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Quantitative biogeography: Decreasing and more variable dynamics of critical species in an iconic meta-ecosystem

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Abstract

Ecosystem stability has intrigued ecologists for decades, and the realization that the global climate was changing has sharpened and focused this interest. One possible early warning signal of decreasing stability is increasing variability in ecosystems over time with increasing climate variability. Determining climate change effects on community stability, however, requires long-term studies of structure and underlying dynamics, including bottom-up and top-down effects in natural ecosystems. Although relevant datasets were rare in the early years of community ecology, such information has increased in recent decades. We investigated spatiotemporal changes in mean and variability of ecological subsidies (nutrients, phytoplankton, prey colonization), performance metrics of a dominant space occupier (mussels) and its primary predator (sea stars), and sea star predation rates on mussels in relation to climatic oscillations, temperature, and disease on rocky shores. The research involved annually repeated multiyear (~1999–2018), multisite (13 sites nested within five regions along ~260 km of the Oregon coast) observations, measurements, and experiments. We analyzed associations between environmental variables and ecological performance of key elements of the sea star-mussel-dominated mid intertidal system. We found that upwelling declined in some regions, but became more variable across all study regions. Air and water temperatures oscillated, but their mean and variation increased through time, with peak values coinciding with the 2014–2016 combined El Niño and Marine Heat Wave. Ecological subsidies generally declined during the study period but increased in variability. Excepting growth rate, mussel (*Mytilus californianus*) performance (condition index, reproductive output) generally decreased and became more variable. Primarily due to a sea star wasting epidemic, reproductive output of the top predator *Pisaster ochraceus* decreased and became more variable, and predation rate on mussels decreased. Analyses indicated that the primary drivers of these changes were temperature-related environmental factors. As declining means and increasing variability of ecological performances can typify destabilizing ecosystems, and environmental trends are toward ever more stressful conditions, the outlook

for this iconic ecosystem is discouraging. Immediate and rapid action to mitigate and ultimately reverse climate change likely is the only option available to prevent an irreversible shift in the future of this, and most other ecosystems.

KEYWORDS
climate change, early warning signals, El Niño-Southern Oscillation, environmental stress, marine heatwave, North Pacific Gyre Oscillation, Pacific Decadal Oscillation, resilience, rocky intertidal, spatiotemporal scale, stability, upwelling

INTRODUCTION

Climate change imposes stresses on ecosystems unlike any seen in recorded history. On land, the litany of ongoing impacts is well known, and includes melting glaciers, mass mortality events, changing biogeographic distributions, drought, flooding, and increasing occurrence of wildfires (IPCC, 2021). In marine ecosystems, similarly profound changes are occurring as changes in wind and current patterns, ocean temperature, stratification, and ocean chemistry have knock-on impacts on physiology, behavior, growth, and survival of organisms (e.g., Doney et al., 2012; Harley et al., 2006; IPCC, 2021). Such impacts in turn can alter population traits (e.g., size structure, abundance, seasonality, phenology, distribution), leading to changed community and ecosystem structure. All these changes have major implications for social and economic systems that, when added to the ecological impacts listed, constitute an existential threat to our global system.

Ecosystems are structured by the integrated effects of abiotic and biotic forces that can vary across multiple spatial and temporal scales, the untangling of which has occupied ecologists for decades. Abiotic factors can vary from microscale to macroscale, but it is the latter across which the impacts of climate change are likely to have the most noticeable effects (Menge, Milligan, et al., 2019; Pessarrodona et al., 2019). For example, increases in conditions varying across large (100s to 1000s of km) scales such as temperature, salinity, or coastal upwelling, can be important determinants of community and ecosystem structure and dynamics, either directly through impacts on survival or indirectly through modulation of biotic processes (Grabowski et al., 2020; Menge & Sutherland, 1987; Sanford, 2013; Whittaker, 1970). Such abiotic factors are exactly those being altered by climate change.

Encapsulated in the concept of "stability," the investigation of biological responses to environmental change has a long history in ecology (Kéfi et al., 2019). Because it takes years to acquire the empirical information needed to assess whether or not biological systems are stable, much early work on this issue has been theoretical (e.g., Holling, 1973; MacArthur, 1955; May, 1973, 1977; Pimm, 1982). More recently, these theories have been tested empirically as appropriate datasets have accumulated (e.g., Bernhardt & Leslie, 2013; Carpenter et al., 2011; Persson et al., 2007; Scheffer & Carpenter, 2003).

Rocky intertidal habitats are ideal for empirical investigation of stability (Donohue et al., 2013, 2016; Menge et al., 2022; Miner et al., 2021; Raimondi et al., 2019; Rindi et al., 2017, 2018). The habitat is compressed to a few vertical meters across a strong immersion/emersion gradient that makes species ranges 'two-dimensional'; organisms are sessile or sedentary and have relatively fast generation times; abundances and sizes of individuals are readily quantified using simple methods; and experimental manipulation is relatively easy (Connell, 1972; Menge, Caselle, et al., 2019; Menge, Milligan, et al., 2019; Paine, 1977, 1994). Further, environmental conditions (temperature, salinity, wave action, water chemistry) are also relatively easily measured (Barth et al., 2007; Chan et al., 2017; Menge et al., 2015). Along the horizontal dimension (i.e., alongshore), habitat boundaries tend to be discrete, with habitable rocky shore habitat punctuated by stretches of unstable substratum such as sand, gravel, or cobble beaches. Thus, the system also lends itself to quantification of metapopulation, meta-community and meta-ecosystem patterns and dynamics (Gouhier et al., 2010, 2011, 2013; Menge et al., 2015). The investigation of multiple local-scale rocky shores across biogeographic scales and quantification of variation in oceanic conditions allows the assessment of pattern and dynamical variation in relation to larger scale environmental variability. Finally, conducting such research over long periods of time allows the resolution of spatiotemporal variation in patterns and dynamics.

Conceptual framework

Climate change, environmental factors, and ecosystems vary across a wide range of temporal scales (e.g., days to weeks for acute events, months to years for more gradual changes)

and spatial scales (e.g., meters to 10s to 100s of meters at local scales, kilometers to 10s of kilometers at regional scales, and 100s to 1000s of kilometers at macroscales). Hence, research that spans these scales can be particularly important for gaining insight into community and ecosystem responses to environmental variability. Temporally, ecological variability and stability is ultimately the most relevant conceptual framework for understanding the influence of changing climate. For decades, research on stability was largely an academic, mostly theoretical exercise, but the advent of climate change has made stability a much more urgent topic. Much research has shown that the resistance and resilience of communities and ecosystems are being tested as never before in recorded history, and in many cases, we face potential tipping points into alternative, usually "undesirable" community states. For this reason, researchers have recently focused on the issues of critical slowing down and decreasing stability of community dynamics, both of which might provide an early warning sign of impending shifts into an alternative state. Gaining such insight requires long-term assessment of both the overall trends (declines may indicate critical slowing down) and in the variability (increases may indicate instability) in various community dynamics. Further, investigation at the mechanistic level, that is, understanding of how the dynamics underlying community structure (e.g., physiology, demographics) change through time, will help us understand the role of climate change in driving any patterns detected.

Spatially, ecologists have long recognized that ecological processes did not necessarily scale up from local to macroscales (e.g., Dayton et al., 1999; Dayton & Tegner, 1984; Levin, 1992; Menge & Olson, 1990; Schneider, 2001; Wiens, 1989). Empirical examples quantifying how species interactions change with scale, for example, are relatively few (but see Hacker et al., 2019; Menge & Menge, 2013; Wootton, 2001). A goal of our research program has been to address this issue using experiment- and measurement-based quantification of ecological processes. These included bottom-up inputs, prey colonization, variation in performance of foundation and keystone species, and rates of predator–prey interactions at local scales nested within regional and coastal scales. As suggested by prior reports, this approach provides a powerful insight into understanding how ecosystem dynamics can scale up from local to macroscales (Hacker et al., 2019; Menge et al., 2003, 2015; Menge & Menge, 2013; Miner et al., 2021; Navarrete et al., 2005; Raimondi et al., 2019). Here, we build on this prior understanding of spatial variation by using mostly lengthier time series to gain stronger insight into spatio-temporal dynamics in this system.

Background: Community resistance and resilience

Three recent studies addressed changes in community structure along the West Coast of North America. Miner et al. (2021) studied patterns of rocky intertidal community change at multiple sites ranging from the Olympic Peninsula in Washington State to San Diego, California. By their definition of community stability (lack of temporal change in a combined species diversity and relative abundance metric), they suggested that northern communities (average of 18 sites northward from Bodega Bay, California) and central communities (average of 20 sites from Pt. Conception to Bodega Bay) were more stable than those in southern communities (Channel Islands, Southern California). They also found that abundance of the key foundation species (the mussel *Mytilus californianus*) did not change during the 2005–2017 study period.

Similarly, using a different sampling procedure (transect-quadrat surveys vs. large fixed grids in Miner et al., 2021), a second study (Gravem et al., unpublished manuscript) found little change in community structure at a mostly different (two sites in common between studies) set of 11 sites from Oregon and northern California. Note that both Miner et al. (2021) and Gravem et al. (unpublished manuscript) were observational studies that examined temporal variability and did not experimentally test the resilience or the processes that underlaid the dynamics of their systems. A third recent study, however, did examine the resilience of low intertidal communities along the Oregon coast (Menge et al., 2022). Using repeated annual disturbance experiments at six sites from 2011 to 2019, this research found diminishing resilience in annually disturbed plots. In intact plots (no disturbances applied), community variability also increased, but community mean state did not change. Thus, as Miner et al. (2021) and Gravem et al. (unpublished manuscript) observed, community structure was persistent, but when perturbed, community dynamics showed evidence consistent with decreasing stability.

Background: Environmental influences

Prior research from our group has shown that several processes are susceptible to climatic and regional environmental variation. For example, delayed upwelling in 2005 had extensive, but short-term (months) effects on nutrient inputs, phytoplankton abundance, and recruitment of sessile invertebrates (Barth et al., 2007). Mussel growth at four central Oregon sites was higher during El Niño and warm-phase Pacific Decadal Oscillation (PDO) conditions than cooler La Niña conditions (Menge

et al., 2008). Mussel recruitment and phytoplankton abundance increased, but intertidal kelp growth decreased, with increasing NPGO (North Pacific Gyre Oscillation = windier) conditions (Menge et al., 2009; Menge, Close, et al., 2021). Analysis of changes in upwelling and its relationship with barnacle and mussel recruitment found that upwelling events are becoming less frequent but stronger and longer in duration, and that barnacle recruitment was declining while mussel recruitment was increasing with these changes (Iles et al., 2012). Elemental composition of four species of intertidal algae varied through time with upwelling and climate mode (ENSO = El Niño-Southern Oscillation, NPGO, PDO), although responses were relatively weak in comparison to highly conserved species-level differences (Close et al., 2020). Miner et al. (2021) found that negative trends in community structure patterns, especially in Southern California, were associated with warmer ocean temperatures. The diminishing resilience noted above (Menge et al., 2022) mostly was associated with variability in upwelling, a key driver of coastal ocean temperature (Iles et al., 2012). Thus, growing evidence suggests that regional to ocean basin-scale environmental variation, often through thermal effects, has influenced several key processes in rocky intertidal communities.

Goals

The impetus for this paper was to discover if key processes underlying the dynamics of rocky intertidal communities have changed through time and, if so, if these changes are related to climatic factors. Below, we analyze temporal changes in abiotic and biotic datasets ranging in length from 10 to >30 years that we have generated in the rocky intertidal meta-ecosystem of the Oregon coast. We then place our results within the conceptual frameworks of stability theory linked to climate change impacts through environmental stress theory (Bernhardt & Leslie, 2013). Our datasets include repeated standardized observations, measurements, and experiments. We first examine local- to regional- to coastal-scale environmental temporal change, including air and water temperature, upwelling, and climatic oscillations including ENSO, NPGO, and PDO. We also include the 2014 sea star wasting (SSW) perturbation as an "environmental factor" as it was a large-scale, "external" coastwide event, although its severity varied at local to regional scales (Hewson et al., 2014; Menge et al., 2016; Miner et al., 2018). We then analyze spatial variation in each metric to determine the scale at which each factor varies, and use this information to generate a network of effects within and between the three scales, coastal, regional, and local.

Ecological data were collected at local scales (10s to 100s of meters), and then summarized at regional (multiple local sites, scales of 1–10s of kilometers) and coastal (multiple regions) scales (10s–100s of kilometers) for comparison to the patterns of large-scale environmental factors including SSW. Our focal system is a dominant subweb in the overall intertidal interaction web: the keystone sea star *Pisaster ochraceus*, its primary prey (mussels: the foundation species *Mytilus californianus*, plus *Mytilus trossulus*, and barnacles: *Balanus glandula*), phytoplankton, which is the primary food resource of these filter-feeding prey species, and nutrients, which drive phytoplankton abundance. We use our results to relate temporal variation to stability patterns of all nonclimate metrics, and to assess which factors do and do not "scale up" and which linkages appear most important in affecting ecological responses. Our overarching hypothesis is that increasing variability in oceanic conditions has caused increased variability in the biological processes underlying our focal interaction web.

STUDY SYSTEM

Our research was conducted at study sites along the Oregon coast (Figure 1, Appendix S1: Table S1). To reduce confusion, we will refer to the five capes by region number, from north to south. When appropriate, sites within capes/regions will be listed by site code, and when a cape has >1 site, also by number from north to south (Figure 1 caption, Appendix S1: Table S1).

Besides often severe, mostly winter-time wave action, the dominant oceanic feature of the Oregon coast is intermittent upwelling from April through September, and predominance of downwelling conditions from October through March (Checkley & Barth, 2009; Hickey & Banas, 2003; Huyer, 1983). All study sites have been described in recent publications (e.g., Close et al., 2020; Hacker et al., 2019; Menge et al., 2015; Menge, Foley, et al., 2021). Briefly, all were wave-exposed rocky intertidal benches with mussel-dominated mid intertidal zones, and fucoid- and barnacle-dominated high intertidal zones. Low zones occurred in two distinct states: invertebrate-dominated (Region 3 sites) or macrophyte-dominated (all other regions) (Menge et al., 2022). Spatial scales ranged from sites (local scales of 1–100s of meters) nested within regions/capes (among-site scales of 1–16 km) to among-capes/regions (scales of 67 to 117 km) (e.g., Hacker et al., 2019; Menge et al., 2009, 2015; Menge, Hacker, et al., 2011).

The prevailing cross-shelf currents during upwelling at northern capes (Regions 1 and 2) are moderately strong in an offshore direction. Cross-shelf currents at Region 3 (CP) are weaker and more retentive nearshore;

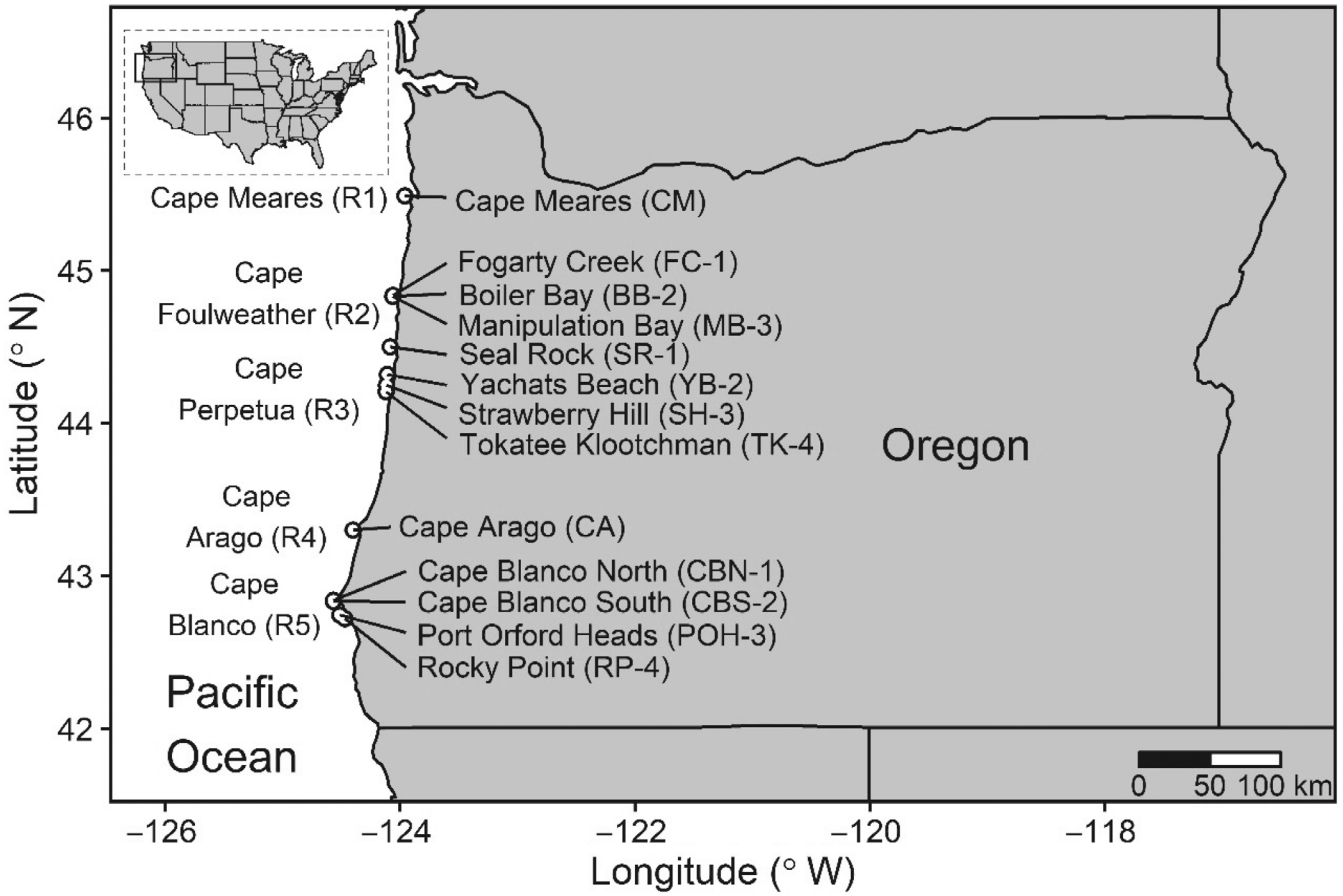

FIGURE 1 Map of sites along the Oregon coast. Sites were nested within capes or regions. Numbered and listed from north to south, these were Cape Meares (Region 1) with single site Cape Meares (CM), Cape Foulweather (Region 2) with sites Fogarty Creek (FC-1), Boiler Bay (BB-2) and Manipulation Bay (MB-3), Cape Perpetua (Region 3) with sites Seal Rock (SR-1), Yachats Beach (YB-2), Strawberry Hill (SH-3), and Tokatee Klootchman (TK-4), Cape Arago (Region 4) with single site CA, and Cape Blanco (Region 5) with sites Cape Blanco North (CBN-1), Cape Blanco South (CBS-2), Port Orford Heads (POH-3), and Rocky Point (RP-4).

and are strongly offshore at Regions 4 and 5 (CA, CB), where the coastal jet is directed southwestward by the abrupt promontory of Cape Blanco (Barth et al., 2000; Barth & Smith, 1998; Kirincich et al., 2005). With variation in coastal geomorphology and shelf width (Menge et al., 2015), these differences are associated with cape-scale differences in phytoplankton abundance. Prior research has shown that exceptionally high levels of phytoplankton occur in Region 3 (CP), moderately high levels at Region 5 (CB), low levels at Regions 1 and 2 (CM, CF), and very low levels at Region 4 (CA) (Barth et al., 2007; Menge et al., 2009, 2015).

METHODS

Environmental data

To characterize environmental conditions occurring during the study period, we assembled datasets for PDO, NPGO, El Niño, upwelling, intertidal sea surface temperature (ISST), intertidal air temperature, nutrients (nitrate plus nitrite or dissolved inorganic nitrogen [DIN]), and phytoplankton (as proxied by chlorophyll *a* [Chl *a*] concentration).

Climate and upwelling indices

Climate variability reflects ocean basin-scale changes so in our system are uniform at the coastal scale (i.e., do not vary at regional and site scales), whereas upwelling is known to vary latitudinally among regions (Menge et al., 2015). We downloaded PDO, NPGO and ENSO (as indexed by version 2 of the Multivariate El Niño-Southern Oscillation Index or MEIv2) data from websites (http://www.jisao.washington.edu/pdo/, http://www.03d.org/npgo/, and https://www.esri.noaa.gov/psd/enso/mei/, respectively). Our focus was on interannual variation in ecological measures (see below) so the

monthly values of each climate measure were averaged by year. We conducted two analyses on climate index data. First, to test for trends in the long-term extent of these measures, we used time series analysis to remove the oscillations in each data set, then conducted linear regressions on the residual variation left in the PDO, NPGO, and MEIv2 indices versus year (see heading of Appendix S1: Table S2 for additional details). Second, to test if trends were present in a time period relevant to our studies, most of which began in 2000, we conducted linear regressions on raw values of each index. As noted above, our ecological data sets are too short (≤28 years) to fully investigate their correspondence to the long-term climatic oscillations such as the PDO (20–30 years, Mantua et al., 1997) and the NPGO (10–15 years; Di Lorenzo et al., 2008). As in previous analyses, however, we used monthly and yearly variation in these metrics to investigate their potential association with variation in ecological measures (e.g., Close et al., 2020; Menge et al., 2008, 2009; Menge, Close, et al., 2021; Menge, Hacker, et al., 2011). ENSO oscillations occur at scales of 4–7 years, so analyses comparing the MEIv2 index and our datasets should include three to five oscillations.

Upwelling analyses used the recently proposed CUTI index (Coastal Upwelling Transport Index; Jacox et al., 2018) (https://oceanview.pfeg.noaa.gov/products/upwelling). Values of this index were available back to 1988 for the west coast of North America at 1° latitude resolution. We focused on the latitudes closest to our study sites (46° N through 42° N) (see Figure 1 for map of sites and capes).

Water and air temperature

Temperature varies mostly at local scales and through time (Menge et al., 2015). Intertidal sea surface and air temperatures were quantified using field-deployable temperature-logging sensors (Onset Corp., Bourne, MA) set to 15-min recording increments. At each site, two to four HOBO Tidbits (±0.2°C accuracy) and/or HOBO Pendants (±0.5°C accuracy) were fastened to the rock after attachment inside small stainless-steel mesh cages that were cleared of fouling organisms monthly. Air and water temperatures (i.e., during exposure at low tide) were separated using a program coupled with tide tables (http://tidesandcurrents.noaa.gov) (e.g., Menge et al., 2015). We note that when air and water temperatures were similar, the distinction could be difficult. Although we deleted identifiably questionable values, some air temperature averages may inadvertently include water temperatures and vice versa. Daily averages of air and water temperature were calculated for each site, and then used to generate weekly, monthly, and annual means.

Nutrients and phytoplankton

Nutrients (DIN) and phytoplankton (Chl *a*) vary mostly at regional and temporal scales (Menge et al., 2015), but were sampled at local site-level scales. Bottle samples ($n = 3$ per collection) for estimation of nutrients (DIN) concentration and phytoplankton (Chl *a*) abundance, have been taken frequently (usually monthly) as far back as 1993 but at most sites since 1999. Methods were detailed in Menge et al. (2015) and Close et al. (2020). Briefly, replicate samples were collected in acid-washed high-density polyethylene bottles from the shore at about 0.5 m depth, filtered through precombusted Whatman glass fiber filters, with filtrate and particulates captured on the filters transferred on ice to the laboratory where they were frozen (−20°C) for later analysis. DIN was quantified spectrophotometrically following methods of Jones (1984) and Strickland and Parsons (1968). Chl *a* was quantified after extraction in acetone using a calibrated Turner Designs model 10 fluorometer.

Ecological changes

Several research objectives aimed to capture processes underlying the dynamics of the focal interaction web. These included annual measures of: (1) rates of prey colonization (mussels: *M. californianus* plus *M. trossulus*; barnacle: *Balanus glandula*); (2) mussel (*Mytilus californianus*) growth, condition, and reproduction; (3) proportion of sea stars (*Pisaster ochraceus*) that were reproductive; and (4) sea star (*P. ochraceus*) predation rate on *M. californianus*.

Prey colonization

Mussels and barnacles are the primary prey of sea stars and whelks in this system and are major space occupiers (Menge et al., 1994; Navarrete et al., 2000; Novak et al., 2017; Paine, 1966, 1974). Starting in 2010, we used annually cleared experimental plots (15 × 15 cm, five replicates per site) to quantify prey colonization rates as prey cover in autumn (settlement is heaviest from August through November; Menge et al., 2009; Menge, Gouhier, et al., 2011; Menge, Hacker, et al., 2011). Annual measures of prey colonization (percentage cover of mussels and the barnacle *Balanus glandula*) were estimated by eye by a single researcher (B. Menge) from photographs

of the plots (e.g., Dethier et al., 1993), in most cases from October of each year.

Mussel growth, condition, and reproduction

As has been reported previously (Blanchette et al., 2007; Menge, 1992; Menge et al., 2008; Rose et al., 2020), estimation of annual mussel growth involved translocating replicate clumps of 30–50 marked mussels (notched at the posterior end with a file). Mussels were deployed by placing them ventral side down to cleared rock surfaces in the mid zone (within the shore level of mussel beds) under plastic mesh cages, allowing them 4–6 weeks to reattach, then removing the cages and collecting after 1 year. Collections and new translocations were done each March or April to obtain annual growth data. Growth rate was estimated by measuring the growth increment (distance in mm from notch to the distal end of the shell) and dividing by initial length and the number of days in the field. Condition index (CI) (Davenport & Chen, 1987) provides a measure of tissue production (CI = tissue weight/shell weight × 100) and was based on dissection of 10 mussels from each clump. Relative reproductive capacity was based on categorical scores assigned during dissection, with 0 = nonreproductive, 1 = reproductive but with small gonads, 2 = moderately large gonads, and 3 = large and ripe gonads.

Sea star reproduction

Estimates of the proportion of reproductive sea stars (*P. ochraceus*) were based on coupling annual measurements of size structure of sea stars at each study site with measurements of gonad size relative to body size. Historically, sampling of gonad and pyloric caecum size involved sacrifice of sampled animals (e.g., Mauzey, 1966). However, Sanford et al. (2009) showed that a nonlethal method of quantification of gonad and pyloric caecum volume using a single arm excised from a sea star explained 98% (gonad) and 93% (pyloric caecum) of the variance calculated from whole animal dissections. Prior studies of *Pisaster* reproductive maturation size (Menge, 1975) found that animals in the San Juan Islands, Washington, were first reproductive between 70 to 110 g wet weight.

To determine whether these earlier estimates of maturation size applied to Oregon *P. ochraceus*, we sampled populations at most sites in 2018 and 2019. Prior to the ∼May sea star spawning period, in late April or early May, we haphazardly selected 20–26 individuals across a range of sizes at all sites but Fogarty Creek (10 in 2019) and Boiler Bay (none sampled because of low population size). After quantifying wet weight and ray length in the field, one arm was removed. We then either field-quantified wet weight of gonad, pyloric caecum, the drained arm, and of the intact animal, or froze the arm for processing in the laboratory for these same measures.

To survey sea star population size structure at all sites we used "belt" transects (Menge et al., 2016). In spring and summer each year, five transect lines were placed parallel to the water's edge in the low zone about 1 m below the mussel bed. When sea stars were abundant (sparse), transects were 5 (10) m in length. Researchers then collected all sea stars in a 2 m wide belt along the transect, and measured arm length (madreporite to the tip of the opposite arm) and wet weight of each individual (using a portable electronic balance, resolution = 0.01 g), and returned them to the transect area. Minimum sample size in most cases was 200 per site per sample period. Data from these surveys were combined with the gonad size results to estimate the proportion of reproductive sea stars (percentage of individuals >100 g wet weight) by site, year, and sample season.

Predation rate by sea stars on mussels

As detailed previously (Menge et al., 2004; Menge, Hacker, et al., 2011; Menge & Menge, 2013), each spring 10 mussel clumps were translocated to the low intertidal zone (i.e., the foraging zone of *P. ochraceus*) using methods identical to those in mussel growth rate measurements. Once mussels were attached, mesh covers were removed, and mussels in each clump were counted. Then half of the clumps were surrounded by a stainless-steel fence (-predators; the control) and, to simultaneously control for mesh effects on flow and allow access by sea stars, half were partially fenced (+predator treatment; the treatment). Mussel counts were made at 2- to 4-week intervals, or in winter as often as possible. Predation rate was calculated as the number of mussels consumed per day.

Data analysis

For data analysis, we used JMPPro v16 (JMP, 2021) and PRIMER-E v7 with PERMANOVA+ (Anderson et al., 2008; Clarke & Gorley, 2015). Most analyses involved calculations of means and standard errors or standard deviations for basic statistics, then used univariate linear and nonlinear regression analyses to test temporal patterns of change. In all cases, we used corrected Akaike Information Criterion (AIC_c) or adjusted R^2 to guide

model selection. In many cases, we show both linear and nonlinear regressions for a given dataset. AIC_c usually identified linear or quadratic equations as the best fit, but in many cases, visual and statistical examination (as indicated by adjusted R^2 values that were often two times higher than those for linear or quadratic regressions) suggested trends were better reflected in third or even fourth order equations. We therefore plotted the nonlinear curves and provide the regression statistics in each such case, although our inferences usually are based on the more robust AIC_c best-fit models.

To analyze the trends in climatic indices, we used the time series module in JMPPro v16 to remove cycles then test the residuals using linear regression. To test the effects of environmental variables on ecological metrics we used multiple regression and multivariate permutational analyses (distance-based linear models in PERMANOVA+ [DistLM]) and ordinations (distance-based redundancy analysis in PERMANOVA+ [dbRDA]). Analyses were conducted at the site, region/cape, and coastal scales. Data were transformed for analyses, using either $\ln(x + 1)$ (count data or percentage data when percentage was well below 100), arcsin transformations (proportions or percentage ranging close to 1.0 or 100, respectively), or square-root transformations for cover data (PRIMER and PERMANOVA+). Tukey honestly significant difference (HSD) tests were used to determine ranks of capes or sites for each metric. We used nested ANOVA [region, site(region)] to determine the scale (coastal, regional, local) at which each factor varied most strongly. Multiple regressions were conducted at regional scales for each ecological metric (Chl *a*, mussel shell growth, CI, and gonad size, prey colonization, sea star reproductive proportion, and sea star predation rate). We also used multiple regression for each factor listed in the previous sentence to construct a summary network of significant links between the factor and all metrics that might be logically expected to have an influence.

RESULTS

Environmental conditions

Our analyses indicate that the coastal ocean has changed substantially in recent decades. Whereas climatic trends were modest, recent upwelling declined in two of four regions and upwelling variability increased at all latitudes. Average temperature-related metrics increased, presumably in response to climate change. Nutrients and phytoplankton mean abundances decreased whereas phytoplankton variability increased. We report temporal results at three scales: site scale refers to patterns at a single site, region scale refers to patterns averaged over the sites within each region, and coast scale refers to results averaged across regions or to a single site when a region represents a single location (i.e., Cape Meares, Region 1 and Cape Arago, Region 4). We detail our results below, first examining temporal patterns then summarizing spatial patterns for each metric.

Climate indices

Long-term average measures of ENSO decreased, whereas NPGO and PDO remained stable through time (Appendix S1: Table S2). NPGO variability increased but no change in variability occurred in ENSO or PDO. In recent decades, ENSO and PDO were in cool phases from 2008 to 2013, then moved into warm phases in 2014–2017 (Appendix S2: Figure S1a). Notably, the first East Pacific marine heat wave (MHW), nicknamed "The Blob" (Di Lorenzo & Mantua, 2016), coincided with the 2015–2016 ENSO, creating a 3+ year long period of exceptionally warm ISST (Appendix S2: Figure S2a–c). The NPGO was strongly positive (windier conditions) in 2002–2003 and 2008–2012 and negative (calmer) in 2015 and 2018–2019 (Appendix S2: Figure S1a). Its cyclical nature (10–15 years) suggests NPGO may increase and again become windier in the coming decade (2020s). In recent decades, mean ENSO and NPGO decreased and their variability increased, but only the change in mean NPGO was significant (Appendix S1: Table S2). In contrast, the mean of PDO increased whereas variability decreased, but neither change was significant. Thus, long-term and short-term NPGO variability increased, and PDO remained stable. In contrast, long-term mean ENSO and short-term mean NPGO decreased and short-term ENSO patterns did not change.

Cross-shelf currents

Upwelling variability increased since 1988 at all Oregon latitudes (Figure 2, Appendix S1: Table S3). Mean upwelling declined at three of five latitudes along the Oregon coast (46° N, 45° N and 43° N) corresponding to Regions 1, 2 and 5 (CM, CF and CB) but did not change in Regions 3 and 4 (CP, CA: Figure 2a, Appendix S1: Table S3, Appendix S2: Figure S1b).

Spatially, and consistent with large-scale latitudinal patterns, upwelling in Oregon intensified equatorward, differing among regions but not sites within regions, with region explaining 73% of the variance (Figure 2a, Appendix S1: Tables S3 and S4). Upwelling did not differ among the three most northern regions (Appendix S1: Table S4; Tukey HSD tests).

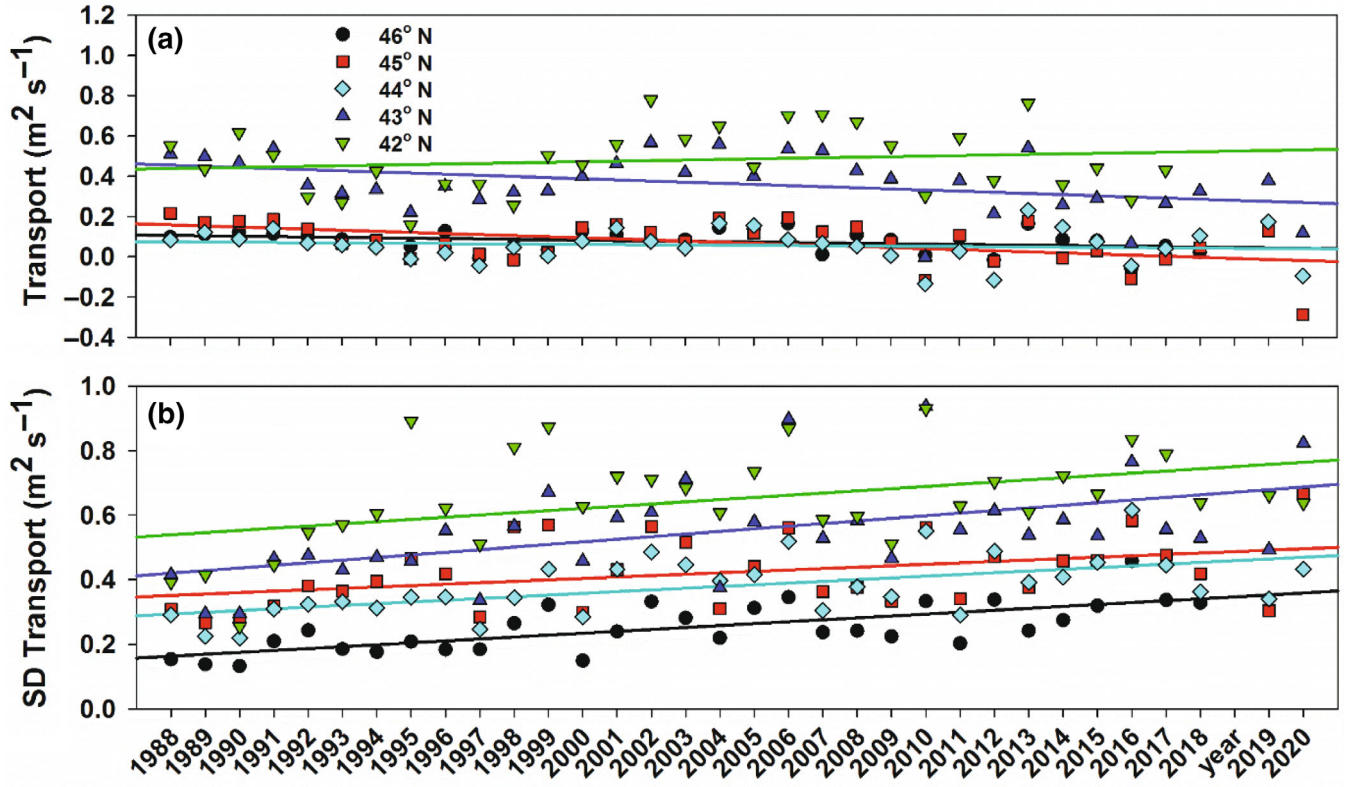

FIGURE 2 Plots of means (a) and SD (b) of upwelling (Coastal Upwelling Transport Index) by year. Lines show linear regressions. *p*-values and adjusted R^2 for each latitude in (a): 46° N, $p = 0.042$, adj. $R^2 = 0.1$; 45° N, $p = 0.005$, adj. $R^2 = 0.21$; 44° N, $p = 0.52$, adj. $R^2 = 0.0$; 43° N, $p = 0.024$, adj. $R^2 = 0.126$; 42° N, $p = 0.29$, adj. $R^2 = 0.005$. *p*-values and adjusted R^2 for each latitude in (b): 46° N, $p = 0.0003$, adj. $R^2 = 0.33$; 45° N, $p = 0.02$, adj. $R^2 = 0.14$; 44° N, $p = 0.0005$, adj. $R^2 = 0.3$; 43° N, $p = 0.002$, adj. $R^2 = 0.25$; 42° N, $p = 0.09$, adj. $R^2 = 0.17$.

Temperature

Temporally, coast-scale linear trends for both mean ISST and air were positive (Figure 3a,c, Appendix S1: Table S5), as were those at the site scale (Appendix S1: Table S6; all first-order coefficients were positive; Appendix S2: Figure S2). However, ISST and air temperature clearly varied nonlinearly (bimodally) at the coastal scale (peaks in 2003–2005 and 2014–2016) with a suggestion of a third peak in 2010 (Figure 3a,c, Appendix S1: Table S5). Variability of coast-scale ISST also increased but reached an asymptote in the 2010s (Figure 3b). In contrast, coast-scale variability of air temperature was unimodal, peaking from ~2007 to 2013, then decreasing (Figure 3d). At the site scale, the unimodal trends for ISST variability occurred at all sites except Rocky Point (RP-4), whereas no trends in variability were detected for air temperature. Thus, mean temperatures increased but variability tended to change nonlinearly, with increasing then decreasing variability occurring from 1999 to 2020.

Spatially, and likely reflecting the higher upwelling of colder water in the two southern regions (Figure 2), mean annual ISST was warmer at northern Regions 1–3 and cooler at southern Regions 4 and 5 (Appendix S1: Table S4; Tukey HSD tests). No regional differences in mean annual air temperature were detected. These spatial differences were much weaker than were those for upwelling, suggesting that thermal variation varies more across larger spatial scales than encompassed by our studies.

Bottom-up inputs

In coastal ecosystems, nutrients and phytoplankton are key drivers of abundances of primary producers (macrophytes and diatoms) and filter-feeding invertebrates (mussels, barnacles, sponges, tunicates), respectively. Means and/or variability of both factors have changed in the past two decades.

Nutrients

Temporally, mean annual DIN increased at the coast scale from 1993 to ~1998 then trended downward to 2017 (Figure 4a; Table 1; Appendix S1: Table S5). The SD of annual DIN also varied nonlinearly, decreasing to ~2000, then increasing to ~2010, then decreasing

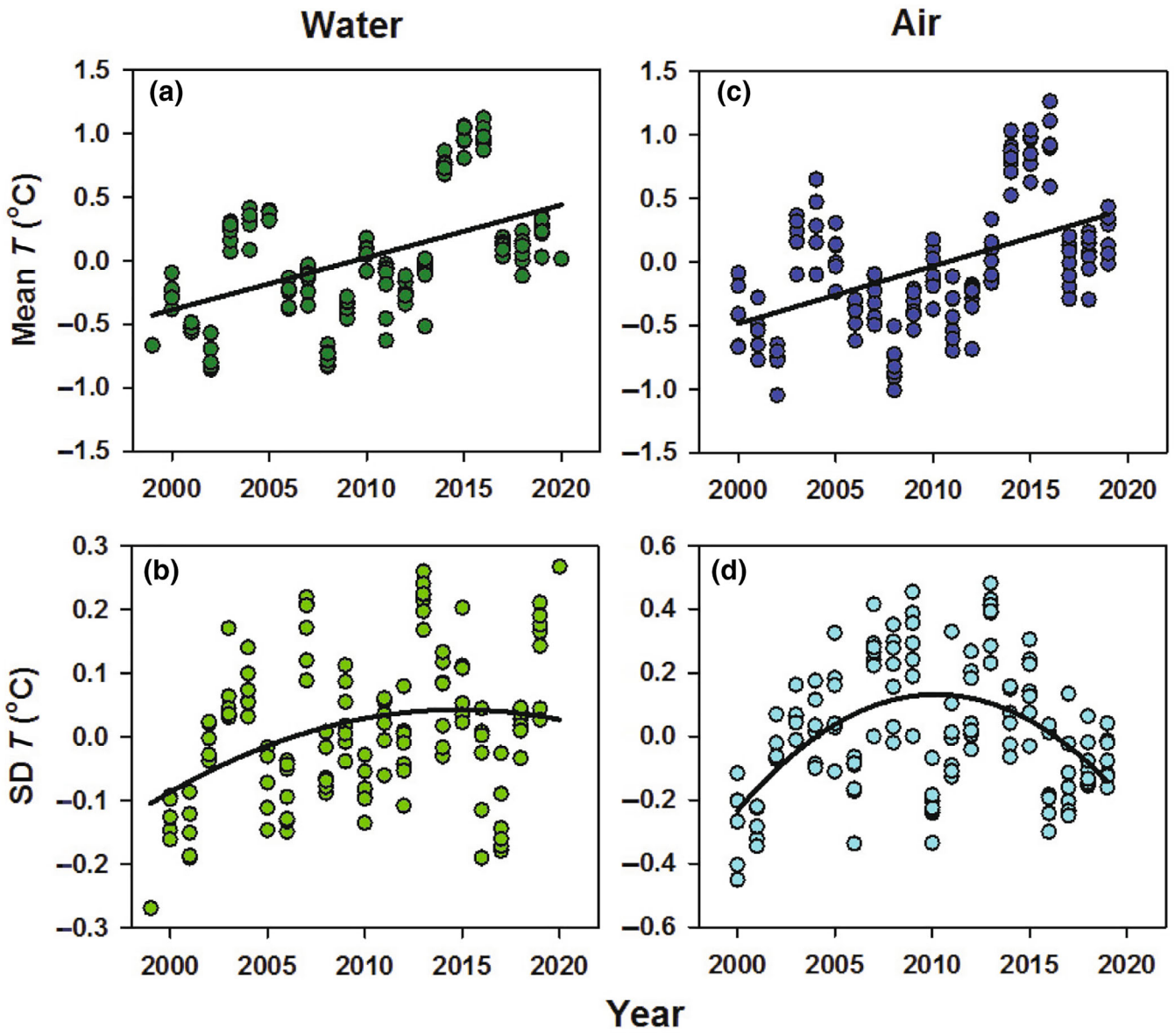

FIGURE 3 Annual mean and annual mean SD temperatures (region-scale averages). (a) Intertidal sea surface water temperature (ISST). Regressions showing long-term increasing trends: (a) ISST (residual) $= -68.77 + 0.034 \times$ year, $F_{(1,143)} = 33.3$, $p < 0.0001$, adj. $R^2 = 0.183$. (b) SD of ISST. (c) Intertidal air temperature: air T (residual) $= -86.9 + 0.043 \times$ year, $F_{(1,183)} = 447.0$, $p < 0.0001$, adj. $R^2 = 0.249$. (d) SD of intertidal air temperature (see Appendix S1: Table S5 for nonlinear coast-scale regressions and Appendix S1: Table S6 for region- and site-scale regressions).

sharply to 2017 (Figure 4b). At more resolved regional and site scales, DIN differed among regions (Appendix S1: Table S4; Appendix S2: Figure S3a), but not among sites. At the region scale, DIN did not vary temporally in Regions 1–3 but did in Regions 4 and 5, where annual average nutrients declined and the SD of annual average nutrients increased (Appendix S1: Table S7). Thus, in general, nutrient variability increased through time at the largest scale, but nutrient abundance decreased (Table 1). These trends were driven by the two southern-most regions. DIN also varied spatially, with a trend toward higher levels of nutrients in southern regions (4 and 5), and low levels in the most northern Region 1 (Appendix S1: Table S4; Tukey HSD test).

Phytoplankton

At the coast scale, phytoplankton (Chl *a*) increased from the early 1990s to ~2000, then declined, while SD of phytoplankton abundance increased (Figure 4c,d; Table 1; Appendix S2: Figure S3b). At regional scales, phytoplankton declined at all capes (but not significantly at CM) whereas temporal trends in variability were weak (Appendix S1: Table S7). Since ~2000, phytoplankton

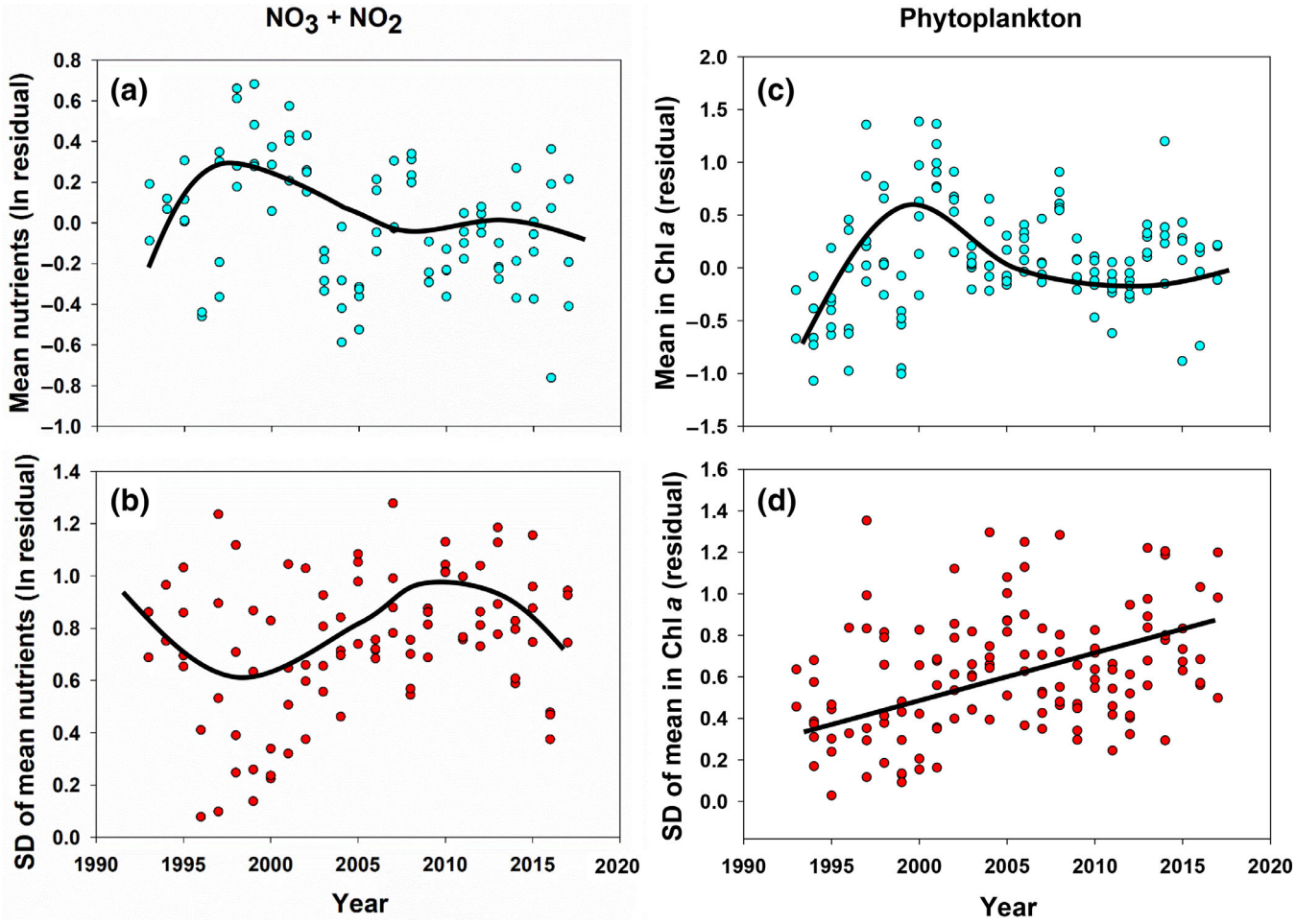

FIGURE 4 Annual average mean $NO_3 + NO_2$ (a), SD of annual mean $NO_3 + NO_2$ (b), annual mean phytoplankton abundance (c), and SD of annual mean phytoplankton abundance (d) from 1993 to 2018. Data are region-scale residuals after removal of effect of site. See Table 1 for best-fit regressions. Statistics for curvilinear fits shown above are in Appendix S1: Table S5.

abundance reached regional lows in 2004 (Region 4), 2010 (3 and 5), 2012 (1, 2 and 4) and 2017 (5) (Appendix S2: Figure S3b). In the most intensively sampled regions (2, 3, 5), annual average growing season phytoplankton (April–September) decreased (Appendix S1: Table S7; variance explained 28%, 55%, and 49%, respectively). Thus, large-scale phytoplankton variability increased but phytoplankton abundance declined after reaching a peak in ~2000 (Figure 4c,d; Table 1).

Spatially, phytoplankton differed strongly among regions (Appendix S1: Table S4). As reported previously (Menge et al., 2009, 2015), spatial variation in phytoplankton was idiosyncratic. Ranked from highest to lowest, Regions were 3 and 5, 1, and 2 and 4 (Appendix S1: Table S4; Tukey HSD test). These patterns are mostly explained by an interaction between variable continental shelf width and upwelling currents, which tend to be retentive in Region 3 (and likely in Region 1) (Kirincich et al., 2005; Menge et al., 2015). Region 4 has strong local offshore surface currents (Figure 2), so likely has low retention of phytoplankton and larvae, while Region 5, where upwelling is relatively strong and the California Current jet is deflected seaward (Castelao & Barth, 2005), often has high phytoplankton in the southward lee of Cape Blanco (Figure 5).

Relation between upwelling regime and bottom-up factors

In coastal upwelling systems, variability in DIN and phytoplankton might be expected to be driven by upwelling and ISST. To determine how this relationship varied in space and time, we tested its strength using the distance-based linear modeling (DistLM) and distance-based redundancy analysis (dbRDA) routines in PERMANOVA+ (Anderson et al., 2008). At region scales, both upwelling (12-month averages of CUTI) and

TABLE 1 Annual bottom-up and ecological metrics regressed by year. Data were mean and SD of region-scale residuals after removing effect of site.

Metric	Years	Statistic	Intercept	Slope (quadratic coefficient)	F	p	N	Adj. R^2
Nutrients	1993–2017	Mean	+28.1	−0.014	10.51	**0.0017**	93	0.104
		SD	−21.3	+0.011	7.83	**0.0063**	92	0.07
Phytoplankton	1993–2017	Mean	−16.9	+0.0086 (−0.0037)	9.11	**0.0002**	139	0.105
		SD	−28.3	+0.014	16.8	**<0.0001**	132	0.108
Mussel growth	1997–2018	Mean	+7.24	−0.0036 (−0.0005)	3.46	**0.035**	109	0.044
		SD	−2.44	+0.0013 (+0.0004)	5.09	**0.008**	109	0.07
Mussel condition index	1999–2018	Mean	+7.67	−0.0038	15.6	**0.0002**	96	0.133
		SD	−1.11	+0.0006	4.61	**0.034**	93	0.038
Mussel gonad size	2002–2018	Mean	+75.9	−0.038	29.0	**<0.0001**	75	0.275
		SD	+9.59	−0.0047 (+0.0042)	12.75	**<0.0001**	75	0.241
Mussel colonization	2011–2019	Mean	+34.9	−0.017 (+0.005)	4.13	**0.029**	27	0.194
		SD	+7.98	−0.004	0.27	0.61	27	0.0
Barnacle colonization	2011–2019	Mean	+106.7	−0.053	18.54	**0.0002**	27	0.403
		SD	+10.3	−0.005	0.31	0.58	27	0.0
Sea star reproductive fraction	2000–2019	Mean	−18.8	−0.0093 (−0.0034)	27.1	**<0.0001**	58	0.48
		SD	−4.25	+0.002 (+0.0004)	6.86	**0.002**	56	0.176
Sea star Predation rate	2007–2019	Mean	+0.0017	−8.43 e−7 (+1.2 e−7)	15.48	**<0.0001**	39	0.432
		SD	+0.00066	−3.26 e−7 (+8.36 e−8)	8.47	**0.001**	39	0.282

Note: Model fit used AIC_c. Units: Nutrients = $\ln(NO_3 + NO_2)$; phytoplankton = ln chlorophyll *a*; mussel growth = ln mm/day/initial length × 1000; condition index (wet tissue weight/shell weight); mussel gonad size = categorical scale 0–3; colonization = arcsin % cover; sea star reproductive fraction = arcsin proportion reproductive; sea star predation rate = mussels eaten/day. The p values <0.05 are shown in boldface.

ISST (12-month average intertidal seawater temperature) contributed to annual and region-scale variation in DIN and phytoplankton (Appendix S2: Figure S4; DistLM sequential tests: pseudo-$F = 5.69_{(CUTI,\ 88\ d.f.)}$, $p = 0.005$, proportion variance explained = 0.061 and pseudo-$F = 4.69_{(ISST,\ 87\ d.f.)}$, $p = 0.016$, proportion variance explained = 0.048, respectively). Surprisingly, total variance explained by this relationship was modest, equaling 11%, meaning most variance in bottom-up processes was explained by other factors. We suspect this relatively weak effect is a function of data resolution: these analyses used annual means and thus did not reflect the well known seasonal, monthly, and even weekly variation that can occur in these metrics (e.g., Huyer, 1983).

Upwelling separated the two southern regions from the three northern regions whereas the temporal variation at each cape was driven primarily by ISST (dbRDA; Appendix S2: Figure S4). Specifically, Regions 4 and 5 (CA, CB) were located below and to the right in ordination space, the direction of stronger upwelling, whereas Regions 1–3 were in the direction of weaker upwelling (upper left). Increasing temperature trended downward and leftward in ordination space. This was the trend for all regions with early years in each time series toward the upper right and later years toward the lower left.

Ecological changes

Prey colonization and mussel performance (growth rate, CI, and reproductive output) declined during 1999–2018. Further, after decades of relatively constant abundance, sea star populations were severely reduced by SSW syndrome in 2014. This event led to a dramatic shift in size structure and thus a decline in reproductive output, as well as to a sharp decrease in the rate of sea star predation on mussels. We detail these changes below, and then analyze their association with climate-related environmental changes.

Prey colonization

Temporally, prey colonization rates generally declined, whereas variability did not change from 2010 to 2019 at the coastal scale (Figure 6). Mussel and barnacle colonization decreased at all regions except Region 5 (mussels)

FIGURE 5 View looking north from study site Port Orford Heads (Region 5 site POH-3) toward Cape Blanco (Region 5 site CB-1) showing dense nearshore phytoplankton bloom (brown water) contrasting to the green water further offshore. Field gear and two researchers in lower right provide scale. Photograph credit: Bruce A. Menge.

and Region 3 (barnacles) and all sites except BB-2, CBN-1 and RP-4 (where mussel colonization was already near 0 across most years) and YB-2 (barnacles) (Appendix S1: Table S8; Appendix S2: Figure S5). Variability (SD) of mussel colonization decreased in Region 2 ($p = 0.049$, adj. $R^2 = 0.172$) but not in Regions 3 and 5. Barnacle colonization variability did not change in any region. At the site scale, mussel colonization variability did not change, and except for decreases at BB-2 and RP-4 and increases at YB-2, barnacle colonization also varied little. However, because variance explained (adj. R^2) was often substantial (Appendix S1: Table S8), small sample size ($n = 9$) at the site scale likely affected the significance of site-scale changes.

Reflecting prior temporal and spatial patterns of mussel recruitment (Broitman et al., 2008; Menge et al., 2009; Menge, Gouhier, et al., 2011; Menge, Hacker, et al., 2011), mean mussel and barnacle colonization variation was context dependent, varying by site within regions and through time (Appendix S1: Table S4). Average mussel colonization was extremely low in Regions 2 and 5 throughout 2011–2019 (Appendix S2: Figure S5; mean percentage cover range: 0.07% at Region 5 sites, 0.2% and 1.0% at Region 2 sites), but was higher at Region 3 sites (5.9% and 22.9%). In contrast, *B. glandula* colonization varied primarily between years (Appendix S1: Table S4). Average barnacle colonization was typically higher than mussel recruitment at all sites across all regions sampled, from 27% and 43% (Region 2), 18.2% and 23.4% (Region 3), and 9.3% and 20.6% (Region 5).

Mussel performance: Growth

Temporally, annual mussel growth rates fluctuated through time at the coast scale, with low rates in the 1990s and mid-2010s, high rates in the mid-2000s, and a suggestion of an increase toward the end of the time series (Figure 7a; Appendix S1: Table S9). Growth rates were relatively invariant until the mid-2010s, when the SD increased (Figure 7b, Appendix S1: Table S9). Growth rate declined in Regions 1 and 2 and at YB-2 in

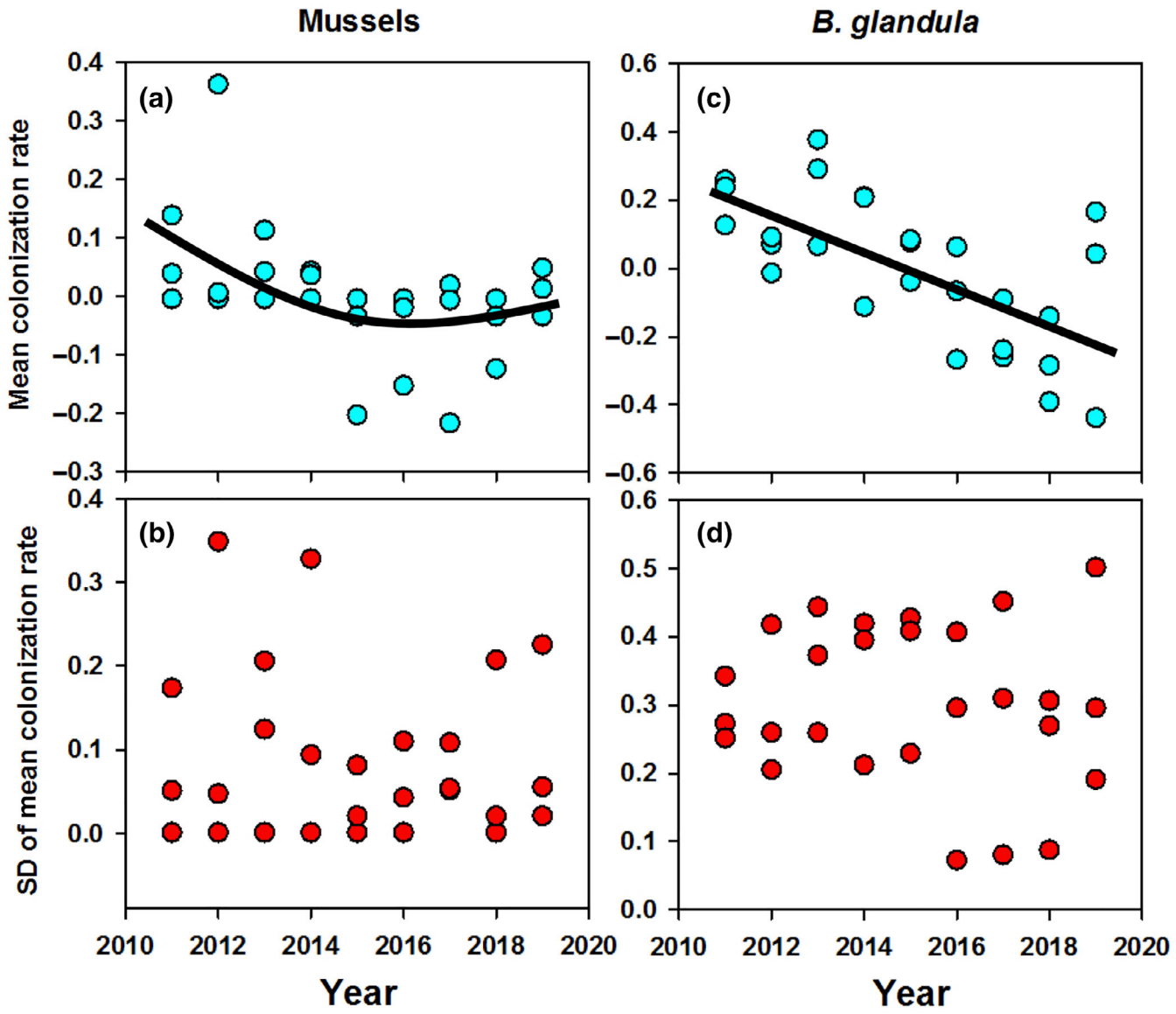

FIGURE 6 Coast-scale colonization rate and SD of primary sea star prey. (a) Mussel mean colonization rate, (b) SD of mean mussel colonization rate, (c) *Balanus glandula* colonization rate and (d) SD of *B. glandula* colonization rate. Data were averaged residuals of means and SD of region-scale annual rates. See Table 1 for regression equations.

Region 3 but increased in Region 5 sites (Appendix S2: Figure S6, Appendix S1: Table S10). No trends in growth rate occurred at SH-3 or TK-4 in Region 3, or in Region 4 (CA). Mussel growth variability also changed spatially, increasing at YB-2 and in Region 5 but decreasing in Region 2 and SH-3 in Region 3 (Appendix S1: Table S10). No trends in variability occurred in Region 1, TK-4 in Region 3 or in Region 4. As suggested by coast-scale patterns, longer term data sets at FC-1, BB-2, and YB-2 showed more complex nonlinear patterns, with increasing then decreasing growth rates at FC-1 and BB-2 (third-order polynomial; Appendix S1: Table S11), and nonlinear decreasing growth rates at YB-2 (quadratic; Appendix S1: Table S11). In general, recent mussel growth rates decreased and became more variable to the north, and either did not change or increased and became more variable to the south.

Spatially, mean mussel growth was context dependent, varying by region × year and site (region). Growth was fastest in Regions 1 and 3, next highest in Region 2, and lowest in Regions 4 and 5 (Appendix S1: Table S4; Tukey HSD test). Growth was different between Region 2 sites (FC > BB) and was greater at one Region 5 site than at the other two sites plus the Region 4 site (POH > CBN, RP, and CA).

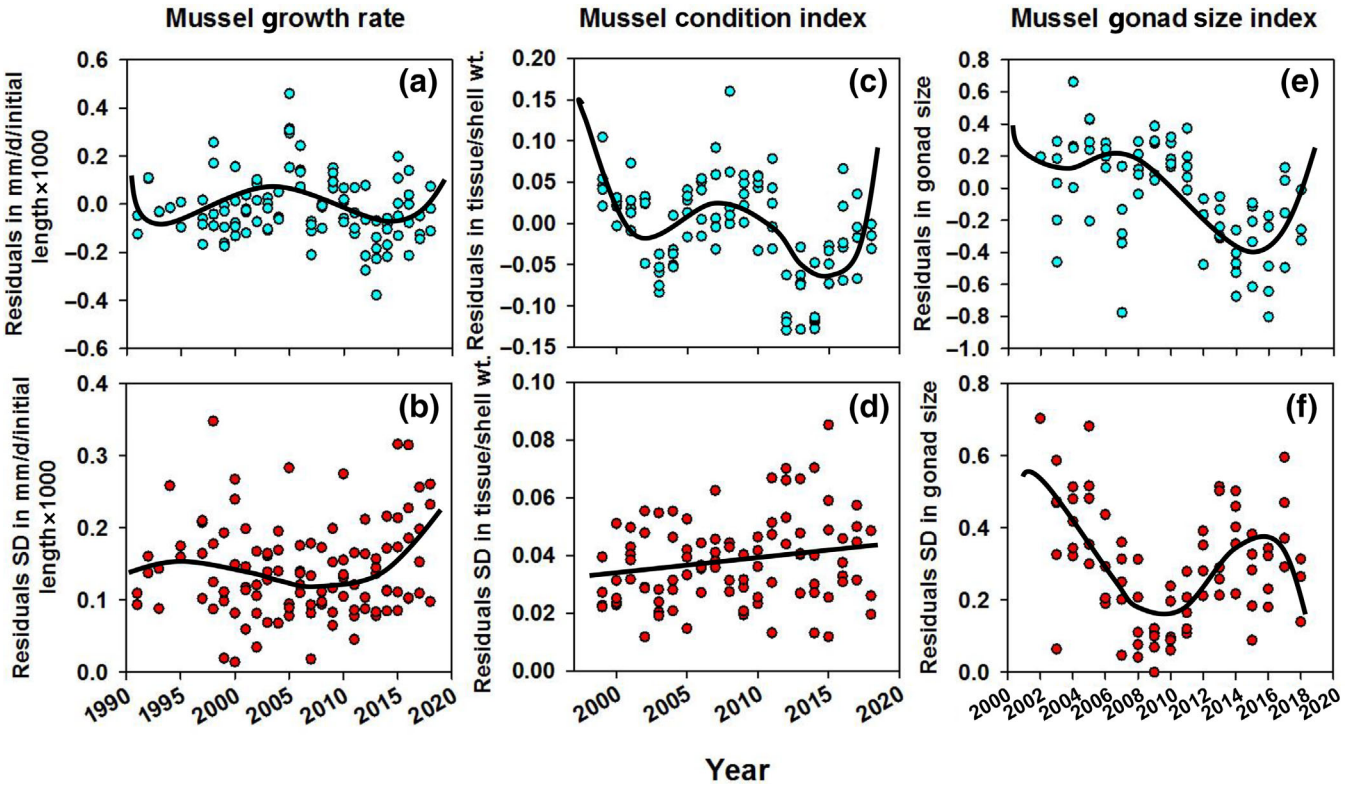

FIGURE 7 Mussel *Mytilus californianus* ecological performance metrics, including (a) mean annual growth rate, (b) SD of growth rate, (c) mean annual condition index (CI), (d) SD of CI, (e) gonad size index, and (f) SD of gonad index. Data are region-scale residuals after removal of site effect. See Table 1 for best-fit regressions, Appendix S1: Table S9 for statistics describing curvilinear fits shown above.

Mussel performance: Condition index

Temporally, mussel CI generally declined at the coast scale from 1999 to 2018 (Figure 7c, Appendix S1: Table S9). As with growth rates, however, these trends clearly varied nonlinearly, with lows in 2003 and 2013–2015 and highs in 1999–1998, the late 2000s, and a suggestion of an increase toward the end of the time series (Figure 7c, Appendix S2: Figure S7). Variability of CI increased through time (Figure 7d). At the region scale, CI declined both linearly and nonlinearly at all but the southern-most Region 5 (Appendix S2: Figure S7, Appendix S1: Tables S12 and S13). Although the strength of the declines in CI was more variable at the site scale, variance explained was relatively high (20% to 54%) across all sites except CBN-1 (no trend) and RP-4 (increasing CI) (Appendix S2: Figure S5, Appendix S1: Table S13). Temporal variability in mussel condition (SD of mean CI) did not change at region scales ($p = 0.22$ or higher) or with the exceptions of POH-3 (positive trending third-order regression, $p = 0.035$, $n = 11$, adj. $R^2 = 0.553$) and SH-3 (negative-trending linear regression, $p = 0.08$, $n = 19$, adj. $R^2 = 0.12$), at site scales.

Spatially, CI patterns varied among regions and through time but not among sites within regions (Appendix S1: Table S4; Tukey HSD test). Here too, CI was highest in Regions 1 and 3, and lowest in Regions 2, 4, and 5.

Mussel performance: Reproduction

Temporally, similar to growth rate and CI, mean gonad size index (GSI) and variability of GSI fluctuated through time at the coast scale (Figure 7e,f). At the region scale and excepting Region 1, mussel GSI declined nonlinearly (Appendix S1: Table S14, Appendix S2: Figure S8). Regional change in variability (SD) was also nonlinear except for Regions 1 and 4 (Appendix S1: Table S14, Appendix S2: Figure S8). Site-scale trends mirrored those at the region scale, with mean GSI decreasing at all sites (but not significantly at SH-3), whereas SD of mean gonad size increased at 7 of 11 sites (Appendix S1: Table S14).

Spatially, regional differences were the same as for CI with strong effects of region and year but not site (Appendix S1: Table S4). GSI in Regions 1 and 3 were greater than those in Regions 2, 4, and 5. Spatial differences in GSI were weaker, however (adj. $R^2 = 0.137$ vs. 0.362 and 0.219 for growth and CI, respectively).

Sea star reproductive performance

Temporally, the proportion of reproductive *P. ochraceus* was nonlinear at the coast scale, with a peak in the early 2010s and the SSW-induced crash from 2014 on (Figure 8a, Appendix S2: Figure S9). Variability in the mean proportion reproductive was also nonlinear, with a low in ~2005 and increasing thereafter (Figure 8b; Table 1). Spatially, proportion of reproductive *P. ochraceus* was context dependent (region × year interaction), between sites within regions, and with year and SSW as covariates (Appendix S1: Table S4).

As in the San Juan Islands (Menge, 1975), Oregon *P. ochraceus* matured reproductively at around 100 g wet weight (Appendix S2: Figure S10). Further, the larger the sea star the more reproductive biomass was produced, reaching ~15%–18% of total body mass in the largest individuals. Not obvious in Appendix S2: Figure S10 is that gonad tissue in individuals in the 0–100 g wet weight size category mostly was gamete free, consisting of just the supportive tissue in which gametes would eventually develop (B. Menge, personal observations). Of 61 individuals sampled in the 0–100 g size category, sex of only 9 (14.8%) could be ascertained and all the latter were >70 g wet weight. Females tended to have larger gonads than males (average [±1SE] gonad indices were 10.4 ± 0.66 vs. 7.8 ± 0.64, respectively) and made up increasing fractions of larger size categories (52% of 100–200 g, 57% of 200–300 g, and 73% of >300 g size groupings). Clearly, size matters with respect to reproductive output of *P. ochraceus*.

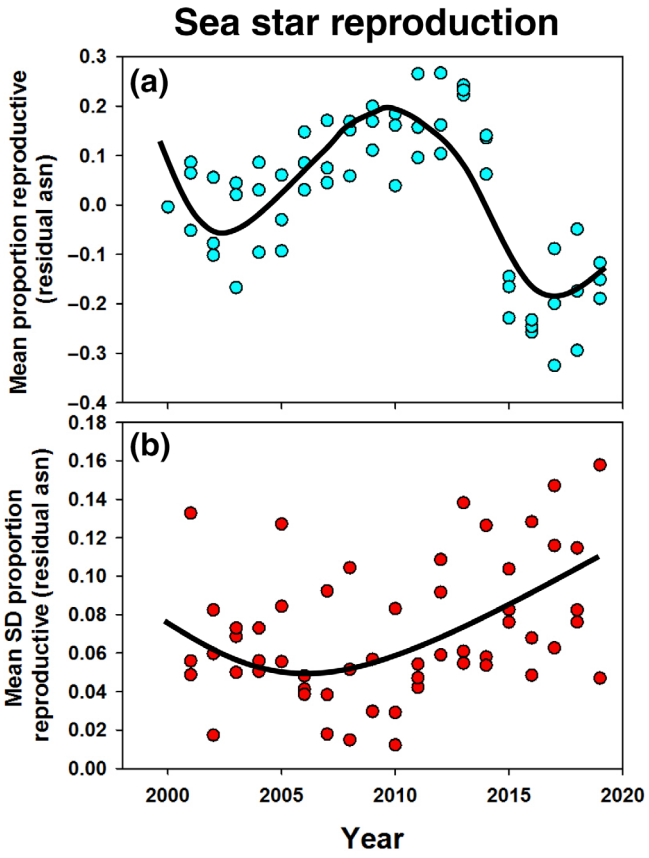

FIGURE 8 Change in reproductive status of the sea star *Pisaster ochraceus* across all sites. (a) Annual mean proportion of sea stars that were reproductive from 2000 to 2019. (b) Annual standard deviation of proportion reproductive. See Table 1 for best-fit regressions. Statistics for curvilinear fits shown above were (a) mean proportion reproductive = $7.8 - 0.0038 \times \text{year} - 0.011 \times (\text{year} - 2009.83)^2 - 9.17\text{e}{-5}(\text{year} - 2009.63)^3 = 9.06\text{e}{-5} \times (\text{year} - 2009.83)^4$, $F_{(4,53)} = 26.5$, $p < 0.0001$, adj. $R^2 = 0.64$. (b) SD of mean proportion reproductive = $-4.25 + 0.0021 \times \text{year} + 0.0004 (\text{year} - 2009.84)^2$, $F_{(2,53)} = 6.86$, $p = 0.002$, adj. $R^2 = 0.176$.

Adult mass mortality likely led to large declines in the production of sea star larvae. Prior to SSW (2001–2014), the proportion of reproductive individuals (i.e., >100 g) among sites ranged from ~40% (BB-2) to nearly 100% (YB-2 and TK-4; Appendix S2: Figure S9). After the 2014 SSW event (2015–2019), proportions ranged from 0% (BB-2) to ~20% (TK-4) among sites. Thus, SSW led to a drastic decrease in reproductive populations, and hence, likely in sea star larval production.

Predation rate

Temporally, predation rate and SD of predation rate decreased nonlinearly at the coast scale (Figure 9; Table 1). Spatially, predation rate varied by region and with SSW but not by site within region or in any interaction (Appendix S1: Table S4).

In 2014, SSW produced an immediate, sharp decrease in sea star predation rates on mussels at all six sites (Appendix S1: Table S15, Appendix S2: Figure S11) and it remained low through 2019 at all sites except YB-2. Thus, at most sites, SSW caused a drastic and lasting change in sea star predation, primarily because the small juveniles replacing the large adults were unable to consume larger prey.

Association between environmental change and ecological trends

Although temporal patterns of some ecological measures varied among regions, most metrics declined at most sites during the study period, especially in the mid to late 2010s (Figures 4 and 6–9, Table 2). Were these trends related to environmental conditions? Our analyses indicate that combined temporal responses of DIN, Chl *a*,

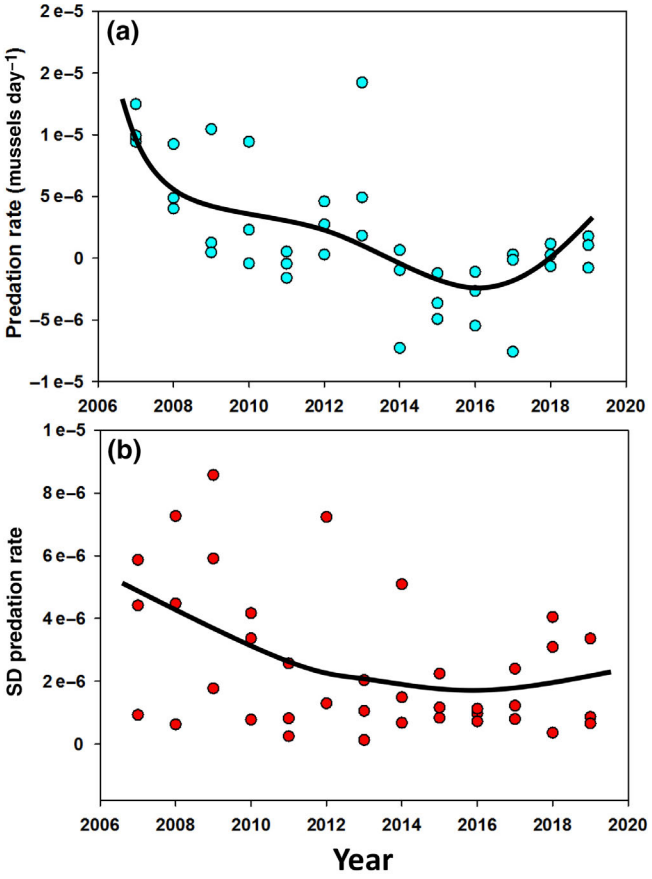

FIGURE 9 Coast-scale patterns of mean annual predation rate and SD of predation rate of *P. ochraceus* preying on *M. californianus* from 2007 to 2019. Each point represents the residuals (effect of site removed) of a region × year value. Statistics for curvilinear fits shown above were: (a) Predation rate = +0.002 − 1.01 e−6 × year − 2.13 e−7 × (year − 2013)^2 + 6.369 e−9 × (year − 2013)^3 + 9.4 e−9 × (year − 2013)^4, $F_{(4,34)} = 9.1$, $p < 0.0001$, adj. $R^2 = 0.46$. (b) SD of predation rate = +0.00066 − 3.26 e−7 × year + 8.36 e−8 × (year − 2013)^2, $F_{(3,36)} = 8.47$, $p = 0.001$, adj. $R^2 = 0.282$.

mussel growth, mussel CI, and sea star reproductive fraction were most strongly associated with upwelling (DistLM sequential test: Pseudo-$F = 13.8$, $p = 0.0001$, variance explained [VE] = 0.20), ISST ($F = 2.68$, $p = 0.03$, VE = 0.038), SSW ($F = 2.60$, $p = 0.039$, VE = 0.031), PDO ($F = 3.88$, $p = 0.006$, VE = 0.052) and NPGO ($F = 5.67$, $p = 0.0005$, VE = 0.07; 55 df total VE = 0.391) (Figure 10). Inspection of the ordination (dbRDA) indicates that upwelling separated the southern Region 5 (CB) from the central and northern Regions 2 and 3 (CF, CP), whereas temperature (ISST) and temperature-related metrics (PDO, NPGO), and SSW were associated with temporal patterns, with warmer years toward the lower left and cooler years toward the upper right of 2D ordination space.

Considered individually, in most cases, the relationship between the ecological metric and environmental factors varied among regions. Phytoplankton abundance, for example, increased with increasing upwelling in Regions 1–3, but not in Regions 4 and 5 (Appendix S1: Table S16). Phytoplankton (Chl *a*) also increased with warm-phase PDO in Regions 2 and 3, with windier NPGO conditions in Regions 2–4, and decreased with cooler air temperatures in Region 3 (Appendix S1: Table S16). Environmental factors and phytoplankton were unrelated in Region 5.

Prey colonization was quantified only in Regions 2, 3, and 5. Mussel colonization decreased with increasing upwelling in all regions, but barnacle colonization did not respond to upwelling (Appendix S1: Table S16). Barnacle colonization was lower with increased food (phytoplankton) in Region 3, but increased with air temperature in Region 3 and with increasing climate indices in Regions 2 (windier NPGO) and 5 (warmer PDO, windier NPGO). Mussel colonization was higher with warmer air temperature in Region 3 and with higher food in Region 2.

Mussel performance (shell growth, CI, and gonad size) responded most consistently and negatively to air temperature (Appendix S1: Table S16). Growth and CI were most affected at the northern regions, whereas reproductive output was affected in all but the northern-most Region 1 (Cape Meares). Based on the R^2 values, CI and gonad size were more tightly associated with increased air temperature than was shell growth. In contrast, ISST effects were minimal and occurred only for shell growth and CI in Region 2 and gonad size in Region 5.

Increasing (windier) NPGO also had negative effects on mussel growth (all but Region 1; CI at Region 4), whereas upwelling effects were mixed and generally weaker (lower R^2s). Shell growth and CI increased with increasing upwelling in Regions 2 (CI), 3 (growth) and 4 (growth). Mussel gonad size increased with upwelling in Regions 1 and 3, and decreased with upwelling in Region 5.

Proportion of reproductive *P. ochraceus* increased with air temperature and decreased with ISST in Regions 3 and 5 (Appendix S1: Table S16). Reproduction increased strongly with increasing (warmer) PDO in Region 2, but decreased in Region 5 (but evidently not statistically significantly). In Region 3, proportion reproductive increased strongly with positive (wavier) NPGO and also increased with upwelling (CUTI). SSW was associated with proportion reproductive only in Region 2, but oddly the relationship was positive.

As has been previously reported (Menge et al., 2016), in all regions sea star predation rate was strongly negatively influenced by SSW, which was the only significant effect in Regions 2 and 3 (Appendix S1: Table S16).

TABLE 2 Temporal trends in (a) environmental drivers and (b) ecological metrics summarized from the figures and supplementary figures in Appendix S2.

	Average trend		Variability trend	
Metric	**Coastwide**	**Regions 2, 3, 5**	**Coastwide**	**Regions 2, 3, 5**
(a) Environmental drivers				
PDO	↑[n]	na	↓[n]	na
NPGO	↓	na	↑	na
ENSO	↓	na	↓[n]	na
Upwelling	↓	↓ ↔ ↔	↑	↑ ↑ ↑
ISST	↑	↑ ↑ ↑[n]	↑	↑ ↑ ↑
Air temperature	↑	↑ ↑ ↑	↑	↑ ↑ ↑[n]
DIN	↓	↔ ↔ ↓	↕	↔ ↔ ↑
(b) Ecological metrics				
Phytoplankton	↓	↓ ↓ ↓	↑	↔ ↔ ↓
Mussel growth	↓	↓ ↕ ↑	↑	↓ ↓[n] ↑
Mussel condition index	↓	↓ ↓ ↔	↑	↔ ↔ ↑
Mussel gonad size	↓	↓ ↓ ↓	↓	↑ ↑ ↑
Mussel colonization	↓	↓ ↓ ↔	↔	↓ ↔ ↔
Barnacle colonization	↓	↓ ↔ ↓	↔	↔ ↔ ↓[n]
Pisaster proportion reproductive	↓	↓ ↓ ↓	↑	↕ ↓ ↔
Predation rate	↓	↓ ↓ ↓	↓	↓ ↓ ↓

Note: Arrows indicate annual mean or variability trends for coastal or regional drivers and metrics, with Regions 2, 3, and 5 shown. Arrows indicate increases, decreases, cyclical trends, or no change (↑, ↓, ↕ or ↔, respectively). [n] indicates a nonsignificant but suggestive trend. na indicates that the given driver was not analyzable at the regional scale.

Abbreviations: DIN, dissolved inorganic nitrogen; ENSO, El Niño-Southern Oscillation; ISST, intertidal sea surface temperature; NPGO, North Pacific Gyre Oscillation; PDO, Pacific Decadal Oscillation.

In Region 5, predation rate also decreased with increasing (warmer) ENSO and warmer air temperatures and increased with increasing PDO and stronger upwelling.

Assessment of variability of factors by scale

Our results facilitate the sorting of the environmental drivers and ecological metrics into the spatial scale at which each varies most significantly (Table 3). Because several metrics covaried (ENSO/PDO, air and water temperature, mussel growth, CI, and gonad index), we used principle coordinates to create combined variables of each. By definition, the climate indices (NPGO, and ENSO/PDO) vary at the largest scale. SSW and, somewhat surprisingly, barnacle colonization also varied at the coastal scale. As noted earlier, upwelling, DIN, Chl *a*, mussel performance, and sea star predation rate all varied primarily by region, whereas mussel colonization and sea star reproduction varied at site scales.

DISCUSSION

After decades of relative stasis in both structure and dynamics (Gravem et al., unpublished manuscript; Menge, Hacker, et al., 2011; Menge et al., 2016, 2022), the Oregon rocky mid intertidal meta-ecosystem has experienced relatively radical changes in environmental conditions, and presumably in response, in ecological processes. The environmental changes are not surprising, of course, because the changing climate has been well documented, both globally and at the scale of the California Current Large Marine Ecosystem (Behrenfeld et al., 2006; Burrows et al., 2011; Doney et al., 2012; Frölicher et al., 2018; Hixon et al., 2010; Iles et al., 2012; Menge et al., 2009; Menge, Hacker, et al., 2011; Raimondi et al., 2019). The changes in ecological processes are surprising however, primarily because we have not yet seen large changes in these ecological communities (Gravem et al., unpublished manuscript; Menge et al., 2022). Our detection of declines and increasing variability in several processes indicates that the changing climate is indeed having an effect on these

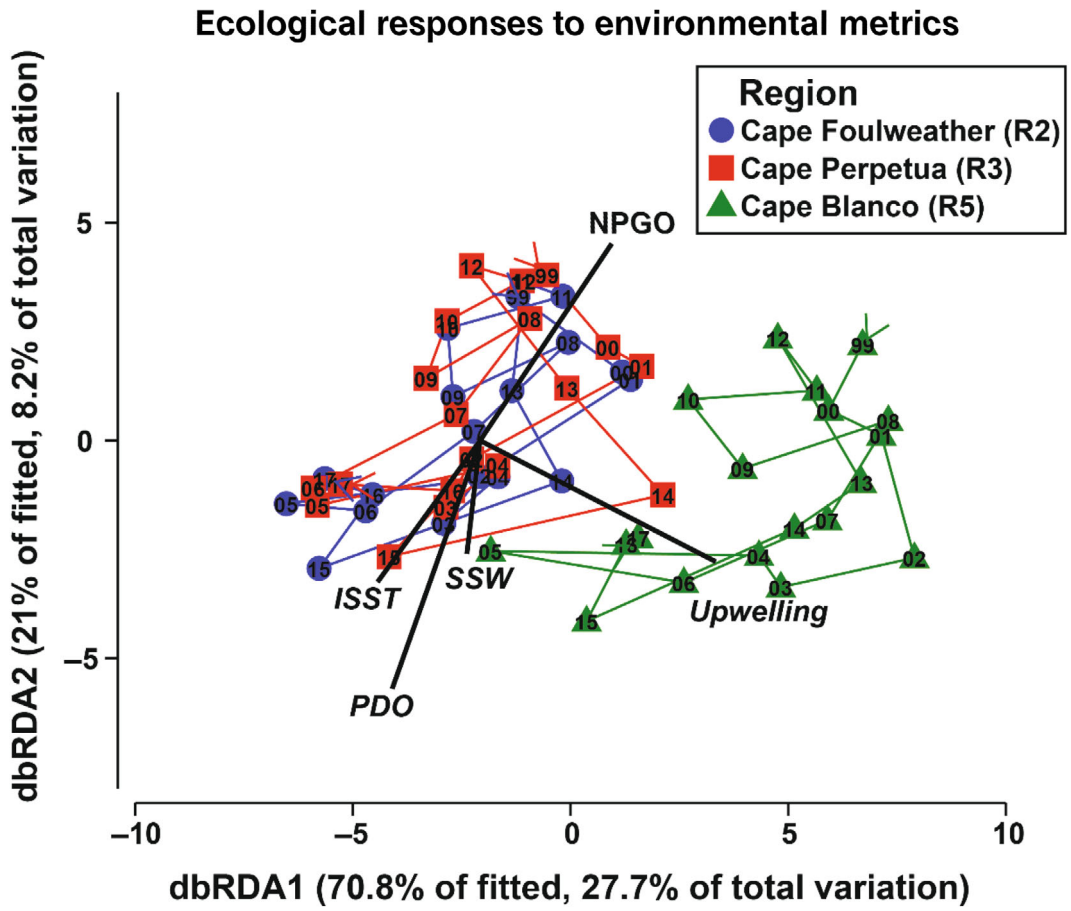

FIGURE 10 Distance-based redundancy ordination of ecological responses (dissolved inorganic nitrogen [DIN], chlorophyll *a* [Chl *a*], mussel growth and condition index, and sea star reproductive proportion) to environmental metrics (Pacific Decadal Oscillation [PDO], North Pacific Gyre Oscillation [NPGO], upwelling, intertidal sea surface temperature [ISST], and sea star wasting [SSW]). Predation rate, prey colonization, and mussel gonad index time series were too short to be included. SD of the environmental metrics, mean air temperature, and El Niño-Southern Oscillation (ENSO) were not significant in preliminary models so were excluded.

communities, and may be an early warning signal (EWS) of more change to come. Below, we first examine our results in the context of community stability theory with advancing climate change, then summarize changes observed in relation to the goals mentioned in the "*Introduction*."

Stability: Responses to environmental drivers

The ultimate goal of these studies was to enable assessment of the stability of key ecological taxa and processes in relation to environmental change and variability. Table 2 summarizes the temporal region- and coast-scale results in these two contexts.

Our data suggest that (1) ecological subsidies (nutrients, phytoplankton, prey colonization), (2) mussel performance, (3) sea star reproductive output, and (4) predation rates have all decreased during the past 10–20 years (Table 2). Further, variability of most ecological metrics has increased over the past 10–30 years (Table 2). Nutrients (DIN), for example, have become increasingly variable over the 2010s, whereas phytoplankton abundance has steadily increased in variability since the mid 1990s. However, mean colonization rate of mussels and barnacles that eat phytoplankton decreased but did not change in variability. Variability in mussel performance has been more complex, with growth measures increasing in some regions but not in others. Mussel performance has also undergone long-term temporal fluctuations, with reproductive output increasing in variability since ~2008. SSW drove a crash in the proportion of reproductive sea stars at all sites. Although SSW is not an environmental factor and it is not clear that it was triggered by climate change, warmer temperatures have been associated with increased speed and severity of the disease (Hamilton et al., 2021). Although most Oregon *Pisaster* populations have recovered in terms of abundance, all populations still consist of mostly immature juveniles, so gamete production will remain low for an indeterminate

TABLE 3 Environmental drivers and ecological metrics sorted by spatial scale at which each varied most strongly, as determined by nested ANOVA (model: x = cape + site(cape) + error).

Factor	Region p-value	Site p-value	p-value	Adj. R^2
Coastal scale				
ENSO/PDO	na	na		
NPGO	na	na		
Temperature (190)	0.084	0.99		
SSW (109)	0.75	0.58		
Barnacle colonization (48)	0.59	0.53		
Regional scale				
Upwelling (190)			<0.0001	0.880
DIN (189)			<0.0001	0.218
Chl-*a* (190)			<0.0001	0.391
Mussel Performance (163)			<0.0001	0.331
Sea star Predation Rate (74)			0.0005	0.187
Site scale				
Mussel Colonization (47)			<0.0001	0.644
Sea star Reproduction (114)			0.011	0.199

Note: Scales were coastal ("large"), region or cape ("meso"), and site ("local"). The climate indices (ENSO, PDO, NPGO) are defined at the ocean basin scale, so were by definition coastal-scale factors. Any metric that did not vary by cape or site(cape) was assigned to coastal scale. ENSO and PDO, air and water temperature, and mussel metrics (growth, condition index, reproduction) covaried, so were analyzed using the first principle component of each set. A metric was defined as varying primarily at the regional scale if site(cape) was not significant, and defined as varying primarily at the site scale if site(cape) was significant. The two factors varying at the site scale also varied significantly at the regional scale (mussel colonization $p < 0.0001$, sea star reproduction $p = 0.0043$). Sample sizes for each analysis are shown in parentheses.

Abbreviations: DIN, dissolved inorganic nitrogen; ENSO, El Niño-Southern Oscillation; ISST, intertidal sea surface temperature; NPGO, North Pacific Gyre Oscillation; PDO, Pacific Decadal Oscillation; SSW, sea star wasting.

amount of time. The collapse of predation rate on mussels is a clear outcome of SSW, and rates are so low across all sites that the decline in variability of predation rate was expected.

Together these changes suggest decreasing stability in multiple ecological processes, including ecological subsidies, space competition, and top-down effects (Table 2). These processes are central to the dynamics of rocky intertidal systems in the California Current system and elsewhere (Bryson et al., 2014; Bustamante et al., 1995; Hacker et al., 2019; Lubchenco & Menge, 1978; Menge, 1976; Menge et al., 1994, 2003, 2004, 2015; Menge & Lubchenco, 1981; Navarrete et al., 2005; Paine, 1966, 1974, 1994; Plass-Johnson et al., 2010; Rilov & Schiel, 2006; Vinueza et al., 2014). Thus, alteration of their dynamics, if severe, seems likely to lead to major disruptions of these systems with reductions in diversity and turnover in species composition, often in directions deemed undesirable.

In fact, although rocky intertidal organisms are adapted to persist and even thrive in the relatively extreme environment of rocky shores, recent evidence indicates that several rocky intertidal ecosystems are expressing signs of decreasing stability. Along the East Coast of the USA, the geographic range of the ecologically critical mussel *Mytilus edulis* has retreated northward (Jones et al., 2009, 2010). This change was associated with major shifts in community composition and predator abundance along the New England coast (Sorte et al., 2017). In these and other cases (e.g., Sanford et al., 2019; Wernberg et al., 2016; Wethey et al., 2011), extreme thermal stress during MHWs was identified as an important cause of shifts in structure and thus in stability.

As noted in the "*Introduction*," the recent report by Miner et al. (2021) showed that the state of rocky intertidal communities along some sections of the United States West Coast became increasingly different from the original mid-2000s "benchmark" state. As they noted, increasing differences from an original state in such communities is to be expected in such a dynamic system, but the differences among regions were unexpected. Specifically, changes in northern and central regions (Washington through central California) were relatively small compared with the larger changes in Southern California. Using their definition of stability (similarity at time t_n to the benchmark state at time t_0) they concluded that northern and central communities were

more stable than southern communities. They also found no change in mussel cover in northern and central regions and declines in cover in the south. Although methodologies of the Miner et al. (2021) study differed from those of Gravem et al. (unpublished manuscript), the conclusions are similar, at least for communities in Oregon and northern California where the Gravem et al. research was done. Structural patterns of rocky intertidal communities in these regions have persisted since at least ~2006. Observations and sporadic samples by the senior author (Menge) suggest such persistence extends back to the early 1980s at Boiler Bay (Region 2) and Strawberry Hill (Region 3) sites.

As in prior research (Menge et al., 2005), however, structural patterns may appear static whereas underlying processes can be dynamic. In the present case, changes in the "hidden" dynamics investigated here seem likely to lead to structural changes if the negative trends we have documented persist. If so, the results of the present paper may presage impending change such as those seen in Southern California (Miner et al., 2021), and, perhaps ultimately, to a shift to an alternative state. In other words, our work potentially reveals EWSs of destabilization of mid intertidal rocky intertidal communities in Oregon.

The issue of EWS has been a core theme in much of recent stability literature (Carpenter & Brock, 2006; Cline et al., 2014; Gsell et al., 2016; Patterson et al., 2021; Scheffer et al., 2009). EWS are thought to accompany the process of critical slowing down, or the reduced resilience of systems to perturbations, that can lead to transitions to alternative states (Menge et al., 2022; Scheffer et al., 2009). Of the several measures of EWS, increasing autocorrelation and increasing variance are widely used. However, neither these nor other measures tested were fully reliable indicators of EWS, and four metrics estimated in five long-term freshwater systems were not strongly correlated (Gsell et al., 2016).

In our case, because estimates of autocorrelation require lengthier time series (ideally >100 observations; Box & Tiao, 1975), we have relied on the more easily estimated changes in variance. Although not all measures increased in variance, and some measures increased at one site or region and decreased at other sites or regions, the bulk of the evidence suggests that key drivers and processes are in fact becoming more variable, and that conditions and performances are worsening (Table 2). Of the drivers, increasing temperatures, increasing temperature variability, and declining and more variable upwelling clearly represent direct and/or indirect stresses to the system. Ecological changes are more complex, but phytoplankton, mussel fecundity, sea star reproductive output, and mussel colonization have all declined or remained extremely low (e.g., mussel colonization in Regions 2 and 5).

A possible path to adaptation to environmental stresses is suggested by the spatial variation in ecological processes; that is, resilience is likely to vary among regions. Specifically, because most processes related to recovery (mussel and sea star growth, prey colonization, phytoplankton abundance) are higher or faster in Region 3 (Cape Perpetua), it is possible that this region will be more resilient to thermal stress, at least compared to other regions.

A parallel experimental community-level study by our group in the low intertidal zone shows diminishing resilience (Menge et al., 2022, which is consistent with these mid intertidal zone species-level results). We found that recovery (resilience) of communities from annually repeated disturbance experiments at the same core sites as in the present study slowed during the 2010s decade and variability in recovery increased. Further, unmanipulated communities showed similar trends of variability, but while community structure declined, these changes were not significant.

Finally, our temperature- and upwelling-related results are consistent with recent evidence in the context of ocean acidification. Specifically, compared to other sites in Oregon and California, mussel growth was relatively high at SH-3 despite reaching more extreme low pH values (Rose et al., 2020), most likely due to high levels of phytoplankton (e.g., Appendix S2: Figure S3). Thus, although pH stress has steadily increased (i.e., pH has decreased) in the California Current system (Hauri et al., 2013), Rose et al.'s work (2020) indicates that this does not seem to have affected performance of adult *M. californianus*. Instead, increasing temperature and decreasing food seems more likely to be the factors underlying decreasing mussel performance.

Environmental trends

Overall increasing mean temperatures are consistent with the intensification of climate change, and the shorter-term fluctuations are typical of temporal variability in weather patterns. The increased thermal variability makes sense given that upwelling has been increasingly variable, and that ISST and air temperatures along the coast partly reflect upwelling conditions (cooler during upwelling, warmer during downwelling).

Nutrients and phytoplankton

The changes in mean phytoplankton abundance reflect prior results showing that, in coastal environments, stronger upwelling was correlated with lower phytoplankton abundance (e.g., Menge et al., 2009). The inferred mechanism is that phytoplankton are moved away from the coast

by the offshore-moving cross-shelf surface currents during upwelling (Botsford et al., 2006), thereby reducing the levels of food for benthic filter-feeders in intertidal and shallow subtidal habitats.

Spatiotemporal ecological trends

Prey colonization

Based on the assumption that temperature would increase and become more variable and thus that food would become more variable, and on our field observations, we expected to discover a decline in prey colonization and, in fact, since 2012 this was what we observed (Figure 5, Table 1). Historically, mussel colonization has been low at BB-2 in Region 2 and all sites in Region 5 (Broitman et al., 2008; Menge et al., 2009). In the 2010s, mussel colonization was almost zero in Regions 2 and 5, and mid decade dropped sharply at Region 3 sites (Appendix S2: Figure S5, Appendix S1: Table S8). Barnacle colonization also declined during this period at all sites except YB-2. The decline in colonization is consistent with the inference in the previous section that larval availability declined during the mid-2010s. Variability of prey colonization, however, did not change during the 2010s (Figure 6). This was not a surprise at Regions 2 and 5 and SH-3 at Region 3, where the extremely low mean recruitment dominated the statistics.

Mussel performance

Prior results indicate that mussel growth should increase with increasing temperature and food abundance (Blanchette et al., 2007; Menge et al., 2008; Rose et al., 2020). Temperature driven increases, however, should be limited to temperatures below the mussel's thermal optimum, and exposure to extreme thermal stress has been shown to cause precipitous decreases in performance and ultimately death (Logan et al., 2012; Moyen et al., 2019). Given the complex changes occurring in thermal conditions and food availability due to climatic oscillations, warming, MHWs, decreasing upwelling, and variable DIN, we did not know what to expect in mussel performance metrics. At the coastal scale, however, we discovered that mean values of all three metrics (growth, CI, and GSI) decreased, whereas their variability increased through time (Table 2). As expected from the many factors that might influence mussel performance, when examined in more detail [e.g., overall nonlinear trends (Figure 7; Appendix S1: Table S9), or region and site scales, Appendix S1: Tables S10–S14, Appendix S2: Figures S6–S8], performance metrics were complex. Overall trends suggested higher levels around 2010 and lower levels before and after that, with stronger dips in performance in the mid-2010s. Variability of growth and gonad size varied approximately inversely to these trends, whereas CI variability increased approximately linearly (Figure 7). Among sites within regions and among regions, trends of mean performance were negative to the north and either neutral or positive to the south. The most consistent decline was in reproductive output, a trend suggesting that the availability of larvae to recruit to adult habitats has grown more limited through time.

Sea star performance

The 2014 SSW event caused mortality in 20+ sea star species, but most massively in *P. ochraceus* and the sunflower star *Pycnopodia helianthoides* (Burt et al., 2018; Gravem et al., unpublished manuscript; Hamilton et al., 2021; Harvell et al., 2019; Menge et al., 2016; Miner et al., 2018). Exceptionally, *Pisaster* mass mortality was followed by similarly explosive recruitment of *Pisaster* "babies" at most Oregon sites in spring 2015 and 2016 (Menge et al., 2016). Because *Pisaster* spawn in May in Oregon (B. Menge, personal observations) and the larvae are in the plankton for about 90 days (Strathmann, 1987), we infer that larval settlement occurred in late summer–early fall 2015. Newly settled individuals are about 1 mm in diameter and essentially undetectable in the field, especially in winter months when low tides are at night and waves are typically high, inhibiting close scrutiny of their habitat. Thus, in an event unlike any seen by the lead author since his career started in the 1960s, recruits observed in spring 2015 clearly had grown during the 2014–2015 winter to detectable sizes of about 10 mm diameter (Menge et al., 2016). Although these recruits restored and often overshot prior *Pisaster* population densities, because individuals must grow to 70 to 110 g wet weight to become reproductive (Menge, 1975; Appendix S2: Figure S10), the mass mortality cost all populations the bulk of reproductive individuals (Appendix S2: Figure S9). At coast, region, and site scales, the mean proportion of populations that were reproductive dropped sharply in 2014/2015 and is slowly increasing, but persists at a low state (Figure 8a; Appendix S2: Figure S9), whereas the variability in proportion reproductive steadily increased since ~2010 (Figure 8b; Table 2).

The implications of these changes are clear; until the recruits reach maturity, reproductive output of *Pisaster* populations should remain suppressed for several years. Recent (2022) field observations (B. Menge, personal observations) indicate that many of the 2015 recruits are

nearing reproductive size at some sites, but most are still subreproductive. This gap in output suggests a possible large reduction in larvae available for recruitment. However, prior to SSW, recruitment to all populations was generally extremely low despite their domination by abundant, large reproductive individuals (Menge et al., 2016). Thus, as we have suggested elsewhere, population replenishment may depend less on larval abundance and more on adult-recruit competition for prey (likely mostly small barnacles, which were unusually abundant in fall 2014). The mechanism underlying recruitment of *Pisaster* warrants more detailed investigation.

Predation rate results indicate that, due to the several years required for *Pisaster* to reproductively mature and approach a size at which they can handle large prey, there is a substantial time lag for recovery of predation effects. As our data suggest, predation rate was beginning to increase by about 2018 and, as of this writing (2022), it had reached prewasting levels at several sites, suggesting a lag of 4–8+ years. Whether or not such fluctuations will continue is unclear.

Summarizing, the largest scale environmental factors that vary regionally, air temperature and ISST, have undergone steady increases since ~2000, with two periods of thermal highs lasting several years each, the latter of which reflects the mid 2010s El Niño and MHW. ISST varied regionally, but weakly, and air temperatures did not vary in space. Unexpectedly, upwelling in the study region has declined but become more variable. Ecological subsidies also changed through time and across space, with nutrients becoming more variable, especially in the last decade, and phytoplankton abundance declining and also becoming more variable. Performance of the species arguably at the center of community dynamics in this system, mussels and the sea star *Pisaster*, also varied spatiotemporally, with temporal mussel performance generally decreasing in northern regions and either unchanging or increasing in southern regions, but with average performance still greater in northern than in southern regions. Sea star reproduction was severely affected by SSW and is still low but showed some signs of recovery from 2014 to 2019. As expected from growth rate differences (sea stars grow fastest in Region 3; Menge, Foley, et al., 2021), reproductive output was higher in Region 3 than in Regions 2 or 5. Predation rate was also sharply reduced due to SSW-caused losses of large sea stars, and has shown only modest recovery since 2015, but the rank order of predation rate in space continues to be as documented prior to 2014. Assuming the recovery of sea star populations continues its current trend, and that epidemic-scale SSW does not return, it is likely that predation rate and reproductive output of sea stars will return to pre-SSW levels in the coming decade in Oregon. While we hope that mussel performance will also rebound in the future, the processes that underlie mussel performance seem to be more sensitive to climate change, and all forecasts indicate continued intensification of climate degradation is in our future. So we suspect the negative trends in mussel performance will persist and may eventually lead to declines in mussel bed coverage as well.

Network of effects

A summary of associations among and between environmental drivers and ecological processes indicates that climatic and environmental drivers have strong and extensive effects on most ecological processes (Figure 11). For example, as expected, temperatures are higher with positive warm phases of combined ENSO/PDO, but barnacle colonization is lower with positive ENSO/PDO. Sea star reproduction, mussel colonization and, more weakly, phytoplankton are all higher with positive (windier) NPGO, but temperature and mussel performance are (weakly) lower with this factor. Also as expected, upwelling is clearly of central importance. Nutrients are high but prey colonization and mussel performance are low with more intense upwelling. Temperature is lower with high upwelling, but this effect is surprisingly weak. Other important strong effects were higher SSW with warmer temperatures, higher mussel colonization with high phytoplankton (consistent with prior effects on mussel recruitment; Menge et al., 2009), higher sea star predation rate with high mussel colonization, and high sea star reproduction with high predation rates.

Most of these linkages are sensible including positive climate-thermal relationship, lower barnacle colonization with warmer climate, positive effects of upwelling on nutrients and negative effects on prey colonization, mussel performance, and temperature, a positive (bottom-up) effect of phytoplankton on mussel colonization, of mussel colonization on predation rate, and of predation rate on sea star reproduction. However, a few linkages seem counterintuitive or contrary to prior results. For example, the increase in SSW with increased temperature regime is consistent with what was observed to the north and south of the central California through the Oregon coast, but contrary to earlier results in these latter regions (Menge et al., 2016; Miner et al., 2018). This contrast may be a partial consequence of the resolution of the temperature data used in the analysis; here we used annual averages (Appendix S2: Figure S2), whereas the earlier analyses used monthly means (e.g., Menge et al., 2016). Annual

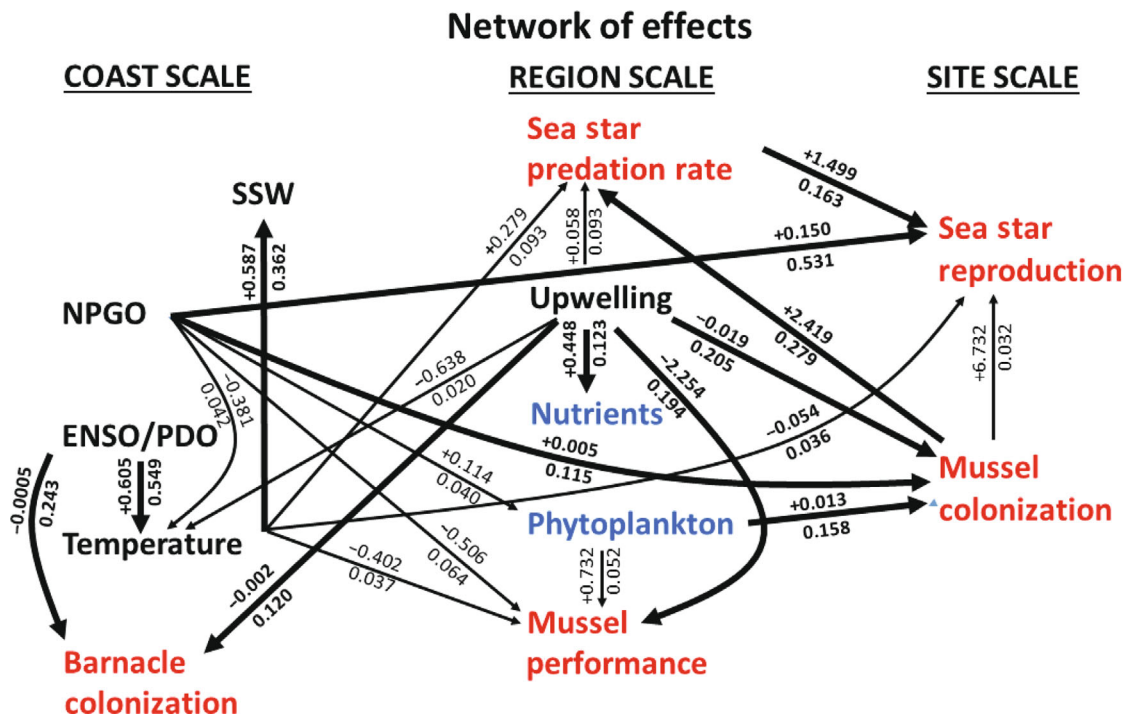

FIGURE 11 Network of effect summarizing results of study based on multiple regressions with each metric as the response variable and all factors that could logically influence each as independent variables. Arrows point to the variable affected. Metrics are arranged by the scale at which they vary the most, with coastal scale encompassing all regions and sites (~spanning 200–300 km), region (cape) scale (~37–75 km), and local (site) scale (~1–15 km). All links shown were statistically significant at $p < 0.05$. Numbers above each line are partial regression coefficients and those below the line are adjusted R^2. Environmental effects (climate, temperature, upwelling, sea star wasting) are shown in black text, bottom-up effects are in blue, and ecological processes in red. Thick lines show the effects with adjusted $R^2 > 0.100$ and thin lines show the effects with adjusted $R^2 < 0.100$.

averages appear to have blurred the shorter-term responses in SSW to temperature, which were strongly associated with colder, not warmer monthly temperatures. Similar issues likely explain the lack of links between SSW and predation rate and sea star reproduction.

The lack of a link between nutrients and phytoplankton is likely to be a consequence of the interaction between these two metrics and continental shelf width and how this modifies coastal currents (see figure 8 in Menge et al., 2015). Shelf width has a negative effect on upwelling strength leading to knock-on reductions in DIN. Basically, a wide shelf off Region 3 causes weakening of near-coast currents, and thus retention of, and high levels of larvae and their food, phytoplankton, blooms of which are huge and deplete nutrients very quickly (leading to an inverse relationship with DIN). In contrast, despite a narrow shelf in Region 5, relatively high levels of Chl *a* also can occur, but these blooms are more likely to be due to the upwelling "shadow" effect south of the Cape Blanco promontory (e.g., Graham & Largier, 1997) than to a modification of upwelling, which is strong in this region. Because nutrients tend to be high in Region 5 (due to strong upwelling) and low in Region 3 (due to rapid use by phytoplankton), these effects are likely to be offset, leading to no relationship between nutrients and phytoplankton in the multiple regressions.

Broader implications

To what extent do our results inform broader discussions of the impact of climate change on Earth's ecosystems? With respect to bottom-up changes, the evidence is mixed but mostly negative. Using satellite-derived estimates of ocean color, Behrenfeld et al. (2006) reported declining global ocean phytoplankton abundance but, more recently (Behrenfeld et al., 2016) indicated that compensatory physiological responses (photo-acclimation) could alleviate these changes by expanding the volume available in the ocean for photosynthesis. Marinov et al. (2010) modeled phytoplankton community structure in relation to nutrients, temperature and light and found that between 45° N and 45° S, declining nutrients and warming led to stronger decreases in (larger) diatoms than in small phytoplankton. On land, future productivity is predicted to decrease in all but cold-temperate regions, with strong negative effects of decreasing

precipitation and increasing maximum temperature (Cao et al., 2021). Although increasing CO_2 has been proposed as potentially beneficial to primary production, recent evidence has suggested that this effect actually has declined since 1982–1996 (Wang et al., 2020).

At higher trophic levels, prediction is difficult due to complexities such as species-level variation in response to the multiple effects of climate change, interactions with other species, the possibility of adaptation or movement to more favorable environments, and many other factors (e.g., Gilman et al., 2010). However, key dominant marine species (e.g., mussels, corals, kelp) have already undergone changes in distribution and abundance in some regions, with likely negative consequences for their consumers or their inhabitants (e.g., Hughes et al., 2017, 2018, 2019; Jurgens et al., 2015; Krumhansl et al., 2016; Munday et al., 2008; Rogers-Bennett, 2007; Rogers-Bennett & Catton, 2019; Sorte et al., 2017; Thomsen et al., 2019; Wootton, 2016). Conversely by buffering oscillations in prey abundance, predators may in some cases mitigate the effects of climate change that lead to boom/bust dynamics (Sala, 2006; Wilmers & Getz, 2005). Much remains to be learned about the long-term impacts of climate change on higher trophic levels as well as lower levels.

CONCLUSIONS

The implications of our results are of serious concern. Our impressions over the decades of research conducted by our group were that this system was resilient and resistant to the progressive changes in climate. Part of this sense was that the system and its component taxa have evolved in an environment that is highly stressful in terms of the physical forces of often large waves, especially in winter, and the thermal challenges often arising during low tides, especially in spring and summer. Further, over the senior author's decades of experience, and that of other researchers conducting long-term research in this system (e.g., Paine, 1994; Paine et al., 2017; Paine & Trimble, 2004; Wootton, 2016; Wootton et al., 2008), many massive disturbances to mussel beds have occurred with eventual full recovery. Our recent work (Menge et al., 2022; this paper) and that of Raimondi et al. (2019) and Miner et al. (2021) suggest that recent environmental shocks may have pushed the system closer to a state from which full recovery may not be possible, at least within the (possibly shortening) time period between major acute disturbances. The changes that have occurred in this system so far have not compromised community appearance (i.e., mussels remain a dominant space occupier at sites they have long dominated, sea stars are rebounding from mass SSW-caused mortality). However, our results suggest that the system may be headed in a direction (loss of mussels, reduced predator abundance) that has already occurred in the New England rocky intertidal zone (Jones et al., 2009, 2010; Sorte et al., 2017) and Southern California (Miner et al., 2021). With the increase of similar catastrophic losses suggested by other recent events (Hamilton et al., 2021; Jurgens et al., 2015; Rogers-Bennett, 2007; Rogers-Bennett & Catton, 2019; Sanford et al., 2019; Thomsen et al., 2019), coastal ecosystems are clearly under assault by climate change. We are encouraged by recent political actions for intensified efforts to attenuate climate change, and hope it is not too late.

AUTHOR CONTRIBUTIONS

Bruce A. Menge designed the research, conducted research, managed and analyzed data, and wrote the paper; Sarah A. Gravem conducted research, managed and analyzed data, and edited the paper; Jonathan W. Robinson conducted research, processed samples, generated data, oversaw collection of data, managed data and edited the paper; Brittany N. Poirson conducted research, processed samples, generated data, oversaw collection of data, managed data, and edited the paper.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Menge et al., 2022) are available in Dryad at https://doi.org/10.5061/dryad.7m0cfxpxj. Climate data obtained from National Centers for Environmental Information (Pacific Decadal Oscillation, http://www.

ncei.noaa.gov/access/monitoring/pdo/), Di Lorenzo et al. (2008) (North Pacific Gyre Oscillation, http://www.o3d.org/npgo/npgo.php), and the National Oceanic and Atmospheric Administration Physical Sciences Laboratory (Multivariate El Niño Index, https://psl.noaa.gov/enso/mei/).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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