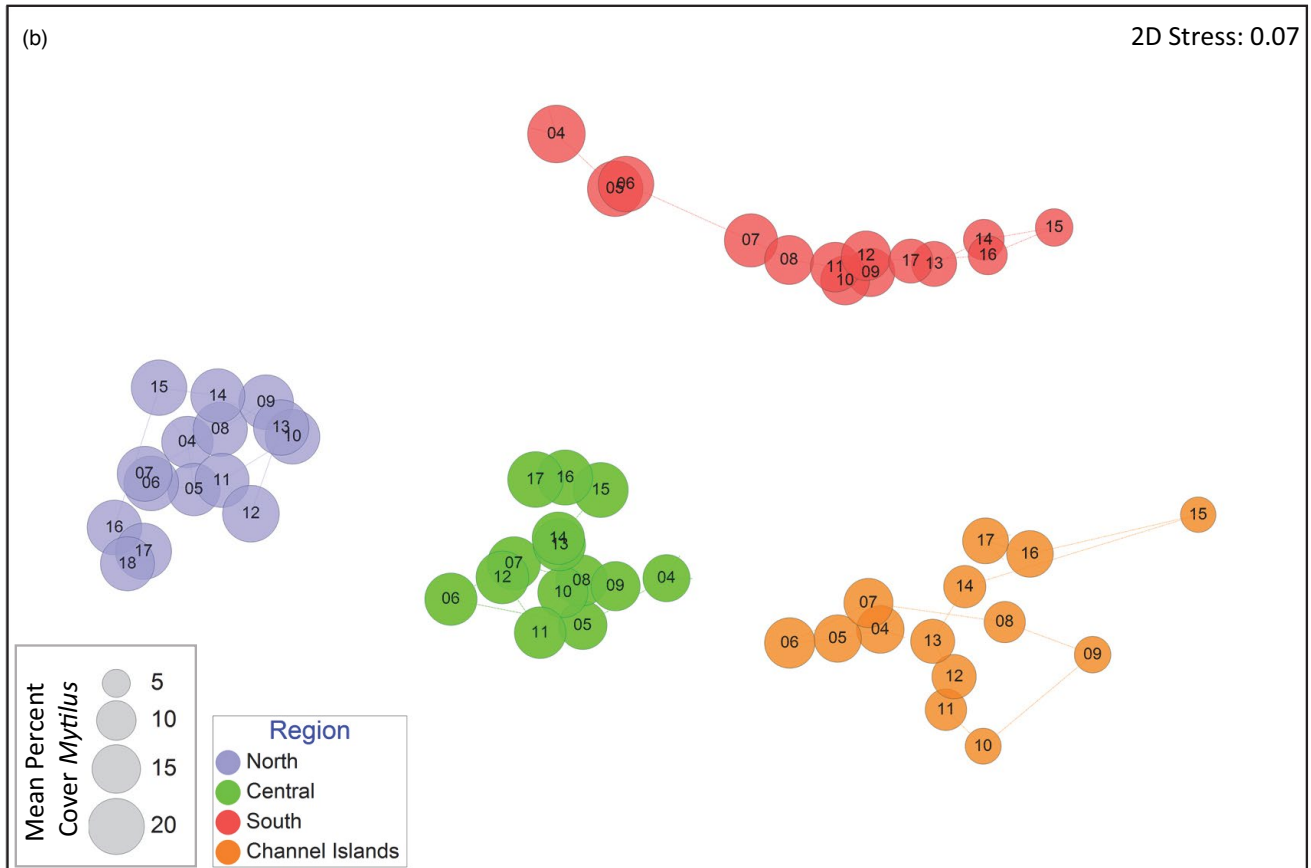
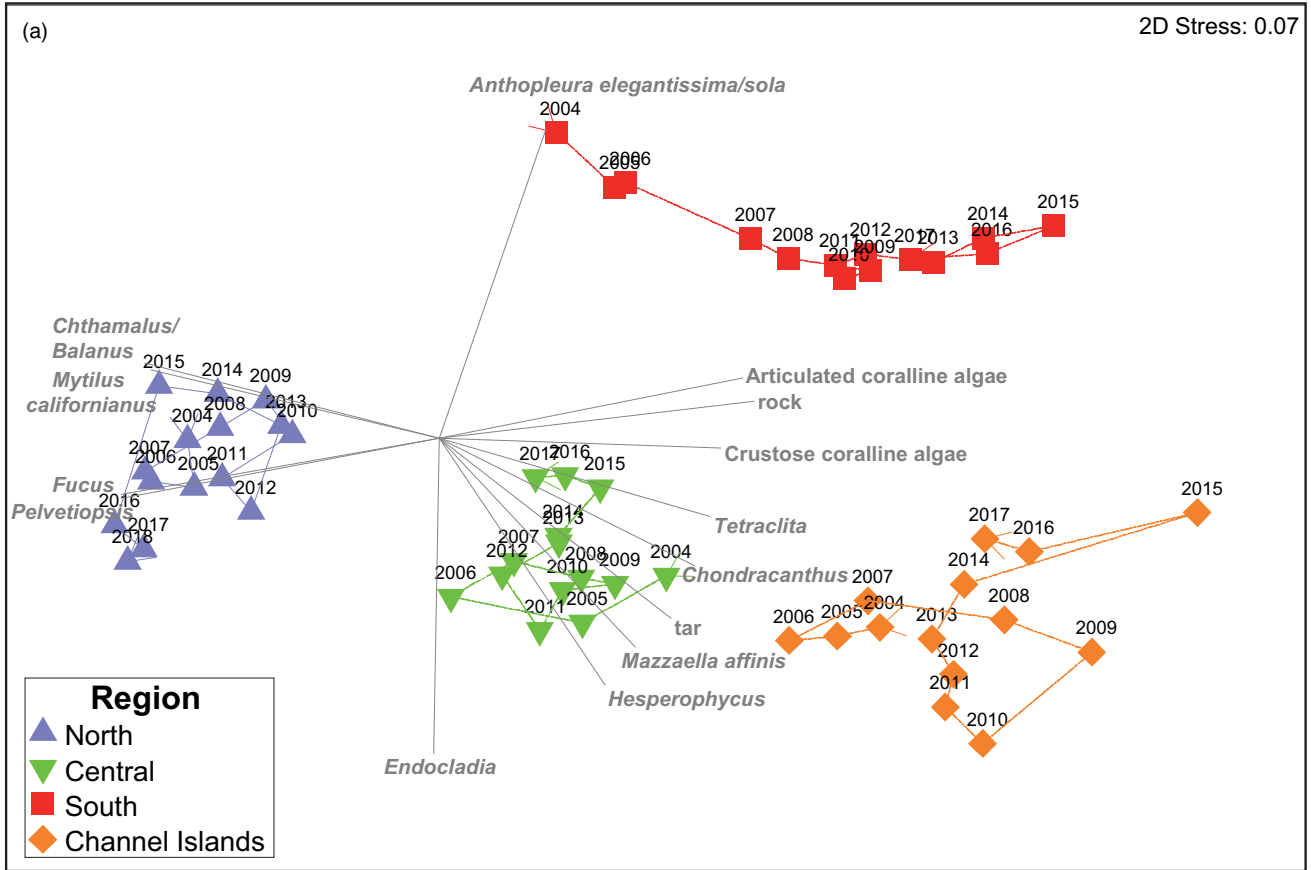


FIGURE 3 Non-metric Multi-Dimensional Scaling plots depicting change in Bray–Curtis similarity and associated community composition over time by region. (a) Species/species groups that are the primary drivers of changes in community similarity over time. Relative contribution of each species to community composition is indicated by the direction and length of each ray. Species listed at the ends of rays correlate with an r^2 value of at least 0.8 (range: 0.8–1) in the direction of the ray. See Table S2 in Supporting Information for full species names and definitions for species categories. (b) Change in percent cover of the mussel, *Mytilus californianus*, averaged across all sites within each region over time. Mussel cover is overlaid on the patterns of change in community similarity depicted in 3(a). Bubble size indicates mean cover for each year. Years are labelled using two-digit abbreviations (e.g. 04 = 2004) to reduce overlap [Colour figure can be viewed at wileyonlinelibrary.com]

(Figure 1). To better understand the drivers behind the observed patterns of community stability, we examined the results from the logistic model designed to predict stability category, which incorporated latitude and five indices of species richness/diversity (see Section 2). Using AICc model selection, the most supported model, which contained three significant ($p < 0.05$) variables: latitude, Margalef's richness (d) and the Shannon–Weiner diversity index (H') (Table 3), predicted stability category with 83% accuracy (correctly predicted state of 53 of 64 sites).

Margalef's (d) is a measure of species richness that includes a calibration by the number of samples, essentially adjusting richness by effort. In our analysis, sites with high d values were more likely

to be classified as having 'higher' long-term community stability (Figure 6a). However, the reverse was true for H' , an index that considers both species diversity and evenness, a measure of the relative abundance of species at a site (Figure 6a). Sites with low H' values were likely to be classified as having 'higher' stability, exhibiting smaller changes in community similarity values over time than sites with high H' values. This was counterintuitive, as species evenness is frequently positively associated with ecological stability (Wittebolle et al., 2009).

3.4 | Community stability and mussel cover

The contrasting relationships between long-term community stability and the two measures of diversity (d and H') may be a consequence of the presence of the mussel, *M. californianus*, a foundation species and competitive dominant on these rocky intertidal shores. Across all sites, mussel cover in permanent plots was negatively related to both H' ($F_{1,62} = 20.71$, $p < 0.001$) and evenness (as J' : $F_{1,62} = 10.39$, $p = 0.002$). When we replaced H' in the logistic model with *M. californianus* cover in permanent plots from an early representative year (2008), mussel cover was a strong predictor of

TABLE 1 Results from mixed-model analysis showing contribution of region and year to long-term stability of intertidal communities

Source	df	F-stat	p value
Region	3	0.28	0.840
Year	10	38.55	<0.001
Region × Year	30	2.63	<0.001

Bold indicates $p < 0.001$.

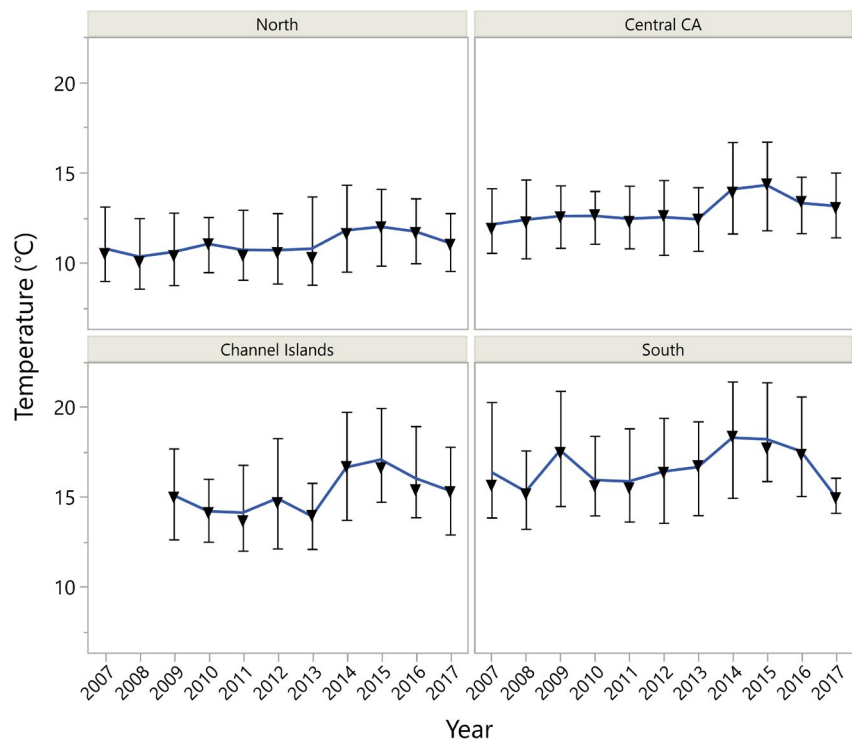


FIGURE 4 Mean (trend line), median (triangles) and 10th and 90th percentiles (bars) of annual water temperature data for each region. Note that 2007–2008 data are shown where available, but only 2009–2017 data were used in analyses to ensure consistency among regions [Colour figure can be viewed at wileyonlinelibrary.com]

Model	<i>p</i> value region	<i>p</i> value temp	<i>r</i> ²	<i>F</i> -stat	BIC	AIC	Delta AIC
Quantile 10	<0.0001	<0.0001	0.72	23.44	173.80	167.2	0.0
PC1	0.0002	0.0003	0.53	10.82	192.46	185.9	18.7
Mean	0.0003	0.0005	0.51	10.29	193.52	186.9	19.7
Median	0.0005	0.0011	0.49	9.50	195.10	188.5	21.3
Quantile 90	0.0063	0.0200	0.40	6.77	20.13	194.7	27.5

TABLE 2 Results for models examining effect of year and temperature metric on regional patterns of community stability. Five models were tested (see Section 2.4.3); the most supported (based on AICc score) included the 10th percentile annual water temperature metric

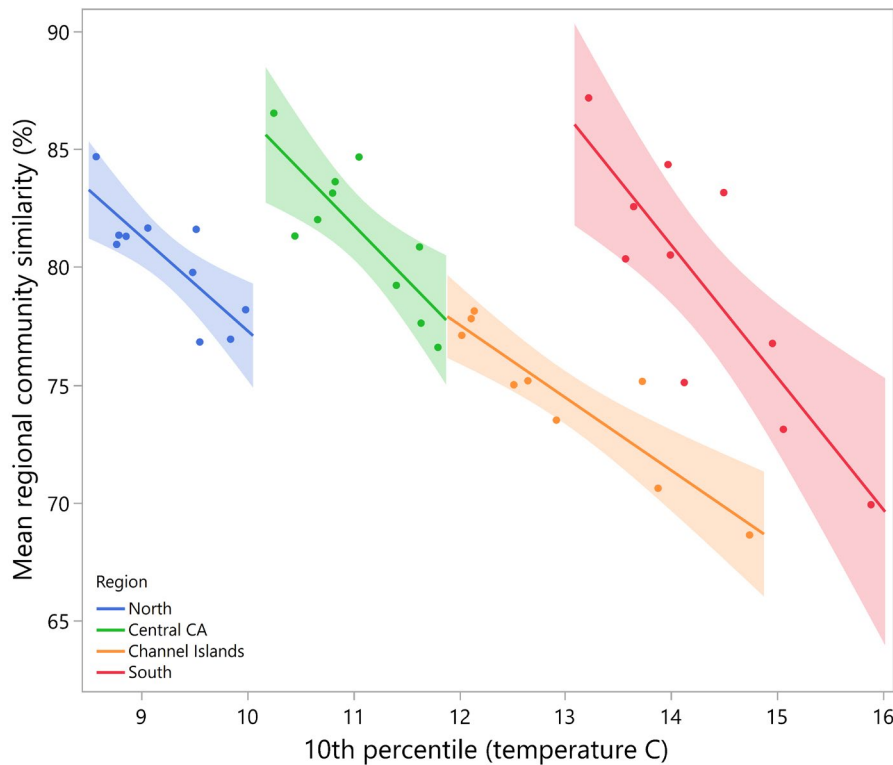


FIGURE 5 Results from the most-supported model examining the relationship between water temperature (10th percentile) and mean regional community stability (= the community similarity values for each site relative to the start year, averaged across all sites in the region) from 2009 to 2017. Shaded area represents the 95% confidence interval around the line [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 3 Results of most-supported logistic model for the association of metrics of diversity/species richness and latitude on long-term community stability category

Source	Estimate	Chi square	<i>p</i> value
Intercept	-15.06	5.42	0.020
Latitude	0.48	8.04	0.005
Mean (<i>d</i>)	1.99	6.04	0.014
Mean (<i>H'</i>)	-5.09	5.05	0.025

long-term community stability; sites with high mussel cover in 2008 were more likely to be classified as having 'higher' community stability over the next 10 years than those with low mussel cover in 2008 (Table 4; Figures 6b and 7a). This pattern was particularly evident at more southern latitudes, where average within-site mussel cover was typically lower and more variable over time compared to northern regions (Figures 3b and 8). Margalef's (*d*) was also associated with community stability (Figures 6a,b and 7b), revealing that once

mussel cover was accounted for in the model, species richness was important for community stability.

4 | DISCUSSION

Long-term, geographically expansive community monitoring surveys play a critical role in assessing how well predictions from experiments and theory explain patterns at broad spatial and temporal scales. A rapidly changing climate requires that we identify meaningful benchmarks against which we can assess ecological shift, and that we work to develop truly comprehensive multivariate assessments of community-level change (Petes et al., 2014). In this study, we examined long-term community stability of rocky intertidal systems utilizing an analytical approach that is applicable to a wide variety of ecosystems. Our findings from this broad-scale, long-term investigation indicate that for ecosystems structured around foundation species, high species diversity and low evenness (driven in part by a high abundance of foundation species) can be complimentary predictors

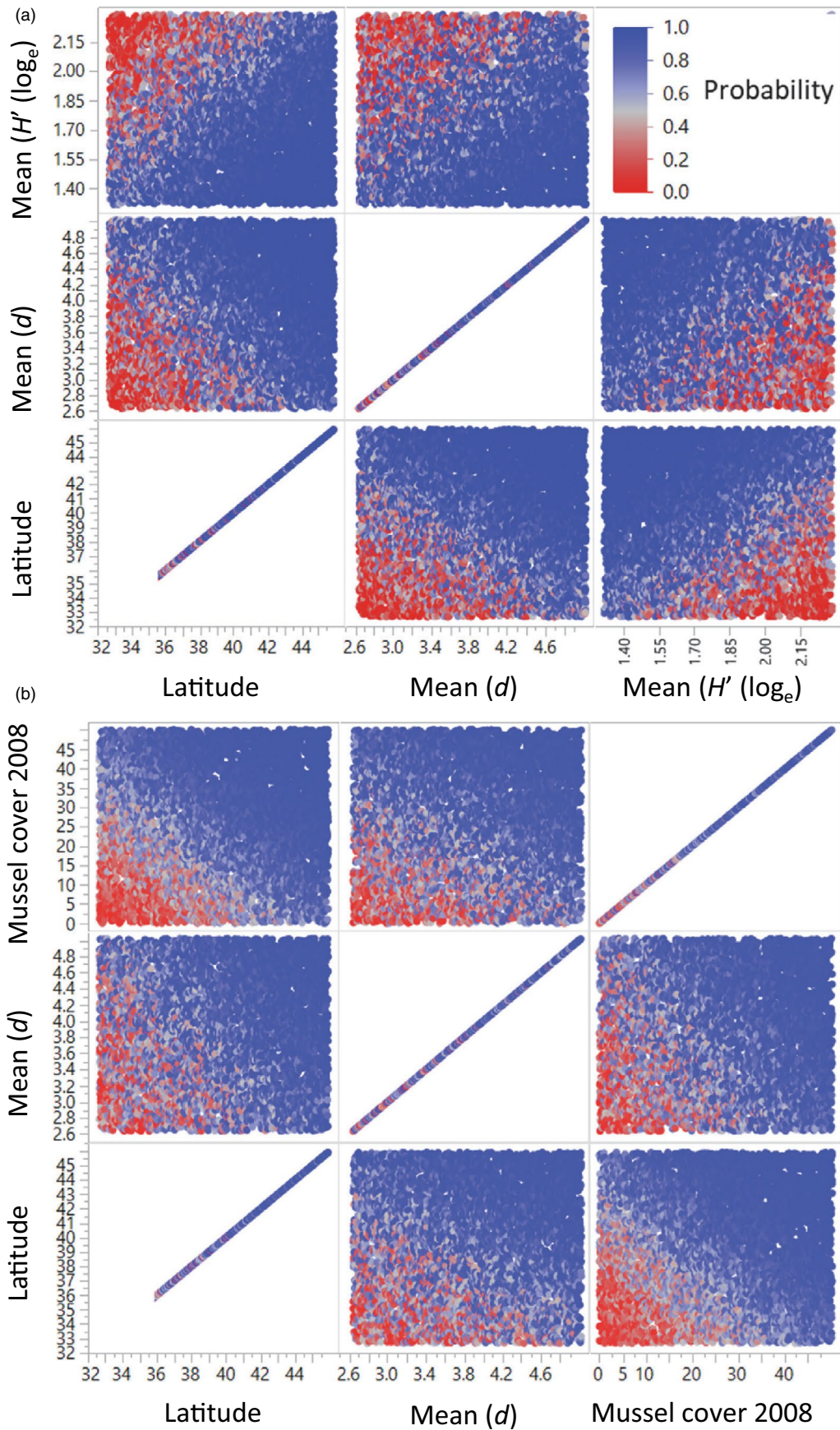


FIGURE 6 Modelled probability of a site being categorized as having 'higher' or 'lower' long-term community stability based on: (a) latitude, d and H' or (b) latitude, d and mussel cover in 2008 [Colour figure can be viewed at wileyonlinelibrary.com]

of long-term community stability and can aid in forecasting how communities will respond to disturbance, such as that resulting from climate change.

TABLE 4 Results of logistic model (see Table 3) with Mussel Cover substituted for Mean (H')

Source	Estimate	Chi square	<i>p</i> -value
Intercept	-18.3712	9.05	0.003
Latitude	0.335392	5.10	0.024
Mussel cover	0.094151	5.20	0.023
Mean (d)	1.248317	4.46	0.035

4.1 | Role of temperature

Ocean temperature can be an important and geographically broad driving agent of disturbance. Our data support a strong association between community change and periods of anomalously warm water conditions in all four regions, collectively spanning over 16 degrees of latitude, with particularly striking levels of change in the southern, warmer regions (Figures 2, 3 and 5). This large-scale pattern may foreshadow substantial changes in marine communities, as more extreme and longer-lasting warm water events are occurring at an increasingly frequent rate with a changing climate (Oliver et al., 2018). The models we used to explore associations between temperature metrics and community change

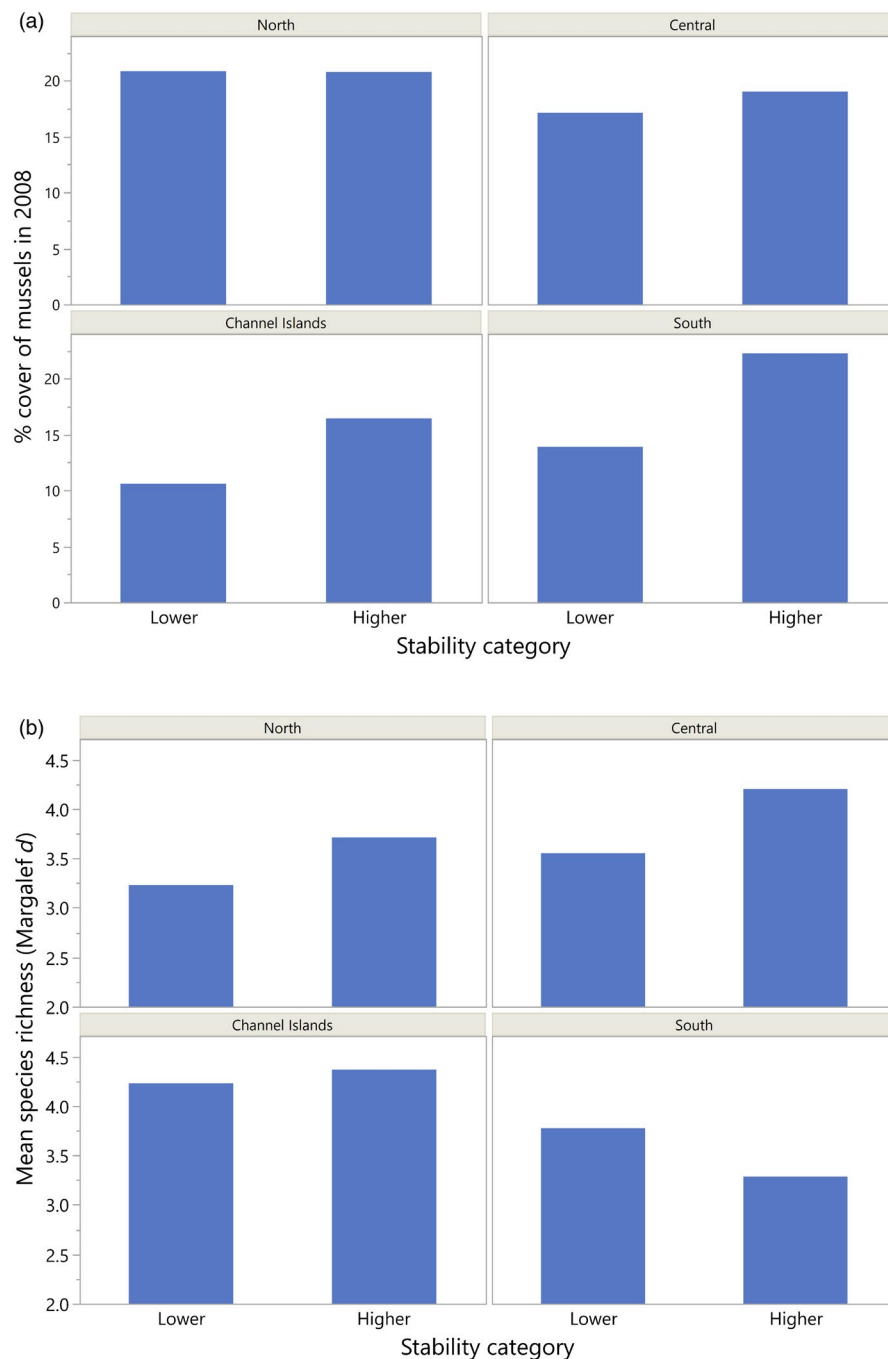
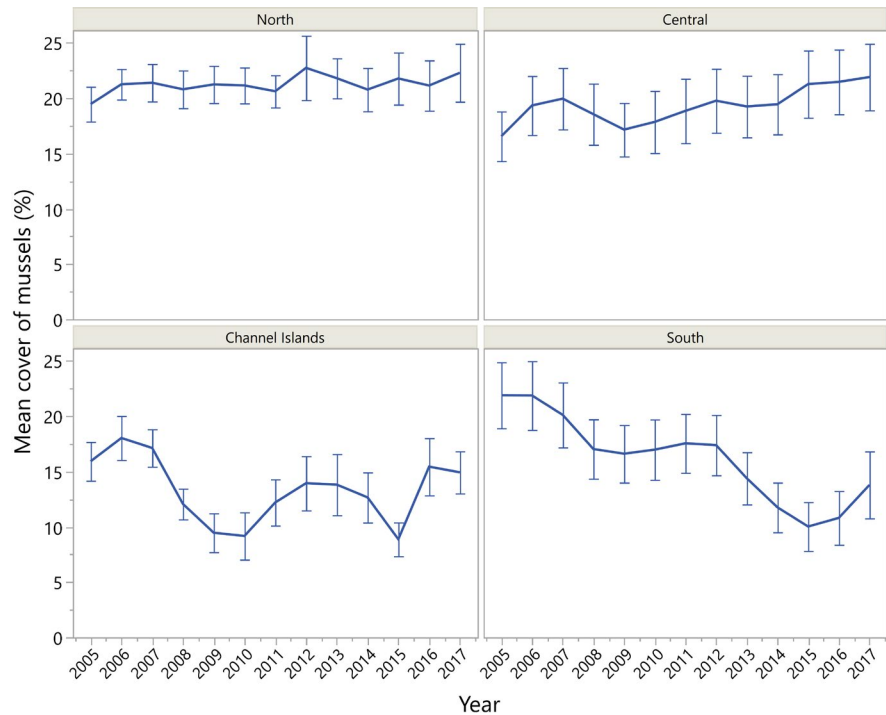


FIGURE 7 Mean values by region and community stability category for two factors associated with community stability: (a) mussel cover and (b) species richness (Margalef's d) [Colour figure can be viewed at wileyonlinelibrary.com]

FIGURE 8 Percent cover of the mussel, *Mytilus californianus*, over time. Data are mean ± 1 SE of all plots in each year for a region. Large error bars reflect the high amount of variability in mussel cover among sites within each region [Colour figure can be viewed at wileyonlinelibrary.com]



indicated that across all regions, warmer water temperatures were associated with a decline in community similarity compared to the benchmark year (Table 2). This correlation is linear, with small temperature changes corresponding to small shifts in community similarity and large temperature changes corresponding to large shifts, suggesting a pattern of incremental change rather than one resulting from tipping points (Figure 5). An unexpected finding was that abnormally high minimum annual temperatures (the coldest 10% of a year's SST) appeared to hold the most explanatory power. This result merits further investigation. In terrestrial systems, climate-change-induced shifts in phenology can result in plant-pollinator, plant-herbivore or predator-prey mismatches, or mistiming of annual life cycles that can have population or ecosystem-level impacts (e.g. Renner & Zohner, 2018; Visser & Gienapp, 2019). Examples of phenological mismatches also exist within marine systems, although research has thus far focused primarily on disruption of trophic interactions (e.g. Bograd et al., 2009; Schmeller et al., 2018). It is likely that rocky intertidal organisms that demonstrate seasonal patterns of growth, feeding and reproduction (Lewis, 1964) might pay a cost for mistimed metabolic or reproductive efforts resulting from spurious temperature cues. Warmer than average sea surface temperatures during typically cool water periods might also be indicative of a relaxation of upwelling during periods when this process, which brings cold, nutrient-rich water to the surface, is typically strong. A relaxation of upwelling can translate to lower nutrient availability and increased delivery of propagules, both of which can result in significant community change (Bograd et al., 2009).

4.2 | Spatial patterns of community stability

Unlike storm events, where damage tends to be patchy within and among sites (Fabricius et al., 2008), warm water events can be spatially pervasive, affecting broad stretches of coastline. Our analysis suggests

that while the general long-term trajectory (decline) of community similarity values in rocky intertidal communities was similar along the entire west coast of North America, the magnitude of decline, and hence implications for community stability, varied greatly among regions. On the southern mainland and Channel Islands, the impact on community stability resulting from large-scale environmental perturbation in the form of elevated water temperature events was more severe than in the central and northern regions. Our results suggest that the composition of communities in the two southern regions is shifting in a direction that less and less resembles communities at these sites from just over a decade ago. During the extreme marine heatwave event of 2014–2016, community composition shifted towards increased cover of bare rock as well as warm-water-tolerant species such as *Tetraclita rubescens* and *Chondracanthus canaliculatus*, and decreased cover of the foundation species, *Mytilus californianus* (Figure 3a,b). Hobday and Pecl (2014) identified the southern California, USA to Baja California, Mexico region as one of the several areas where ocean temperatures are rising at rates among the fastest on the planet. They argue that these 'marine hotspots' should be used as windows into the future for other regions, and we should focus on studies aimed at developing effective management and adaptation measures in these 'hotspots'. Our data highlight the potential risk to intertidal communities in this region and we echo this call for more studies that closely examine southern California rocky intertidal communities for clues to the conditions or mechanisms that affect long-term stability.

4.3 | Interpreting diversity metrics in systems with spatially dominant species

A primary focus of conservation ecology has been understanding the link between species diversity and ecosystem stability

(Loreau & Mazancourt, 2013; Tilman et al., 2014). Large bodies of data show strong relationships between community stability and both richness and evenness (Shade, 2017; Wilsey & Polley, 2004; Wittebolle et al., 2009). High species richness may increase chances of functional redundancy such that decline or loss of one species can be buffered by the presence of other species with similar community roles (Schmera & Erős, 2012; Wohl et al., 2004). Under fluctuating environmental conditions, species-rich communities may be stabilized by asynchronous responses of species within the same functional group (Loreau & Mazancourt, 2013). Within functionally redundant groups of species, high evenness has been found to increase the likelihood that ecosystem function will remain intact through environmental fluctuations (Wittebolle et al., 2009).

Our data indicate that in the open coast rocky intertidal ecosystem, there is a negative relationship between community stability and evenness. While this finding is counter to the most prevalent expectation that lower evenness should result in decreased stability (Wittebolle et al., 2009), it supports the findings of a handful of studies that found the reverse to be true. In these examples, one or a few stable dominant species were associated with increased overall community stability (Grman et al., 2010). Most intertidal systems are heavily influenced by foundation species (Angelini et al., 2011; Dayton, 1972; Ellison, 2019) which are, by definition, abundant and 'disproportionally important to the continued maintenance of community structure' (Dayton, 1972). Persistence of a foundation species therefore by definition stabilizes the local community (Lamy et al., 2020), and because of their abundance, drives down evenness values. In systems structured around a single, spatially dominant foundation species, in the absence of functional redundancy, changes in abundance of this species can have large impacts on community attributes (Lamy et al., 2020). This is the case with the mussel, *M. californianus*, a foundation species found on rocky shores across all biogeographical provinces represented in this study (Dayton, 1972; Smith et al., 2006). While other mussels co-occur with *M. californianus*, the only candidate for functional redundancy in terms of individual size and abundance is the congener *Mytilus trossulus*. However, compared to *M. californianus*, *M. trossulus* is almost always much less common and exhibits more temporally variable abundance on exposed coastal shores, in part due to its high susceptibility to predation (Menge et al., 1994; Sanford & Worth, 2010). It also has lower thermal tolerance than *M. californianus* in both air and water (Dowd & Somero, 2013). Thus, a replacement for declining *M. californianus* populations is unlikely and, where this critical species declines, substantial community-level change is all but certain.

In this study, we used non-destructive sampling methods that did not capture changes in the interstitial community within the mussel beds—those species directly dependent on *M. californianus* for habitat, food or protection from predation or physical stress (Suchanek, 1992). Instead, we examined the stabilizing role of mussels within the broader community of species attached to the primary substrate. Our data suggest that in systems containing

spatially dominant foundation species, traditional interpretation of diversity indices that incorporate both community-level richness and evenness might not be appropriate for predicting long-term community stability. While species richness does appear to be linked to long-term community stability, the pattern for evenness is likely the opposite for systems dominated by one or a few species, and low evenness values can indicate an abundant and stable presence of spatially dominant foundation species. Because several of the planet's most important marine ecosystems (e.g. oyster beds, kelp forests, coral reefs, seagrasses, mangroves: reviewed in Angelini et al., 2011; Ellison, 2019) are structured around single foundation species that are sensitive to ocean warming, acidification and other effects of climate change (Gaylord et al., 2015; Wernberg et al., 2016), prospects for long-term stability in these ecosystems might be low.

4.4 | Community succession and stability

One of the conclusions from this study—that as a spatially dominant foundation species in rocky intertidal communities, mussels exert an important stabilizing force on community structure over time—is an idea that was first demonstrated by the extensive work exploring succession and stability of climax communities 40 years ago (e.g. Connell & Slatyer, 1977; Paine & Levin, 1981; Sousa, 1984). Our work expands upon these canonical studies by assessing contrasting predictions of two fundamental categories of models of community stability: (a) a stable climax community is less rich than communities in earlier stages of succession (e.g. intermediate disturbance hypothesis, Sousa, 1979) and (b) communities with high diversity are more stable than communities with low diversity (e.g. diversity stability hypothesis; e.g. Ives & Carpenter, 2007). Our results show that both high species richness and mussel cover were associated with increased community stability in temperate rocky intertidal systems (Figure 6). In the regions that experienced greater community change (South and Channel Islands), abundance of *M. californianus* appeared to be more important than richness in predicting community stability, lending support to the idea that climax communities afford overall stability to a system (Figure 7a). By contrast, in regions where mussel cover remained generally high (i.e. in which climax communities are common; North and Central regions), species richness appeared to be more important for predicting community stability (Figure 7b). Thus, elements of both types of community stability models were supported, though the relative strength of support varied regionally.

4.5 | Concluding remarks

Here we examined the relationship between temporal shifts in community composition and sea water temperature over a large spatial scale. However, we do not assert that water temperature is the only potential driver of community change. Because it is relatively inexpensive and simple to monitor, sea water temperature is currently the only factor consistently measured on a broad scale for intertidal

ecosystems (although important gaps exist). High priority should be placed on designing and implementing inexpensive, simple methods for measuring other key factors known to influence species' distributions and survivorship, such as sea water pH, wave climate, humidity, air temperature, organismal body temperature and prevalence of fog. Combining reliable, high-frequency and spatially explicit data for these key physical factors with long-term biological monitoring data from programmes such as MARINE will give us the most power to detect and potentially mitigate community shifts (Petes et al., 2014).

In the face of a changing climate and accompanying ecological uncertainty, management agencies are challenged to create forward-looking plans, which can effectively address the local impacts of regional or global phenomena (Petes et al., 2014; Rilov et al., 2019). The ability to identify factors that contribute broadly to community stability has important implications for resource management and conservation and our analysis adds to the toolbox of methods that can be used to effectively allocate management effort across time and space (Rilov et al., 2019).

ACKNOWLEDGEMENTS

We thank Lisa Gilbane, our MARINE programme manager, for her vision and support of this long-term monitoring effort. Funding for this effort was provided by the Bureau of Ocean Energy Management, the California Ocean Protection Council, the David and Lucille Packard Foundation and the National Park Service. We also thank the many non-author researchers, technicians, students and volunteers who helped collect and manage data. Site access and field support were provided by the University of California Natural Reserve Systems (Bodega, Landels-Hill Big Creek, Coal Oil Point, and Santa Cruz Island), The Nature Conservancy, and the Olympic Coast, Gulf of Farallones, Monterey Bay and Channel Islands National Marine Sanctuaries. We are also grateful to the Makah Tribe and Quinault Indian Nation, the Sea Ranch Association, Hopkins Marine Reserve, the Pebble Beach Company, El Sur Ranch, Hollister Ranch and Vandenberg Air Force Base for access to sites. Authors have no conflicts of interest to declare.

AUTHORS' CONTRIBUTIONS

P.T.R. designed the study; C.M.M., J.L.B., K.A., B.H.B. S.C.F., J.R.S., S.G.W. and P.T.R. collected the data; P.T.R. analysed the data; C.M.M. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

The data underlying this study have been uploaded to DataONE and are accessible here: https://doi.org/10.6085/AA/marine_ltm.20.1.

ORCID

C. Melissa Miner  <https://orcid.org/0000-0002-4032-3846>

Jennifer L. Burnaford  <https://orcid.org/0000-0003-2159-2335>

Karah Ammann  <https://orcid.org/0000-0002-6200-1944>

Steven C. Fradkin  <https://orcid.org/0000-0002-6528-1961>

Peter T. Raimondi  <https://orcid.org/0000-0001-5235-1441>

REFERENCES

- Alheit, J., & Bakun, A. (2010). Population synchronies within and between ocean basins: Apparent teleconnections and implications as to physical-biological linkage mechanisms. *Journal of Marine Systems*, 79(3), 267–285. <https://doi.org/10.1016/j.jmarsys.2008.11.029>
- Ambrose, R. F., Engle, J. M., Raimondi, P. T., Wilson, M., & Altstatt, J. A. (1995). *Rocky intertidal and subtidal resources: Santa Barbara County mainland*. Final Report to the Minerals Management Service. (No. OCS Study MMS 95-0067).
- Ambrose, R. F., & Smith, J. R. (2005). *Restoring rocky intertidal habitats in Santa Monica Bay*. Technical Report for the Santa Monica Bay Restoration Commission.
- Angelini, C., Altieri, A. H., Silliman, B. R., & Bertness, M. D. (2011). Interactions among foundation species and their consequences for community organization, biodiversity, and conservation. *BioScience*, 61(10), 782–789. <https://doi.org/10.1525/bio.2011.61.10.8>
- Arnoldi, J.-F., Loreau, M., & Haegeman, B. (2016). Resilience, reactivity and variability: A mathematical comparison of ecological stability measures. *Journal of Theoretical Biology*, 89, 47–59. <https://doi.org/10.1016/j.jtbi.2015.10.012>
- Bindoff, N. L., Cheung, W. W. L., Kairo, J. G., Aristegui, J., Guinder, V. A., Hallberg, R., Hilmi, N., Jiao, N., Saiful Karim, M. D., Levin, L., O'Donoghue, S., Purca Cuicapusa, S. R., Rinkevich, B., Suga, T., Tagliabue, A., & Williamson, P. (2019). Changing ocean, marine ecosystems, and dependent communities. In H. O. Pörtner, D. C. Roberts, V. Masson-Delmotte, P. Zhai, M. Tignor, E. Poloczanska, K. Mintenbeck, A. Alegria, M. Nicolai, A. Okem, J. Petzold, B. Rama, & N. M. Weyer (Eds.), *IPCC Special Report on the Ocean & Cryosphere in a Changing Climate*, 447–587.
- Blanchette, C. A., Miner, C. M., Raimondi, P. T., Lohse, D., Heady, K. E. K., & Broitman, B. R. (2008). Biogeographical patterns of rocky intertidal communities along the Pacific Coast of North America. *Journal of Biogeography*, 35(9), 1593–1607. <https://doi.org/10.1111/j.1365-2699.2008.01913.x>
- Bograd, S. J., Schroeder, I., Sarkar, N., Qiu, X., Sydeman, W. J., & Schwing, F. B. (2009). Phenology of coastal upwelling in the California Current. *Geophysical Research Letters*, 36(1), 1–5. <https://doi.org/10.1029/2008GL035933>
- Brierley, A. S., & Kingsford, M. J. (2009). Impacts of climate change on marine organisms and ecosystems. *Current Biology*, 19(14), R602–R614. <https://doi.org/10.1016/j.cub.2009.05.046>
- Cavole, L., Demko, A., Diner, R., Giddings, A., Koester, I., Pagniello, C., Paulsen, M.-L., Ramirez-Valdez, A., Schwenck, S., Yen, N., Zill, M., & Franks, P. (2016). Biological impacts of the 2013–2015 warm-water anomaly in the Northeast Pacific: Winners, losers, and the future. *Oceanography*, 29, 273–285. <https://doi.org/10.5670/oceanog.2016.32>
- Clarke, K. R., Somerfield, P. J., & Chapman, M. G. (2006). On resemblance measures for ecological studies, including taxonomic dissimilarities and a zero-adjusted Bray–Curtis coefficient for denuded assemblages. *Journal of Experimental Marine Biology and Ecology*, 330(1), 55–80. <https://doi.org/10.1016/j.jembe.2005.12.017>
- Connell, J. H., & Slatyer, R. O. (1977). Mechanisms of succession in natural communities and their role in community stability and organization. *The American Naturalist*, 111(982), 1119–1144. <https://doi.org/10.1086/283241>
- Croll, D. A., Maron, J. L., Estes, J. A., Danner, E. M., & Byrd, G. V. (2005). Introduced predators transform subarctic islands from grassland to Tundra. *Science*, 307(5717), 1959–1961. <https://doi.org/10.1126/science.1108485>
- Dayton, P. K. (1972). Toward an understanding of community resilience and the potential effects of enrichments to the benthos at McMurdo Sound, Antarctica. In B. Parker (Ed.), *Proceedings of the Colloquium on Conservation Problems in Antarctica* (pp. 81–96). University of California, San Diego, Scripps Institution of Oceanography, La Jolla, CA; Allen Press.

- Doney, S. C., Ruckelshaus, M., Emmett Duffy, J., Barry, J. P., Chan, F., English, C. A., Galindo, H. M., Grebmeier, J. M., Hollowed, A. B., Knowlton, N., Polovina, J., Rabalais, N. N., Sydeman, W. J., & Talley, L. D. (2012). Climate change impacts on marine ecosystems. *Annual Review of Marine Science*, 4(1), 11–37. <https://doi.org/10.1146/annurev-marine-041911-111611>
- Donohue, I., Hillebrand, H., Montoya, J. M., Petchey, O. L., Pimm, S. L., Fowler, M. S., Healy, K., Jackson, A. L., Lurgi, M., McClean, D., O'Connor, N. E., O'Gorman, E. J., & Yang, Q. (2016). Navigating the complexity of ecological stability. *Ecology Letters*, 19(9), 1172–1185. <https://doi.org/10.1111/ele.12648>
- Donohue, I., Petchey, O. L., Montoya, J. M., Jackson, A. L., McNally, L., Viana, M., Healy, K., Lurgi, M., O'Connor, N. E., & Emmerson, M. C. (2013). On the dimensionality of ecological stability. *Ecology Letters*, 16(4), 421–429. <https://doi.org/10.1111/ele.12086>
- Dowd, W. W., & Somero, G. N. (2013). Behavior and survival of *Mytilus* congeners following episodes of elevated body temperature in air and seawater. *Journal of Experimental Biology*, 216, 502–514. <https://doi.org/10.1242/jeb.076620>
- Ellison, A. M. (2019). Foundation species, non-trophic interactions, and the value of being common. *Science*, 13, 254–268. <https://doi.org/10.1016/j.isci.2019.02.020>
- Fabricius, K. E., De'ath, G., Puotinen, M. L., Done, T., Cooper, T. F., & Burgess, S. C. (2008). Disturbance gradients on inshore and offshore coral reefs caused by a severe tropical cyclone. *Limnology and Oceanography*, 53(2), 690–704. <https://doi.org/10.4319/lo.2008.53.2.0690>
- Freund, M. B., Henley, B. J., Karoly, D. J., McGregor, H. V., Abram, N. J., & Dommenges, D. (2019). Higher frequency of Central Pacific El Niño events in recent decades relative to past centuries. *Nature Geoscience*, 12(6), 450–455. <https://doi.org/10.1038/s41561-019-0353-3>
- Frölicher, T. L., & Laufkötter, C. (2018). Emerging risks from marine heat waves. *Nature Communications*, 9(1), 1–4. <https://doi.org/10.1038/s41467-018-03163-6>
- Gaylord, B., Kroeker, K. J., Sunday, J. M., Anderson, K. M., Barry, J. P., Brown, N. E., Connell, S. D., Dupont, S., Fabricius, K. E., Hall-Spencer, J. M., Klinger, T., Milazzo, M., Munday, P. L., Russell, B. D., Sanford, E., Schreiber, S. J., Thiagarajan, V., Vaughan, M. L. H., Widdicombe, S., & Harley, C. D. G. (2015). Ocean acidification through the lens of ecological theory. *Ecology*, 96(1), 3–15. <https://doi.org/10.1890/14-0802.1>
- Grimm, V., & Wissel, C. (1997). Babel, or the ecological stability discussions: An inventory and analysis of terminology and a guide for avoiding confusion. *Oecologia*, 109(3), 323–334. <https://doi.org/10.1007/s004420050090>
- Grman, E., Lau, J. A., Schoolmaster, D. R., & Gross, K. L. (2010). Mechanisms contributing to stability in ecosystem function depend on the environmental context: Stabilizing mechanisms in grasslands. *Ecology Letters*, 13(11), 1400–1410. <https://doi.org/10.1111/j.1461-0248.2010.01533.x>
- Harley, C. D. G., Randall Hughes, A., Hultgren, K. M., Miner, B. G., Sorte, C. J. B., Thornber, C. S., Rodriguez, L. F., Tomanek, L., & Williams, S. L. (2006). The impacts of climate change in coastal marine systems: Climate change in coastal marine systems. *Ecology Letters*, 9(2), 228–241. <https://doi.org/10.1111/j.1461-0248.2005.00871.x>
- Harms, S., & Winant, C. (1998). Characteristic patterns of the circulation in the Santa Barbara Channel. *Journal of Geophysical Research*, 103(C2), 3041–3065.
- Hawkins, S. J., Moore, P. J., Burrows, M. T., Poloczanska, E., Mieszkowska, N., Herbert, R., Jenkins, S. R., Thompson, R. C., Genner, M. J., & Southward, A. J. (2008). Complex interactions in a rapidly changing world: Responses of rocky shore communities to recent climate change. *Climate Research*, 37(2–3), 123–133. <https://doi.org/10.3354/cr00768>
- Hawkins, S. J., Sugden, H. E., Mieszkowska, N., Moore, P. J., Poloczanska, E., Leaper, R., Herbert, R., Genner, M. J., Moschella, P. S., Thompson, R. C., Jenkins, S. R., Southward, A. J., & Burrows, M. T. (2009). Consequences of climate-driven biodiversity changes for ecosystem functioning of North European rocky shores. *Marine Ecology Progress Series*, 396, 245–259. <https://doi.org/10.3354/meps08378>
- Hillebrand, H., Bennett, D. M., & Cadotte, M. W. (2008). Consequences of dominance: A review of evenness effects on local and regional ecosystem processes. *Ecology*, 89(6), 1510–1520. <https://doi.org/10.1890/07-1053.1>
- Hillebrand, H., Langenheder, S., Lebret, K., Lindström, E., Östman, Ö., & Striebel, M. (2018). Decomposing multiple dimensions of stability in global change experiments. *Ecology Letters*, 21(1), 21–30. <https://doi.org/10.1111/ele.12867>
- Hobday, A. J., & Pecl, G. T. (2014). Identification of global marine hotspots: Sentinels for change and vanguards for adaptation action. *Reviews in Fish Biology and Fisheries*, 24(2), 415–425. <https://doi.org/10.1007/s11160-013-9326-6>
- Hodgson, D., McDonald, J. L., & Hosken, D. J. (2015). What do you mean, 'resilient'? *Trends in Ecology & Evolution*, 30(9), 503–506. <https://doi.org/10.1016/j.tree.2015.06.010>
- Howard, J., Babij, E., Griffis, R., Helmuth, B., Himes-Cornell, A., Neimier, P., Orbach, M., Petes, L., Allen, S., Auad, G., Auer, C., Beard, R., Boatman, M., Bond, N., Boyer, T., Brown, D., Clay, P., Crane, K., Cross, S., ... Xue, Y. (2013). Oceans & marine resources in a changing climate. *Oceanography & Marine Biology: An Annual Review*, 51, 71–192.
- Ingrisch, J., & Bahn, M. (2018). Towards a comparable quantification of resilience. *Trends in Ecology & Evolution*, 33(4), 251–259. <https://doi.org/10.1016/j.tree.2018.01.013>
- Isbell, F. I., Polley, H. W., & Wilsey, B. J. (2009). Biodiversity, productivity and the temporal stability of productivity: Patterns and processes. *Ecology Letters*, 12(5), 443–451. <https://doi.org/10.1111/j.1461-0248.2009.01299.x>
- Ives, A. R., & Carpenter, S. R. (2007). Stability & diversity of ecosystems. *Science*, 317(5834), 58–62. <https://doi.org/10.1126/science.1133258>
- Kapsenberg, L., & Hofmann, G. E. (2016). Ocean pH time-series and drivers of variability along the northern Channel Islands, California, USA. *Limnology and Oceanography*, 61, 953–968. <https://doi.org/10.1002/lno.10264>
- Keeling, R. E., Körtzinger, A., & Gruber, N. (2010). Ocean deoxygenation in a warming world. *Annual Review of Marine Science*, 2, 199–229. <https://doi.org/10.1146/annurev.marine.010908.163855>
- Kéfi, S., Dominguez-García, V., Donohue, I., Fontaine, C., Thébault, E., & Dakos, V. (2019). Advancing our understanding of ecological stability. *Ecology Letters*, 22, 1349–1356. <https://doi.org/10.1111/ele.13340>
- Lamy, T., Koenigs, C., Holbrook, S. J., Miller, R. J., Stier, A. C., & Reed, D. C. (2020). Foundation species promote community stability by increasing diversity in a giant kelp forest. *Ecology*, 101(5), e02987. <https://doi.org/10.1002/ecy.2987>
- Lewis, J. R. (1964). *The ecology of rocky shores*. The English Universities Press Ltd.
- Loreau, M., & de Mazancourt, C. (2013). Biodiversity and ecosystem stability: A synthesis of underlying mechanisms. *Ecology Letters*, 16, 106–115. <https://doi.org/10.1111/ele.12073>
- Menge, B. A., Berlow, E. L., Blanchette, C. A., Navarrete, S. A., & Yamada, S. B. (1994). The keystone species concept: Variation in interaction strength in a Rocky Intertidal Habitat. *Ecological Monographs*, 64(3), 249–286. <https://doi.org/10.2307/2937163>
- Miner, C. M., Burnaford, J. L., Ambrose, R. F., Antrim, L., Bohlmann, H., Blanchette, C. A., Engle, J. M., Fradkin, S. C., Gaddam, R., Harley, C. D. G., Miner, B. G., Murray, S. N., Smith, J. R., Whitaker, S. G., & Raimondi, P. T. (2018). Large-scale impacts of sea star wasting disease (SSWD) on intertidal sea stars and implications for recovery. *PLoS ONE*, 13(3), e0192870. <https://doi.org/10.1371/journal.pone.0192870>
- Narayan, N., Paul, A., Mulitza, S., & Schulz, M. (2010). Trends in coastal upwelling intensity during the late 20th century. *Ocean Science*, 6(3), 815–823. <https://doi.org/10.5194/os-6-815-2010>

- Oliver, E. C. J., Donat, M. G., Burrows, M. T., Moore, P. J., Smale, D. A., Alexander, L. V., Benthuyssen, J. A., Feng, M., Sen Gupta, A., Hobday, A. J., Holbrook, N. J., Perkins-Kirkpatrick, S. E., Scannell, H. A., Straub, S. C., & Wernberg, T. (2018). Longer and more frequent marine heatwaves over the past century. *Nature Communications*, 9(1), 1–12. <https://doi.org/10.1038/s41467-018-03732-9>
- Paine, R. T., & Levin, S. A. (1981). Intertidal landscapes: Disturbance and the dynamics of pattern. *Ecological Monographs*, 51, 145–178.
- Petes, L. E., Howard, J. F., Helmuth, B. S., & Fly, E. K. (2014). Population synchronies within and between ocean basins: Apparent teleconnections and implications as to physical–biological linkage mechanisms. Science integration into US climate and ocean policy. *Nature Climate Change*, 4, 671–677. <https://doi.org/10.1038/NCLIMATE2312>
- Raimondi, P. T., Ammann, K., Gilbane, L., Whitaker, S., & Ostermann-Kelm, S. (2018). *Regional assessment of the rocky intertidal monitoring programs at Channel Islands National Park & Bureau of Ocean Energy Management sites: Power analysis for cover of sessile species & counts of selected mobile species*. Natural Resource Report NPS/MEDN/NRR. National Park Service, Fort Collins, Colorado.
- Raimondi, P. T., Wilson, C. M., Ambrose, R. F., Engle, J. M., & Minchinton, T. E. (2002). Continued declines of black abalone along the coast of California: Are mass mortalities related to El Niño events? *Marine Ecology Progress Series*, 242, 143–152. <https://doi.org/10.3354/meps242143>
- Reguero, B. G., Losada, I. J., & Méndez, F. J. (2019). A recent increase in global wave power as a consequence of oceanic warming. *Nature Communications*, 10(1), 1–14. <https://doi.org/10.1038/s41467-018-08066-0>
- Renner, S. S., & Zohner, C. M. (2018). Climate change and phenological mismatch in trophic interactions among plants, insects, and vertebrates. *Annual Review of Ecology, Evolution, and Systematics*, 49(1), 165–182. <https://doi.org/10.1146/annurev-ecolsys-110617-062535>
- Rilov, G., Mazaris, A. D., Stelzenmüller, V., Helmuth, B., Wahl, M., Guy-Haim, T., Mieszowska, N., Ledoux, J.-B., & Katsanevakis, S. (2019). Adaptive marine conservation planning in the face of climate change: What can we learn from physiological, ecological and genetic studies? *Global Ecology and Conservation*, 17, e00566. <https://doi.org/10.1016/j.gecco.2019.e00566>
- Rogers, H., Hille Ris Lambers, J., Miller, R., & Tewksbury, J. J. (2012). ‘Natural experiment’ demonstrates top-down control of spiders by birds on a landscape level. *PLoS ONE*, 7(9), e43446. <https://doi.org/10.1371/journal.pone.0043446>
- Sanford, E., Sones, J. L., García-Reyes, M., Goddard, J. H. R., & Largier, J. L. (2019). Widespread shifts in the coastal biota of northern California during the 2014–2016 marine heatwaves. *Scientific Reports*, 9(1), 1–14. <https://doi.org/10.1038/s41598-019-40784-3>
- Sanford, E., & Worth, D. J. (2010). Local adaptation along a continuous coastline: Prey recruitment drives differentiation in a predatory snail. *Ecology*, 91(3), 891–901. <https://doi.org/10.1890/09-0536.1>
- Schmeller, D. S., Weatherdon, L. V., Loyau, A., Bondeau, A., Brotons, L., Brummitt, N., Geijzendorffer, I. R., Haase, P., Kuemmerlen, M., Martin, C. S., Mihoub, J.-B., Rocchini, D., Saarenmaa, H., Stoll, S., & Regan, E. C. (2018). A suite of essential biodiversity variables for detecting critical biodiversity change. *Biological Reviews*, 93(1), 55–71. <https://doi.org/10.1111/brv.12332>
- Schmera, D., & Erős, T. (2012). Does functional redundancy of communities provide insurance against human disturbances? An analysis using regional-scale stream invertebrate data. *Hydrobiologia*, 693, 183. <https://doi.org/10.1007/s10750-012-1107-z>
- Seed, R., & Suchanek, T. H. (1992). Population & community ecology of *Mytilus*. In E. M. Gosling (Ed.), *The mussel Mytilus* (pp. 87–169). Elsevier Science Publishers.
- Shade, A. (2017). Diversity is the question, not the answer. *The ISME Journal*, 11(1), 1–6. <https://doi.org/10.1038/ismej.2016.118>
- Smith, J. R., Fong, P., & Ambrose, R. F. (2006). Dramatic declines in mussel bed community diversity: Response to climate change? *Ecology*, 87(5), 1153–1161.
- Sousa, W. P. (1979). Disturbance in marine intertidal boulder fields: The non-equilibrium maintenance of species diversity. *Ecology*, 60, 1225–1239.
- Sousa, W. P. (1984). Intertidal mosaics: Patch size, propagule availability, and spatially variable patterns of succession. *Ecology*, 65(6), 1918–1935. <https://doi.org/10.2307/1937789>
- Suchanek, T. H. (1992). Extreme biodiversity in the marine environment: Mussel bed communities of *Mytilus californianus*. *The Northwest Environmental Journal*, 8(1), 150–152.
- Tilman, D., Forest, I., & Cowles, J. M. (2014). Biodiversity & ecosystem functioning. *The Annual Review of Ecology, Evolution, & Systematics*, 45, 471–493.
- Underwood, A. J., Chapman, M. G., & Connell, S. D. (2000). Observations in ecology: You can't make progress on processes without understanding the patterns. *Journal of Experimental Marine Biology and Ecology*, 250(1–2), 97–115. [https://doi.org/10.1016/S0022-0981\(00\)00181-7](https://doi.org/10.1016/S0022-0981(00)00181-7)
- Valdivia, N., González, A. E., Manzur, T., & Broitman, B. R. (2013). Mesoscale variation of mechanisms contributing to stability in rocky shore communities. *PLoS ONE*, 8(1), e54159. <https://doi.org/10.1371/journal.pone.0054159>
- Visser, M. E., & Gienapp, P. (2019). Evolutionary and demographic consequences of phenological mismatches. *Nature Ecology Evolution*, 3, 879–885. <https://doi.org/10.1038/s41559-019-0880-8>
- Ware, R. (2009). *Central orange county areas of special biological significance public use monitoring program*. Prepared for the City of Newport Beach Public Works.
- Wernberg, T., Bennett, S., Babcock, R. C., de Bettignies, T., Cure, K., Depczynski, M., Dufois, F., Fromont, J., Fulton, C. J., Hovey, R. K., Harvey, E. S., Holmes, T. H., Kendrick, G. A., Radford, B., Santanagarcon, J., Saunders, B. J., Smale, D. A., Thomsen, M. S., Tuckett, C. A., ... Wilson, S. (2016). Climate-driven regime shift of a temperate marine ecosystem. *Science*, 353(6295), 169–172. <https://doi.org/10.1126/science.aad8745>
- Wilsey, B. J., & Polley, H. W. (2004). Realistically low species evenness does not alter grassland species–richness–productivity relationships. *Ecology*, 85(10), 2693–2700. <https://doi.org/10.1890/04-0245>
- Witman, J. D., Lamb, R. W., & Byrnes, J. E. K. (2015). Towards an integration of scale and complexity in marine ecology. *Ecological Monographs*, 85(4), 475–504. <https://doi.org/10.1890/14-2265.1>
- Wittebolle, L., Marzorati, M., Clement, L., Balloi, A., Daffonchio, D., Heylen, K., De Vos, P., Verstraete, W., & Boon, N. (2009). Initial community evenness favours functionality under selective stress. *Nature*, 458(7238), 623–626. <https://doi.org/10.1038/nature07840>
- Wohl, D. L., Arora, S., & Gladstone, J. R. (2004). Functional redundancy supports biodiversity & ecosystem function in a closed & constant environment. *Ecology*, 85, 1534–1540. <https://doi.org/10.1890/03-3050>

SUPPORTING INFORMATION

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

How to cite this article: Miner CM, Burnaford JL, Ammann K, et al. Latitudinal variation in long-term stability of North American rocky intertidal communities. *J Anim Ecol*. 2021;90:2077–2093. <https://doi.org/10.1111/1365-2656.13504>