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A unified meta-ecosystem dynamics model: Integrating herbivore-plant subwebs with the intermittent upwelling hypothesis

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Abstract

Determining the relative influence of biotic and abiotic processes in structuring communities at local to large spatial scales is best understood using a biogeographic comparative-experimental approach. Using this approach, previous work suggests that intertidal community dynamics (top-down and bottom-up effects) vary unimodally along an upwelling-based productivity gradient, termed the Intermittent Upwelling Hypothesis (IUH). Evidence consistent with the IUH comes from the sessile invertebrate/predator (SIP) subweb in certain rocky intertidal communities, but whether this pattern extends to macrophyte/herbivore (MH) subwebs is unknown. Here we ask: Are MH subwebs also structured as predicted by the IUH? What is the relative importance of herbivory and predation in structuring these communities? Under what conditions do ecological subsidies like nutrients or propagule production drive community dynamics? And are omnivorous interactions important? We hypothesize that MH subwebs are driven by a new construct, the Grazing-Weakening Hypothesis (GWH), which states that MH interactions weaken monotonically with increasing nutrients, with strong (weak) herbivory and low (high) macrophyte productivity at low (high) nutrients. We explored local-to-large spatial scale dynamics of both subwebs using a biogeographic comparative-experimental factorial field experiment testing joint and separate effects of herbivores and predators between two continents. Experiments at 10 sites ranging from persistent upwelling to persistent downwelling regimes ran for 26–29 months in Oregon and California, and New Zealand (NZ) South Island. For the MH subweb, results were consistent with the GWH: herbivory declined and macrophytes increased with increasing nutrients. As expected, results for the SIP subweb were consistent with the IUH: predator effect size was unimodally related to upwelling. Overall, herbivory explained more variation in community structure than did predation, especially in NZ. Omnivory was weak, sessile invertebrates outcompeted macrophytes, and ocean-driven subsidies provided the basic template driving ecosystem dynamics. We propose a unified meta-ecosystem dynamics model combining MH and SIP results: with increased upwelling, sessile invertebrates and underlying dynamics vary unimodally (as in the IUH), while herbivory decreases and macrophytes generally increase. While this model was based on research in temperate ecosystems varying in upwelling regime, its wider applicability remains to be tested.

KEYWORDS

biogeographic experiments, bottom-up, comparative-experimental approach, ecological subsidies, Grazing-Weakening Hypothesis, herbivore-macrophyte subweb, Intermittent Upwelling Hypothesis, New Zealand, Oregon, predator–sessile invertebrate subweb, top-down, unified meta-ecosystem dynamics model

INTRODUCTION

The structure and dynamics of ecological communities are driven by biotic and abiotic forces, and research aims to determine the relative impacts of each category and which components of each are preeminent. Among biotic factors, an early focus was on the importance of competition as a determinant of structure (Clements et al., 1926; Connell, 1961; Gleason, 1926; Grinnell, 1917). The trophic cascade concept developed by Hairston et al. (1960) proposed that community structure was controlled by top-down effects: by controlling herbivore abundance, predators facilitated high plant abundance. While this idea was met with skepticism (Ehrlich & Birch, 1967; Murdoch, 1966), events since have provided overwhelming support for the frequency and importance of trophic cascades (e.g., Borer et al., 2005; Carpenter et al., 1985, 1987; Estes & Palmisano, 1974; Power, 1992; Ripple & Beschta, 2012; Ripple & Larsen, 2000; Terborgh & Estes, 2010; Terborgh et al., 2001, 2008).

Another idea was that bottom-up factors, for example, nutrients, determined the abundance and/or diversity of higher trophic levels (Carpenter et al., 1987; Hall et al., 1970; Hunter & Price, 1992; McQueen et al., 1989; Oksanen et al., 1981). This perspective broadened the three-trophic-level, trophic cascade model envisioned by Hairston et al. (1960). Since nutrient-dependent productivity was known to vary, the bottom-up view provided a mechanistic basis for varying numbers of trophic levels or complexity of food webs.

The environment may set the pace of species interactions

The environmental conditions in which a meta-ecosystem is embedded can resolve seemingly contrasting top-down and bottom-up perspectives. In the nearshore temperate marine environment, for example, wind-driven upwelling regimes can be major determinants of coastal currents, nutrient levels, and primary production, and are well-known to have impacts on species interaction magnitude and consequently on community structure (e.g., Bustamante et al., 1995; Hacker et al., 2019; Menge & Menge, 2013; Menge et al., 1997, 2003, 2004, 2015; Navarrete et al., 2005; Sellers et al., 2021). The Intermittent Upwelling Hypothesis (IUH) conceptual framework was proposed to explain how environmental conditions can regulate several components of rocky intertidal ecosystems. On temperate rocky shores, wind-driven upwelling or downwelling currents often regulate key rates of ecological subsidies (nutrients, phytoplankton, and propagules) that ultimately influence the growth rates and abundance of species and alter the strength of top-down control (Menge & Menge, 2013, 2019). In the IUH, high subsidy rates are more likely under intermittent upwelling, when winds and currents alternate between upwelling that brings nutrients to the surface waters, fueling phytoplankton blooms, and relaxation periods during wind cessation or downwelling that moves surface waters shoreward, both of which can hold blooms close to shore (Botsford et al., 2006). A source of variation in coastal oceanic regimes can occur when the upward flow does not reach below the thermocline, as can happen, for example, during El Niño events that deepen the thermocline (e.g., Chavez, 1996). When upwelling events occur at approximately weekly scales, phytoplankton (food) pulses are made available to nearshore shallow-water benthic primary consumers. In contrast, under persistent downwelling or persistent upwelling, rates of subsidy inputs are typically low; persistent downwelling moves nutrient-depleted surface waters shoreward, thereby inhibiting primary production, while persistent upwelling transports nutrients and phytoplankton offshore, making them unavailable to nearshore primary consumers (Botsford et al., 2006). Overall, the IUH suggests that the bottom-up processes of primary productivity are pivotal in all conditions. Evidence consistent with this idea was presented along with its conceptual development and in a recent study of barnacle recruitment in South Africa and Australia (Lathlean et al., 2019). However, IUH-related research thus far has focused only on the sessile invertebrate/predator (SIP) subweb (sea stars/whelks/barnacles/mussels) of intertidal communities. Whether or not the macrophyte/herbivore (MH) subweb (limpets/chitons/snails/micro- and macrophytes) dynamics are also consistent with the IUH, and thus, the importance of the environmental conditions in structuring entire communities, remains untested.

One or two models?

Based on the idea that sessile invertebrates and macrophytes would respond differently to increasing upwelling, Menge and Menge (2013) speculated that the MH subweb diverges from the predictions of the IUH. Theory and evidence, for example, indicates that two ecological subsidies (propagules and phytoplankton) vary unimodally with increasing upwelling (Botsford et al., 2006; Lathlean et al., 2019; Menge & Menge, 2013, 2019). However, a third key subsidy, nutrients, should increase monotonically with increasing upwelling (e.g., Huyer, 1983), likely with different impacts on the MH subweb. That is, steady input of nitrate and other nutrients during upwelling should facilitate uptake by macrophytes, thereby increasing productivity. In concept, this bottom-up effect should flow up through the food web, enabling faster growth and higher densities of herbivores (Oksanen et al., 1981). With trophic feedback, herbivore abundance should also increase monotonically with upwelling. However, time lags inherent in growth responses and recruitment of herbivores will doubtless vary, leading to some uncertainty in how strongly increasing or decreasing abundance of macrophytes and herbivores covary. Furthermore, with high nutrient inputs, macrophyte productivity may at least temporarily swamp the ability of herbivores to respond. Literature evidence (see meta-analysis in Sellers et al. [2020]) suggests that, in fact, swamping of herbivory by high macrophyte productivity may be the rule, and thus that top-down control through herbivory may be stronger at low productivity. This abundance-based analysis is similar to the diversity-based “Grazer-Reversal Hypothesis” (Proulx & Mazumder, 1998), with the difference being the Grazer-Reversal Hypothesis proposes that herbivory reduces diversity, not abundance, in unproductive environments and increases it (thus the “Reversal”) in productive environments. To avoid confusion, we will term the abundance-based hypothesis the “Grazing-Weakening Hypothesis,” or GWH. Ultimately, we are left with competing hypotheses for how top-down control should vary with upwelling; control by predators may vary unimodally (IUH), whereas control by herbivores may decline monotonically (GWH) with upwelling. Testing these competing hypotheses in a single design should facilitate integrating them into a unified theory of meta-ecosystem dynamics that includes both subwebs.

We illustrate these ideas in Figure 1. The top portion shows SIP and MH subwebs, with top-down effects by predators on the former and by herbivores on the latter (thick black arrows). In temperate intertidal systems, bivalves typically dominate competition (open arrows) with subordinate species (e.g., barnacles and macrophytes). Subordinate sessile invertebrates can facilitate the dominant sessile invertebrates (Menge, 1976, 1995; Menge et al., 2011), while among the macrophytes, both competition and facilitation can occur (e.g., Barner et al., 2016). Populations of sessile invertebrates and macrophytes are replenished by recruits/juveniles or spores/sporelings, respectively, which are susceptible to mortality from small predators, bulldozing grazers, and consumption by filter-feeding sessile invertebrates (for the latter two, blue arrows with “-?”). Thus, omnivory (grazers eating barnacles, bivalves eating algal spores) may potentially be a significant process in addition to predation and herbivory. Settling invertebrate recruits can be preemptively excluded by solid stands of macrophytes (black arrow from macrophyte module to juveniles) (Menge, 1976). Furthermore, when extremely dense, phytoplankton blooms can suppress growth of macrophytes (Figure 1a; black arrow from phytoplankton to macrophytes) (e.g., Kavanaugh et al., 2009).

Figure 1 reflects our hypothesis that the IUH applies to the SIP subweb (left side of Figure 1a) while the GWH applies to the MH subweb (right side of Figure 1a). As originally hypothesized, the unimodal dynamics of the IUH are phytoplankton-dependent, while macrophyte dynamics are hypothesized to be nutrient-dependent as determined by the upwelling regime (Figure 1b). As discussed above, macrophyte productivity is proposed to be driven monotonically by nutrient inputs, which, due to swamping effects, cause declining top-down control (i.e., grazing rates) from high levels in downwelling-dominated systems to lower levels in upwelling-dominated systems (e.g., Sellers et al., 2020). Thus, while both subwebs are driven by bottom-up dynamics, each depends on different subsidies.

Integrating SIP and MH subwebs

Experiments testing top-down control typically focus on either herbivore–plant or predator–prey interactions as the direct effect influencing community structure. In aquatic systems, however, consumers are often omnivorous (e.g., Briscoe & Sebens, 1988; Diehl, 1993; France, 2012; Menge & Lubchenco, 1981; Vadas, 1990), and in space-

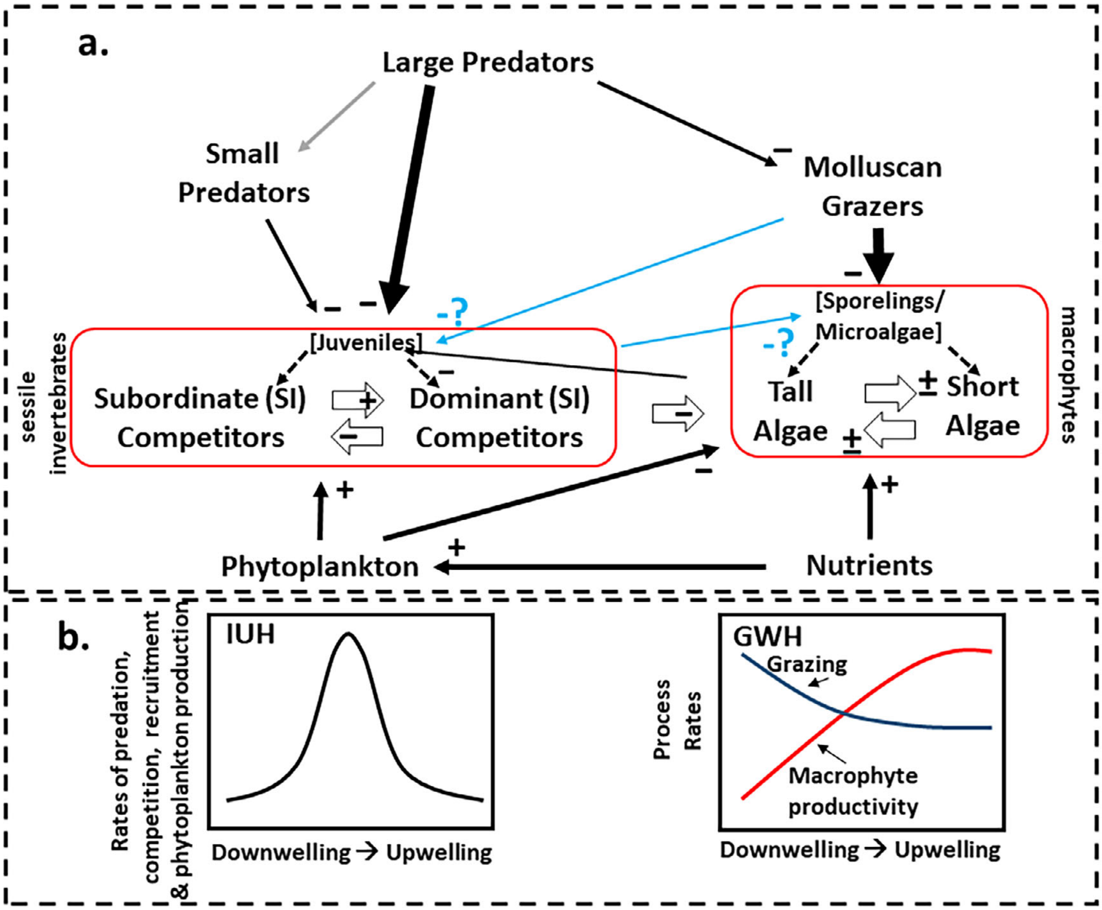

FIGURE 1 Upwelling-driven models of community structure and conceptual links between upwelling and process rates. The top diagram (a) shows the predator–sessile invertebrate and herbivore-macrophyte subwebs and actual or possible interaction links within and between each. Taxa are shown as functional groups. Blue arrows and question marks indicate links of unknown strength. Minus and plus signs indicate negative or positive effects. (b) The lower left diagram shows the predictions of the Intermittent Upwelling Hypothesis (IUH), and the lower right diagram shows the predictions of the Grazing-Weakening Hypothesis (GWH). For the IUH, key rates of interactions and inputs are shown. For the GWH, key process rates are grazing and macrophyte production. SI, sessile invertebrates.

limited systems, the basal level can include both animals and plants (Figure 1a). Here, our focus is on whether or not herbivory and predation interact synergistically, antagonistically, or independently in influencing community structure, and if omnivory links between SIP and MH subwebs are strong.

To examine these possibilities, we used the comparative-experimental approach (Coleman et al., 2006; Dayton, 1971; Freidenburg et al., 2007; McPeek, 1998; Menge et al., 1994, 2019; Rilov & Schiel, 2011). This method uses identically designed and executed experiments carried out at multiple sites along an environmental gradient. To encompass downwelling- to upwelling-dominated environmental regimes, we conducted the research in different large marine ecosystems (LMEs; Sherman, 1991) but at similar latitudes and in communities with functionally and taxonomically similar biotas. Specifically, our nested design included two replicate sites within each of four upwelling regimes arrayed across the coasts of Oregon (OR) and northern California (CA), and the South Island of New Zealand (NZ; Figure 2). We contrasted three regimes: (1) strong but "intermittent" upwelling (i.e., cross-shelf surface) currents alternate between upwelling (seaward) currents and downwelling (landward) currents that occurred in both OR and NZ (central OR and West NZ coasts, respectively), (2) persistent downwelling that occurred in NZ (east coast), and (3) persistent upwelling that occurred in OR (southern coast) and northern CA (see Menge & Menge, 2013; Menge et al., 2003, 2015 and the methods for more oceanographic information). Prior research determined that oceanic conditions can account for up to ~50% of the variance in predator–prey and competitive interactions in these systems (Menge & Menge, 2013) and, in OR, a similar amount of variance in community structure and dynamics (Hacker et al., 2019; Menge et al., 2015).

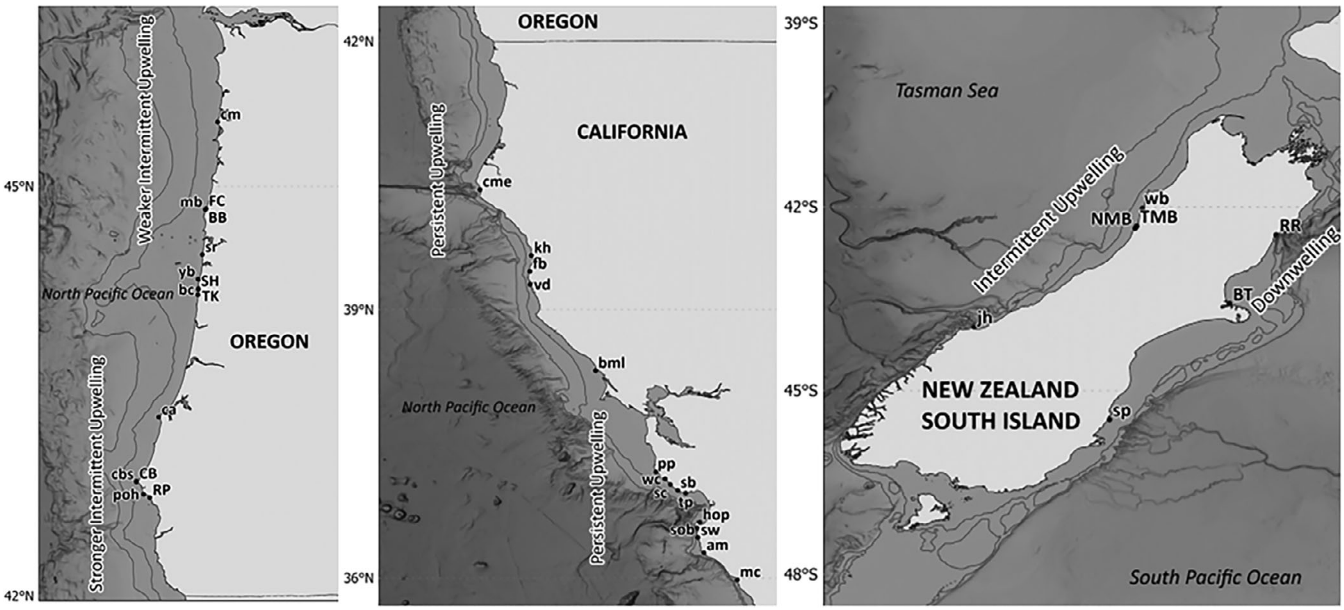

FIGURE 2 Maps showing locations of core (all capital letters) and ancillary (lower case letters) sites in Oregon (OR), California, and New Zealand (NZ) South Island. Core OR sites are Fogarty Creek (FC), Boiler Bay (BB) on Cape Foulweather (CF; northern region), Strawberry Hill (SH), and Tokatee Klootchman (TK) on Cape Perpetua (CP, central region), and Cape Blanco North (CB) and Rocky Point (RP) on Cape Blanco (southern region). Core NZ sites are Twelve-Mile Beach (TMB) and Nine-Mile Beach (NMB) on the intermittently upwelled west coast and Raramai (RR) and Box Thumb (BT) on the predominantly downwelled east coast. See Table 1 heading for names and codes for ancillary sites. All OR sites and regions have intermittent upwelling, but upwelling intensity is greater in the southern region. Note that the latitudes are comparable but in different hemispheres.

Control by consumers or ecological subsidies?

In rocky intertidal communities, top-down control of prey abundance is common but not universal (review in Menge, 2000; also Bryson et al., 2014; Connell, 1961, 1970; Dayton, 1971; Lubchenco & Menge, 1978; Menge, 1976; Menge & Menge, 2013; Paine, 1966, 1974; Sellers et al., 2020). In theory, factors underlying variation in top-down effects can include environmental stress (Bruno et al., 2003; Connell, 1975; Menge & Sutherland, 1987; Silliman & He, 2018) and nutrients/productivity, that is, bottom-up effects (Menge, 2000; Oksanen et al., 1981). Examples of both stress and nutrient/productivity effects on top-down dynamics are available from both LMEs under consideration (e.g., Menge & Menge, 2013; Menge, Olson, et al., 2002; Petes et al., 2008; Sanford, 1999). Here we focus on the nutrient/productivity effects on community structure, having chosen our sites to have similar wave exposures and moderate thermal stress.

Impacts of grazing, mostly by limpets, have also been studied in both systems (Dayton, 1971; Dunmore & Schiel, 2003; Farrell, 1988; Freidenburg et al., 2007; Guerry & Menge, 2017; Harley, 2003; Haven, 1973; Menge, 2000; Menge et al., 1999; van Tamelen, 1996), but generalities are somewhat unclear. For example, at single sites in the Pacific Northwest, limpet grazing was strong in high intertidal zones (above mussel beds; Farrell, 1988; Harley, 2003). Similarly, grazing was strong among multiple mid-intertidal sites (within and just below mussel beds; sites in OR and Washington; Dayton, 1971; Freidenburg et al., 2007). However, in the low intertidal zone (multiple sites in OR; Freidenburg et al., 2007; Menge, 2000), grazing strength varied among capes (10s to 100s of km; strong at two sites with relatively low nutrients, weak at 2–3 sites with higher nutrients). In NZ, in a variety of experiments varying in length (3, 6, and 6 months) and zone (high, mid, and low), limpet grazing was either stronger in persistently downwelled sites than in intermittently upwelled sites in high and low zones (Guerry & Menge, 2017), did not differ between coasts/upwelling regimes (Menge et al., 1999), or was strong in the mid-intertidal on the persistently downwelled east coast (but no experiments were done on the west coast; Dunmore & Schiel, 2003). Hence, overall, grazing impacts varied in strength in both OR and NZ LMEs, but somewhat inconsistently in relation to upwelling regimes depending on the study. Also, variable experiment durations make comparisons of how limpet grazing may be influencing community structure difficult. Finally, the importance of predation may change with geography, so it is possible that these inconsistent findings are influenced by interactive effects of predators and grazers on rocky intertidal communities or, additionally, that consumer size is also important. For example, although whelks and sea stars were of similar size in both systems, limpets were larger in NZ as we document below.

Is omnivory important?

The interaction web modeled in Figure 1a includes examples of trophic-level omnivory (feeding on more than one trophic level), with predators consuming both mobile herbivores and sessile invertebrates, and herbivores consuming primary producers and bulldozing or perhaps consuming juvenile stages of sessile invertebrates (e.g., Dayton, 1971; Hawkins, 1983). Filter-feeders can consume larval barnacles and mussels, as well as algal spores (Alfaro, 2006; Lehane & Davenport, 2004; Santelices & Martínez, 1988). Intraguild predation (e.g., Holt & Polis, 1997; Polis & Holt, 1992) can also occur, with large predators (e.g., sea stars) consuming small predators (e.g., whelks) and both consuming sessile invertebrates. However, sea star consumption of whelks was infrequent in both systems (NZ north island, <1% [Paine, 1971]; four sites on SINZ, 4.8% [11 whelks consumed by 231 *Stichaster australis*; B. Menge, personal observations, 1994–2010]; OR, ~2% or 7 of 377 *Pisaster ochraceus* [Navarrete & Menge, 1996]), so we do not consider intraguild predation further.

Research questions

Tests of the relative impact of herbivores versus predators are rare (but see Lefcheck & Duffy, 2015). Due to favorable organismal size and abundance scales, and compact habitat scales, such tests are probably most feasible in aquatic systems. In these OR, CA, and NZ meta-ecosystems, we ask: (1) Are both subwebs structured as predicted by the IUH? That is, are the dynamics of the MH subweb similar to or different from those of the SIP subweb, or is the MH subweb structured as predicted by the GWH? (2) What is the relative importance of the top-down effects of predators versus herbivores in controlling community structure? (3) Under what conditions are bottom-up or top-down dynamics dominant? (4) Finally, does omnivory influence community dynamics, and link the subwebs, or are the subwebs linked via interactions at the basal level?

METHODS AND MATERIALS

Study systems

Research was done on wave-exposed rocky benches on the OR and northern CA coast, located in the CA Current LME, and NZ, located in the NZ Shelf LME (Figure 2). Experiments were done in OR and NZ, and supplementary data on nutrients and macrophyte cover were obtained in CA by the PISCO consortium. Tidal ranges were 3.0–3.5 m in OR and CA and 2.1 (east coast) to 3.4 m (west coast) in NZ (Appendix S1: Table S1). OR/CA experiences mixed semi-diurnal tides (i.e., successive low or high tides are of unequal height, with one "good" low tide per day during spring tide periods), while NZ tides are semi-diurnal (daily low and high tides are of similar height). Except for Nine-Mile Beach in NZ, sites used in this study have lengthy histories of continuous ecological research, beginning in 1983 in OR, the 1990s in CA, and 1994 in NZ.

Environment

Experiments in NZ and OR were conducted between October 2004 and October 2007 and May 2005 and August 2007, respectively. CA and NZ data on nutrients and chlorophyll *a* (chl *a*) were obtained in 1999–2002 and have been collected in OR continuously since 1999. The research included environmental and ecological measurements and identically designed and conducted experiments in both LMEs, with initiation offset by 6 months so that each was begun in the respective spring in each LME (Appendix S2: Figure S1).

Upwelling regimes and shelf width

Oceanic conditions in the two LMEs have been detailed elsewhere (e.g., Menge & Menge, 2013; Menge et al., 1997, 1999, 2003, 2011, 2015; Schiel, 2004, 2011; Stevens et al., 2021). Briefly, the OR/CA coast is characterized by intermittent upwelling, with a reversing, conveyor belt-like cross-shelf flow pattern (Appendix S1: Table S2). Upwelling events typically deliver temporally varying pulses of cold, nutrient-rich water nearshore, and then via subsequent cross-shore flows to offshore shelf waters, while the alternating downwelling-driven events deliver warmed, nutrient-poor surface waters to the nearshore. Periods between upwelling cessation and downwelling onset are termed "relaxations" and are also conditions that can deliver materials to the coast as the uneven sea level generated by upwelling processes evens up with shoreward water movement. In this study, upwelling was stronger at the southern OR and CA sites, and weaker at the four central OR sites.

Coastal currents interact with shelf width to modify retention of subsidies along the coast (Kirincich et al., 2005). The shelf is relatively wide in the Cape Perpetua (CP) or "central" region (sites SH and TK) and relatively narrow at all other sites (Menge et al., 2015), generating weak and retentive currents in the CP region and stronger, less retentive offshore currents elsewhere (see bathymetry in Figure 2).

In NZ, east coast sites are dominated by persistent downwelling, while west coast sites experience intermittent upwelling (Menge et al., 2003; Appendix S1: Table S2). Shelf width also differs between coasts, being narrow at the east coast sites and wide at the west coast sites (Menge et al., 2003). It thus seems likely that the west coast sites have retentive oceanic regimes for the same reason as those at CP; the wide shelf likely weakens upwelling currents. On the east coast, downwelling flows occur shoreward, so they would also transport particles toward the coast, at least in surface waters.

We quantified upwelling regimes using two measures: a high-resolution (to 0.25° [28 km] latitude) dataset used in analyses of OR and NZ data in which we used the Ekman cross-shelf transport component (e.g., see Close et al., 2020), and in analyses including CA data, the globally available Bakun upwelling index (Bakun, 1975). Units of both are cubic meters of water per second per 100 m of coastline. These metrics were highly correlated ($p < 0.0001$, adj. $R^2 = 0.92$), indicating that using these alternatives should give comparable results. Although an updated upwelling index (CUTI; Jacox et al., 2018) is available for CA Current sites, it has not yet been extended to NZ. We calculated the monthly average upwelling index at each site for the period of study in each LME. Upwelling intermittency was calculated as in Menge and Menge (2013, p. 290 and Appendix B: figs. B2 and B3), and shelf width was determined as detailed in Menge et al. (2015) for both OR and NZ. Data for 100-m isobaths were obtained using the ETOPO1 database (see Appendix S1: Table S2).

Water temperature

Seawater temperature was quantified using Onset HOBO TidBit (Onset Computer, Bourne, MA) replicate temperature loggers ($n = 2$ or 3) placed in situ in the low intertidal zone at each site. Loggers recorded at 15-minute (OR) to hourly (NZ) intervals, which were averaged to daily, then to monthly values for analysis. We used a detiding program (Menge et al., 2003) to separate air from water temperatures (hereafter termed intertidal sea surface temperature, or ISST).

Nutrients and phytoplankton

Nutrients ($NO_3 + NO_2$) and phytoplankton (proxied by chl *a*) were quantified using replicate ($n = 3$–5) bottle samples taken during low tides (see details in Menge et al., 1997, 1999, 2003, 2015). We used data averaged across upwelling months (April–September in OR, October–March in NZ). Nutrient data were only available from 1999 to 2002 for NZ, so we limited our comparisons of nutrients to upwelling months in those years in both NZ and OR.

Prey recruitment

We considered prey recruitment to be an external (environmental) input in our analyses (see below). We quantified barnacle and mussel recruitment using standard collectors to test for associations between recruitment and experimental communities. Barnacle recruitment was determined using 10 × 10 cm PVC plates covered with Saf-T-Walk (3M, Maplewood, MN), a rubbery rugose tape used as an anti-slip surface on boats. Such collectors have been widely used (e.g., Broitman et al., 2008; Dudas et al., 2009; Farrell et al., 1991; Menge, 1992; Menge & Menge, 2013, 2019; Menge et al., 1999, 2003, 2010, 2011, 2015; Navarrete et al., 2005, 2008; Pfaff et al., 2011, 2015) and provide an index of barnacle recruitment. Mussel recruitment was similarly determined using plastic mesh balls (Tuffies), also in wide use (references in previous sentence). Collectors ($n = 5$ replicates each) were placed in the lower mid-intertidal zone near the experiments at all sites in both LMEs and replaced monthly in OR and monthly to quarterly in NZ. Samples were processed in the laboratory by counting recruits under a microscope. Barnacle recruits could usually be identified to species, but OR mussel recruits were difficult to identify to species, likely included both *Mytilus californianus* and *M. trossulus*. NZ mussel recruits of *Perna canaliculus* and *A. ater maioriensis* were distinguishable, but *Mytilus galloprovincialis* and *Xenostrobus pulex* are very similar. In analyses, we combined all acorn barnacle and mussel recruits as "barnacle recruits" and "mussel recruits," respectively. We used data from the recruitment seasons (~April–November in OR, October–March in NZ) for 2003 through 2006.

Similar biota and functional roles among systems

The biota in each LME consisted of similar groups, including some of the same genera, but few species occurred in both LMEs (Appendix S1: Table S3). Each LME had similar functional groups of macrophytes, sessile invertebrates (mytilid mussels, acorn, and stalked barnacles), grazing herbivores (limpets and chitons), and predators (whelks and sea stars). Furthermore, each functional group consisted of morphologically similar species; both LMEs had larger and smaller species of mussels and barnacles, limpets and whelks of similar size and appearance, and similar apex sea star predators known to be dietary generalists and to consume similar prey (for details, see Menge et al., 1994, 1999, 2003; Navarrete & Menge, 1996; Novak, 2010, 2013; Paine, 1971; Schiel, 2004, 2011). A few taxa occurred in, or were abundant in, one system but not the other. For example, (1) surfgrass (e.g., *Phyllospadix* spp.) does not occur in NZ (but did not colonize our OR plots); (2) gooseneck barnacles *Pollicipes polymerus* are abundant in OR, but comparable stalked barnacles *Calantica villosa* and *C. spinosa* were sparse at NZ sites and mostly restricted to cryptic habitats; (3) the large chiton *Katharina tunicata* is abundant in OR, but similar-sized chitons (e.g., *Eudoxochiton nobilis*) were sparse at our NZ sites; and (4) herbivorous fish and crabs can have effects at some sites in NZ (e.g., Rilov & Schiel, 2006; Taylor & Schiel, 2010). We have never observed crabs at our NZ sites, nor have we seen evidence of their activity or that of fish (e.g., broken or cracked mussel shells or bitten off barnacles), so we feel it unlikely they had effects in our experiments. Crabs are sparse at our OR/CA sites, and possible fish predators seem restricted to calmer waters, and again, we have seen no signs of predation by these taxa at our sites. Despite these differences, the similarities remain striking, and researchers familiar with one system quickly become comfortable working in the other.

In this study, because few species occurred in both systems, we focused on interactions at the functional-group or "trait-based" level. The taxa listed in Appendix S1: Table S3 were sorted into 10 functional groups, including crustose algae, filamentous algae, turf-forming algae, blade-forming algae, large brown algae, chthamaloid barnacles, balanoid barnacles, gooseneck barnacles, mussels, and "other" (consisting mostly of sea anemones).

Community patterns among upwelling regimes

Abundances

To provide the broader community context for the experiments, at all sites we quantified community structure, defined as abundance of sessile and mobile species, using three methods. In NZ, we conducted horizontal (i.e., parallel to the water's edge) transect-quadrat surveys for sessile organisms and small mobile organisms (e.g., Lubchenco & Menge, 1978; Menge, 1976). In OR and CA, we conducted vertical transect-quadrat surveys (i.e., perpendicular to water's edge, spanning the intertidal zones). In the horizontal transect-quadrat method, 0.25 m^2 quadrats divided into 0.04 m^2 subquadrats were placed at 3-m intervals along 30-m transect tapes placed in the center of the low-mid zone (i.e., the ~1 m-wide zone just below mussel beds) parallel to the water's edge. Abundance, quantified as percent cover of all sessile taxa, was estimated from photographs using the subquadrats (each covering 4% of the 100% of the quadrat area) as a guide to facilitate abundance scaling to the 1% level. Mobile organisms were then counted in each 0.25 m^2 quadrat to provide density estimates. Mobile organism abundance estimates in vertical transect-quadrat photographic surveys (OR, CA) were done similarly; although transects ran from the low-mid zone to the high zone, we used only data from the low zone (i.e., the ~1 m below the mussel bed). In OR and NZ, we also used larger belt transects in areas of sea star habitat (typically just below mussel beds or in channels) to quantify sea star abundance (e.g., Menge et al., 2011, 2016). Belt transects consisted of replicated 2 × 10 or 2 × 5 m plots placed parallel to the water's edge in which all sea stars were counted, weighed, and measured. Here, we present averages of percent cover data across 2015–2020 (6 surveys, OR and CA) and 1995–2016 (11 surveys, NZ), small mobile species (including limpets and chitons) density data from 2006 to 2016 (11 surveys, OR) and 2008 to 2016 (3 surveys, NZ), and sea star density data from 2005 to 2007 (3 surveys, OR), and 2000 to 2019 (4 surveys, NZ).

Limpet size

Because herbivore size could be related to herbivore impact as well as herbivore density, we quantified limpet size using two methods. In NZ, we measured species-specific limpet length directly in the field at each site using rulers and calipers. All accessible limpets (some were in crevices) in the vicinity of each transect were measured with the goal of measuring at least 200 individuals of each species. In OR, we measured limpets in photographs of experimental treatments (see below) using rulers placed at the edge of each plot as a scale. We used photographs taken in the second year of the experiment (i.e., after limpets recolonizing plots had grown to sizes like those of limpets in the vicinity) to ensure that sizes were representative.

Comparative experiments testing top-down control among upwelling regimes

Experimental timing

In OR, the experiments testing predator × herbivore effects started in May 2005 at six sites, two each in three regions (from north to south, Capes Foulweather [hereafter northern region], Perpetua [central region], and Blanco [southern region]). In NZ, experiments began in October 2004 at four sites, two each on East and West coasts. Depending on the site, and how quickly an endpoint was reached (i.e., when little change occurred during several consecutive monitoring visits), experiments ran for 21–26 months in OR and 22–29 months in NZ (Appendix S2: Figure S1). Although sampling was often monthly, for easier analysis and comparison, we averaged samples by season (termed a "sample period") in each LME with OR sample periods lagged 6 calendar months after NZ sample periods. In sample periods 2–7, seasons were summer, fall, winter, spring, summer, and fall. Because recovery was slow on the NZ East coast, the last two sample periods (8 and 9) were 6 and 12 months long (Appendix S2: Figure S1).

Experimental design

All experiments were established in the lower mid zone, transitional between typically mussel-dominated mid zones and algal-dominated low zones. Plots ranged in tidal height from about 0.8 to 1.8 m (Appendix S1: Table S1). Reflecting the different tidal range between NZ east and west coasts, experiment heights were slightly lower at east coast sites than at west coast sites (Appendix S1: Table S1). The basic unit was a 25 × 25 cm square experimental plot, which was cleared of all biota using scrapers and wire brushes. Oven cleaner (NaOH) was then applied to remove most of the remaining algal and animal tissue. Treatments were (1) controls that allowed herbivore and predator access (abbreviated = +H+P), (2) predator exclusion (herbivores present, predators absent = +H−P), (3) herbivore exclusion (herbivores absent, predators present = −H+P), and (4) consumer exclusion (herbivores absent, predators absent = −H−P). Three control treatments, all +H+P, were included. To control for stainless-steel fences and antifouling paint (see below), we used partial (two-sided) fence controls (FC) and partial (strips with gaps) paint control barriers (PC). Plots with stainless steel lag screws at each corner served as marked plot controls (MP). MPs, FCs, and PCs allowed entry by limpets, chitons, whelks, sea stars, and crabs. The efficacy of the paint exclusion and fence methods to exclude or allow entry by limpets, the main herbivore group, was high (Appendix S2: Figures S2 and S3). Limpets were abundant in control (+H+P) and predator effect treatments (+H−P), and low in herbivore effect and consumer effect treatments (−H+P and −H−P). The design was blocked, with each block including all treatments, and with five replicate blocks per site. Blocks were spaced out on the shore, with 3–10 m between each block.

Predator effects (+H−P) were tested by fastening four-sided stainless steel mesh fences or "open cages." Fences hindered entry by certain benthic predators (whelks, sea stars; but not crabs or fish) but allowed grazers (limpets, chitons) to enter (by crawling underneath cage edges) or recruit to the cages. Those few whelks entering cages (species shown in Appendix S1: Table S3) were removed at each monitoring visit. The only sea stars found in OR cages were one *Pisaster ochraceus* at SH (once) and occasional *Leptasterias* sp. at FC. No sea stars were found in NZ cages during monitoring visits.

Herbivore effects (−H+P) were tested by attaching a 3- to 5-cm-wide strip of Z-Spar (Pettit Paint A-788 Splash Zone marine epoxy) around each plot, smoothing the edges to ensure a continuous smooth surface was available to grazers, and applying a layer of copper-based antifouling paint (Coastal Copper 250 Ablative Antifouling Bottom Paint, 1st Marine Products) (e.g., Figure 3). Prior research has shown that this effectively excludes limpets but does not impede whelks, sea stars, or crabs (Cubit, 1984; Freidenburg et al., 2007; Guerry, 2008; Guerry & Menge, 2017; Guerry et al., 2009; Menge, 2000). Herbivorous snails (e.g., species shown in Appendix S1: Table S3) are also not deterred by the paint, but at all OR and NZ sites, they were either sparse (*Tegula*, *Lunella*, *Melagraphia*, and *Diloma*) and/or very small and unlikely to have much effect (littorines, *Risselopsis*). Consumer effects (−H−P) were tested by combining paint strips and stainless-steel fences (e.g., Figure 3). Fences were attached to the rock and then surrounded by the Z-spar/paint barriers.

After initiation, abundances in plots were determined visually in the field or photographically during each monitoring visit by the senior author. Because prior experiments showed that changes were typically initially rapid and slowed over time, the frequency of visits varied, ranging from monthly during the first months of the experiment and extending to 3 (OR) to 12 (NZ) months. During monitoring visits, we removed invading grazers or predators from exclusion plots, repainted barriers as needed, and repaired damaged cages. In total, we analyzed 4711 samples across all combinations of LME ($n = 2$) × region ($n = 5$) × site ($n = 2$ per region) × treatments ($n = 6$) × replicates ($n = 5$) × sample dates (7–9 in NZ, 17–19 in OR, depending on region).

Data analysis

To organize our results and categorize datasets, we have assembled each according to region, inclusive dates, the sites used, and in which figure(s) and/or table(s) analyses each dataset was used in Table 1. The table heading lists

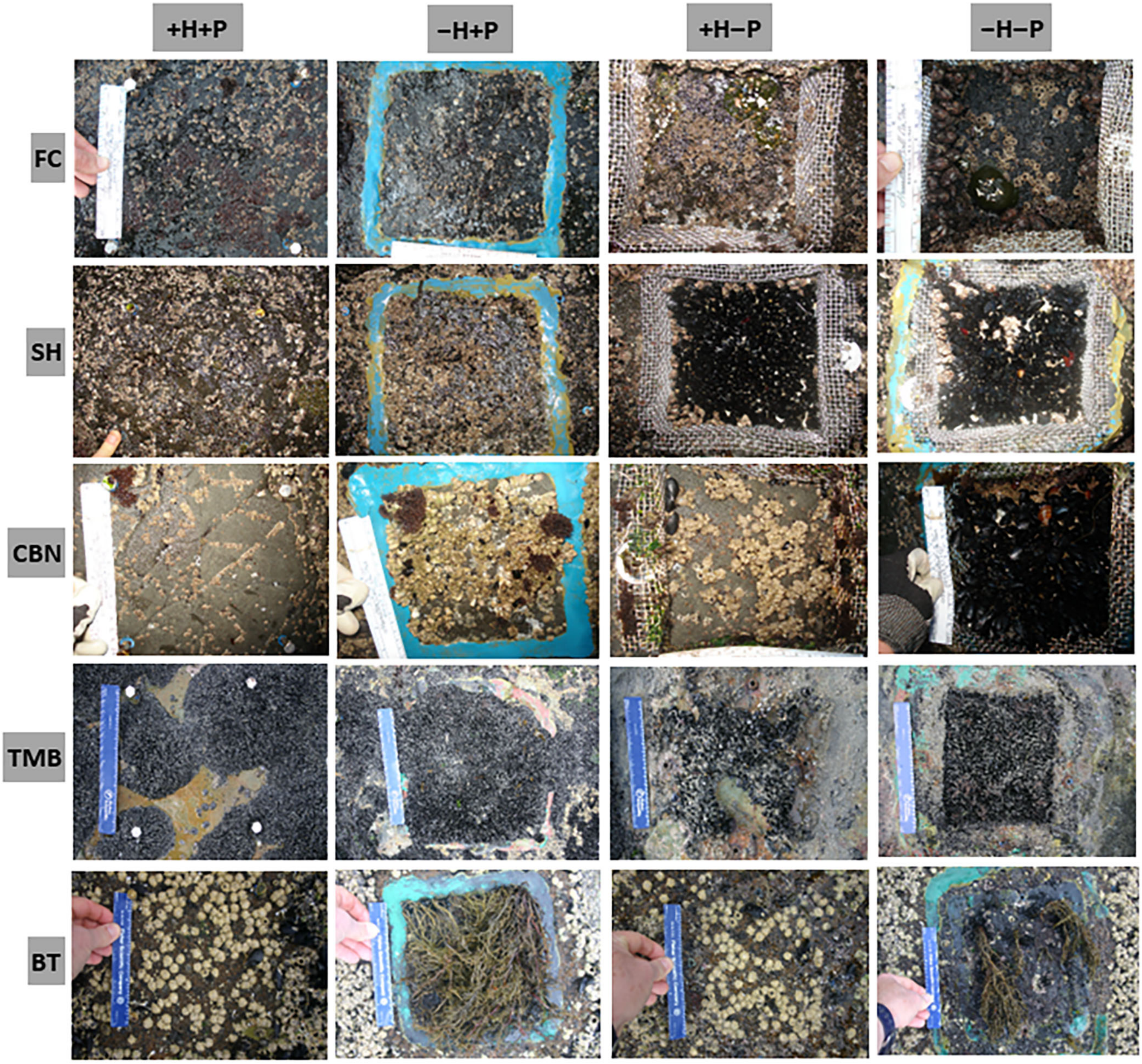

FIGURE 3 Photos of treatment examples at one site per region in Oregon and New Zealand. See Figure 1 for site codes and text for treatment codes. Organisms visible in photos include acorn barnacles (tan to white in most photos), mussels (black organisms in SH, CBN, and TMB photos), and brown algae (BT photos). From top to bottom rows, respectively, visible devices are lag screws of marked plots, paint squares excluding herbivores, fences excluding predators, and paint and fences excluding predators and herbivores. BT, Box Thumb; CBN, Cape Blanco North; FC, Fogarty Creek; SH, Strawberry Hill; TMB, Twelve-Mile Beach. Photo credit: Authors Menge, Richmond, and Noble.

all sites used, including core sites in each region and sites from which supplementary data were collected.

Data were analyzed using JMP v16.1.0 (SAS Institute, Inc., 2021–2022), PRIMER 7, and PERMANOVA+ for PRIMER (Anderson & Gorley, 2008). We used natural log-transformed data (ln $(x + 1)$) in JMP analyses and square root transformations in PRIMER analyses. We chose not to use arc-sine transformations because percent covers could range >100% due to algal layering or overgrowth. Factors in the PERMANOVA model included the nested spatial effects crossed with the time and treatment effects, including LME (large-scale effects of OR and NZ as a random factor), region nested within LME (mesoscale effects of cape or coast as a random factor), and site nested within region (local-scale effects of site, often as a random factor), predator treatment, herbivore treatment, time point, and their interactions. Because large LME effects masked the experimental effects of

TABLE 1 Summary of datasets by region, date, specific sites sampled, and analyses in which the datasets were incorporated.

Dataset	Region	Dates	Sites	Analyses in:
Experiment	Oregon	May 2005–August 2007	Core sites	Figures 5, 6, 8–11, 13; Appendix S2: Figures S14–S16, S20, S21; Appendix S1: Tables S5–S8, S11
	New Zealand	October 2004–October 2007	Core sites	Figures 5, 7–11, 13; Appendix S2: Figures S17, S18, S20, S21; Appendix S1: Tables S5–S7, S9, S11
Upwelling	Oregon	July 2005–August 2007	Core sites	Figures 8, 10–13; Appendix S2: Figures S7 and S19; Appendix S1: Tables S10 and S11
	New Zealand	December 2004–October 2007	Core sites	Figures 8, 10–13; Appendix S2: Figure S19; Appendix S1: Tables S10 and S11
Shelf width	Oregon		Core sites	Appendix S1: Tables S2 and S10; Appendix S2: Figure S19
	New Zealand		Core sites	Appendix S1: Tables S2 and S10; Appendix S2: Figure S19
Water temperature	Oregon	July 2005–August 2007	Core sites	Figure 8; Appendix S2: Figures S5 and S19; Appendix S1: Table S10
	New Zealand	December 2004–October 2007	Core sites	Figure 8; Appendix S2: Figures S5 and S19
Nutrients & Phytoplankton	Oregon	April–September 1999–2002	Core sites + CM, MB, SR, YB, BC, CA, CBS, POH and CA sites CMe, KH, FB, VD, BML, PP, WC, SC, SHB, TP, Hop, SWC, Sob, AM, MC	Figure 12; Appendix S2: Figures S6 and S7
	New Zealand	October–March 1999–2002	Core sites + SP, JH, and WB	Figure 12; Appendix S2: Figures S6 and S7
Prey recruitment	Oregon	April–November 2003–2006	Core sites	Figure 8; Appendix S2: Figures S8 and S19; Appendix S1: Table S10
	New Zealand	October–March 2003–2006	Core sites	Figure 8; Appendix S2: Figures S8 and S19; Appendix S1: Table S10
Community structure surveys				
Percent cover	Oregon and California	Summer 2015–2020	Core sites plus CA sites	Figure 3; Appendix S2: Figure S9
	New Zealand	Summer 1995–2016	Core sites + SP, JH and WB	Figure 4; Appendix S2: Figure S10
Small mobile species	Oregon	Summer 2006–2016	Core sites	Figure 3
	New Zealand	Summer 2008–2016	Core sites	Figure 4
Sea stars	Oregon	Summer 2005–2007	Core sites	Figure 3
	New Zealand	Summer 2000–2019	Core sites	Figure 4
Limpet size & density	Oregon	July 2006–August 2007	Core sites	Figure 8; Appendix S2: Figures S2, S11, S13, S19; Appendix S1: Table S10
	New Zealand	October 2008	Core sites	Figure 8; Appendix S2: Figures S3, S12, S13, S19; Appendix S1: Table S10

Note: Core sites in Oregon were Fogarty Creek (FC), Boiler Bay (BB), Strawberry Hill (SH), Tokatee Klootchman (TK), Cape Blanco North (CBN), and Rocky Point (RP); those in New Zealand were 12-Mile Beach (TMB), Nine-Mile Beach (NMB), Raramai (RR), and Box Thumb (BT). Additional sites in Oregon were Cape Meares (CM), Manipulation Bay (MB), Seal Rock (SR), Yachats Beach (YB), Bob Creek (BC), Cape Arago (CA), Cape Blanco South (CBS), and Port Orford Heads (POH). California sites included Cape Mendocino (CMe), Kibesillah Hill (KH), Fort Bragg (FB), Van Damme State Park (VD), Bodega Marine Lab (BML), Pigeon Point (PP), Waddell Creek (WC), Scott Creek (SC), Sandhill Bluff (SHB), Terrace Point (TP), Hopkins Marine Station (Hop), Stillwater Cove (SWC), Soberanes Point (Sob), Andrew Molera State Park (AM), and Mill Creek (MC). Additional New Zealand sites were Shag Point (SP), Jackson Head (JH), and Woodpecker Bay (WB).

interest, we ran subsequent PERMANOVAs for each LME (as above without LME). Estimates of variance components converted into percent variance explained (see Table 2 footnote) were used to examine the relative importance of each factor and interaction. We visualized temporal changes in experimental communities using nonmetric multidimensional scaling (nMDS) to plot centroid-based vectors of averaged consumer treatments among sites through time to show community development patterns.

Inclusion of block and all three control treatments in the overall analysis did not allow the model to run due to insufficient degrees of freedom. We therefore conducted preliminary analyses testing for differences among the three control treatments and found no differences among them either as main effects or in interactions (Appendix S1: Table S4). Similarly, we tested block (i.e., replicate) effects and found it was not significant as a main effect or in most interactions except (the Site(Region(LME)) × Block interaction; $p = 0.0001$, 11.6% of the variance; Appendix S1: Table S5). This decision likely made our relevant analyses conservative, with some factors identified as not significant when in fact they might have been.

We used two methods to estimate effect sizes of top-down control, assess upwelling regime influences on these effect sizes, and determine if results vary with procedure. In Method One, we conducted nMDS on functional group abundances by site and treatment (averaging MP, PC, and FC to obtain a single value for the +H+P treatment) and saved *x* and *y* coordinates for centroids of each by treatment and replicate (control [+H+P], herbivore effect [−H+P], predator effect [+H−P] and consumer effect [−H−P]). We used these coordinates to calculate vector distances between control and exclusion treatments, which served as our estimate of effect size. We visualized the association between all site-by-treatment combinations in 2D space using nMDS and overlaid environmental metrics to assess the relationship between each site-by-treatment combination and the environment. Finally, we regressed herbivore, predator, and consumer effect sizes against upwelling to determine if the experimental results were consistent with expectations of the combined IUH/GWH model (Figure 1).

In Method Two, we summarized temporal variation in community structure in each treatment and site by calculating how individual functional groups varied during the experiment. After square-root transforming percent cover of all functional groups, we standardized each to its maximum value, then took the average across the groups by each replicate, site, treatment, and sample period to calculate a community index. We then examined linear, quadratic, and cubic regressions (by site and treatment) for the average community index versus time and found that cubic regressions provided the best fit to the data. Next, we used the second-order coefficient (i.e., the slope) of the cubic regressions to estimate the effect sizes of herbivore exclusion, predator exclusion, and consumer exclusion, and plotted the slopes against the average Bakun upwelling index at each site. We also plotted the third-order coefficient versus upwelling to determine the rate of deceleration or acceleration of the effects of each consumer group. To visualize which taxa were most closely associated with patterns observed in the cubic regressions, we used nMDS and plots of temporal changes for each functional group.

We used principal coordinates analysis to ordinate the environmental regimes (upwelling, intermittency, shelf width at 100-m depth, ISST, mussel and barnacle recruitment, limpet density, and shell length) to determine which environmental factors were most closely associated with each site. We assessed the association between average experimental results using nMDS with an overlay of environmental factors and distance-based linear models (DistLM).

RESULTS

Environmental conditions

A detailed comparison of upwelling regimes can be found in Menge and Menge (2013). Below, we summarize upwelling conditions at each site during this experiment, and brief summaries of seawater temperature, nutrients, phytoplankton abundance, and prey recruitment that we later used to investigate whether the upwelling regime affected intertidal communities.

Upwelling, upwelling intermittency, and shelf width

The most strongly upwelled experimental sites were located in southern OR (Appendix S1: Table S2). Levels of (intermittent) upwelling at the central and northern region sites were comparable to those on the NZ west coast. NZ east coast sites were strongly downwelled. Intermittency was greatest on the NZ west coast, next highest in southern OR, similar in the central and northern OR regions, and lowest on the NZ east coast. Shelves were widest in central OR, similar in northern OR and the NZ west coast, lower in the southern OR, and narrowest on the NZ east coast, especially RR.

TABLE 2 PERMANOVA test of spatial effects (LME, Region nested within LME, Site nested with Region nested within LME), herbivory and predation, and time period.

Source	df	SS	MS	Pseudo-F	P (perm)	Unique perms	Factor	Variance components	Percentage of variance explained
Main effects									
LME	1	69,023	69,023	4.68	0.097	60	Random	16.1	9.42
Region (LME)	3	58,301	19,437	2.23	**0.046**	9543	Random	9.6	5.62
Site(Region [LME])	5	47,319	9463.7	65.5	**0.0001**	9910	Random	12.2	7.14
Time	8	1.62E+05	20,277	4.77	**0.0057**	9914	Fixed	17.0	9.95
Herbivory	1	46,282	46,282	4.92	0.34	6	Fixed	13.2	7.72
Predation	1	13,427	13,427	2.58	0.50	6	Fixed	6.3	3.69
Two-way interactions									
Herbivory × Predation	1	1408.6	1408.6	4.77	0.2	199	Fixed	3.3	1.93
LME × Time	8	34,040	4255.1	3.24	**0.0001**	9903	Random	10.3	6.03
LME × Herbivory	1	9407.9	9407.9	3.03	0.14	9920	Random	7.7	4.51
LME × Predation	1	5205.4	5205.4	6.61	**0.037**	9897	Random	6.5	3.80
Time × Herbivory	8	21,262	2657.7	5.73	**0.004**	9942	Fixed	8.9	5.21
Time × Predation	8	6970.8	871.35	1.93	0.09	9950	Fixed	3.9	2.28
Region (LME) × Time	22	39,353	1788.8	1.74	**0.0056**	9887	Random	6.6	3.86
Region (LME) × Herbivory	3	12,158	4052.5	4.19	**0.021**	9938	Random	7.3	4.27
Region (LME) × Predation	3	2979.7	993.23	0.55	0.82	9956	Random	−3.7	−2.17
Site(Region [LME]) × Time	36	36,172	1004.8	6.95	**0.0001**	9811	Random	9.9	5.79
Site(Region [LME]) × Herbivory	5	5184.7	1036.9	7.18	**0.0001**	9921	Random	5.3	3.10
Site(Region [LME]) × Predation	5	9677.4	1935.5	13.40	**0.0001**	9915	Random	7.6	4.45
Three-way interactions									
LME × Herbivory × Predation	1	295.52	295.52	0.396	0.71	9966	Random	−2.9	−1.70
LME × Time × Herbivory	8	3710.5	463.81	1.06	0.45	9952	Random	1.3	0.76
LME × Time × Predation	8	3615.1	451.89	2.21	**0.022**	9952	Random	4.2	2.46
Time × Herbivory × Predation	8	1032.4	129.06	1.06	0.46	9955	Fixed	0.7	0.41
Region (LME) × Time × Herbivory	22	12,317	559.88	3.86	**0.0001**	9917	Random	6.9	4.04
Region (LME) × Time × Predation	22	5034.2	228.83	0.72	0.85	9903	Random	−3.2	−1.87
Region (LME) × Herbivory × Predation	3	2816	938.66	1.22	0.36	9940	Random	2.4	1.40
Site(Region [LME]) × Time × Herbivory	36	5128.9	142.47	0.99	0.52	9806	Random	−0.7	−0.41
Site(Region [LME]) × Time × Predation	36	11,277	313.25	2.17	**0.0001**	9834	Random	6.2	3.63
Site(Region [LME]) × Herbivory × Predation	5	4116.3	823.26	5.70	**0.0001**	9941	Random	6.6	3.86
Four-way interactions									
LME × Time × Herbivory × Predation	8	978.6	122.32	0.76	0.68	9950	Random	−2.4	−1.40

(Continues)

TABLE 2 (Continued)

Source	df	SS	MS	Pseudo-F	P (perm)	Unique perms	Factor	Variance components	Percentage of variance explained
Region (LME) × Time × Herbivory × Predation	22	3724.2	169.28	1.12	0.37	9920	Random	2.0	1.17
Site(Region [LME]) × Time × Herbivory × Predation	36	5441.5	151.15	1.05	0.37	9848	Random	1.8	1.05
Residual	607	87,698	144.48				Random	12.0	9.42
Total	942	1.0467E+06							

Note: Percent cover data were square root transformed and converted into Bray–Curtis similarities for analysis. The PERMANOVA used Type III (partial) sums of squares with permutation of residuals under a reduced model and 9999 permutations. Fixed effects are summed to zero for mixed terms. LME, region, and site were random and time, herbivory, and predation were fixed. Variance components were estimated as the square root of the estimate for each factor and the residuals. Percent variance explained is the proportion of the sum of variance components made up by each factor × 100. Bold values are significant at $p < 0.05$. Abbreviations: LME, large marine ecosystem; MS, mean square; SS, sums of squares.

Water temperature

In OR, mean monthly seawater temperatures were generally cooler but also less variable than in NZ (Appendix S2: Figure S4). Low temperatures occurred both in upwelling seasons, especially June through August, and in winter (December–February). NZ water temperature was highly seasonal with summer highs and winter lows. The NZ west coast variability was more moderate than on the east coast, with winter lows of ~11–12°C and summer highs of ~16–18°C compared to east coast winter lows of ~6–9°C and summer highs of ~14–18°C.

Nutrients

NZ nutrient data were only available from 1999 to 2002, so we limited OR data to those years for comparison (Appendix S2: Figure S5a). Nutrient levels were vastly different between LMEs, ranging from ~11 to 17 μM in OR and from ~1 to −1.5 μM in NZ. This variability is due in large part to differences in upwelling within and between LMEs (Appendix S2: Figure S6a). When OR and NZ sites are combined, nutrient levels increased asymptotically with increasing upwelling (Appendix S2: Figure S6a). Note that in OR, at least, the greatest variability in nutrient levels occurred at the sites with relatively more intermittent upwelling.

Phytoplankton

NZ chl *a* was estimated only from two upwelling seasons between 1999 and 2002 (1999 and 2000, 2001 and 2002), so we limited OR data to the 2000 and 2001 upwelling seasons (Appendix S2: Figure S5b). In OR, as documented previously (Menge et al., 2009), phytoplankton abundance was low in the northern region and high in the central and southern regions. NZ sites had far lower phytoplankton abundance on both west and east coasts. As with nutrients, phytoplankton abundance increased nonlinearly with upwelling but in OR was highly variable regardless of intermittency (Appendix S2: Figure S6b). Abundance of chl *a* increased with increasing nutrients, but this relationship was also highly variable (Appendix S2: Figure S6c).

Prey recruitment

Prey recruitment rates during the study period varied spatiotemporally within and among regions. Excepting NZ east coast sites and TMB on the west coast, magnitudes of barnacle and mussel recruitment were comparable between LMEs (Appendix S2: Figure S7). Barnacle recruitment was relatively high in northern and central OR regions and the NZ west coast compared to the southern OR region and the NZ east coast (Appendix S2: Figure S7a–e). Mussel recruitment rates in OR were similar across regions during this period, while NZ west coast sites had far higher levels of mussel recruitment than NZ east coast sites and OR sites (Appendix S2: Figure S7f–j). At several sites in each region, prey recruitment declined from 2003 to 2006 (Appendix S2: Figure S7a,c,d,f–h and NMB in i).

General patterns of community structure from surveys

Abundances

In OR, community structure varied mostly among regions, as has been reported previously (e.g., Menge & Menge, 2013;

Menge et al., 1994, 1997, 2015). Macrophytes covered most space in northern and southern regions, while sessile invertebrates, especially barnacles, occupied 30%–40% of space in the central region compared to the typical <5% cover at other regions (Figure 4). Free space (bare rock plus encrusting algae) availability was similar across sites, ranging from ~15% to 25%. Limpet abundance was relatively low in the northern region, intermediate in the central region, and the highest in the southern region. Whelk abundances were highest in the central region and similarly abundant in northern and southern regions, while sea star abundances were highest at SH in the central region but generally similar among other sites (Figure 4).

At the functional group scale, several differences between sites within regions emerged (Appendix S2: Figure S8). Large brown algae were more dominant at BB than at FC in the northern region, stalked barnacles (*P. polymerus*) and mussels differed inversely at TK and SH in the central region, and turf-forming and bladed algae differed inversely at CBN and RP in the southern region. The relatively high abundance of mussels at RP was anomalous, occurring at just two of five replicate transects, and likely resulted from the occurrence of sea star wasting in 2014 (B. Menge, personal observations, 1994–2010; S. Gravem, personal observations, 2015–2020).

In contrast, community structure at all NZ sites was dominated by sessile invertebrates, with barnacles dominating east coast site RR, mussels dominating west coast site NMB, and similar abundances of each at east coast BT and west coast TMB (Figure 5). At all sites, macrophytes were relatively sparse and free space availability ranged from ~10% to 30%. Limpet abundances were highest at east coast site RR, similar at east coast BT and west coast TMB, and lower at west coast site NMB, while whelk abundances were highest at NMB and similarly low at the other three sites (Figure 5). As previously reported (Menge et al., 1999, 2003; Menge, Sanford, et al., 2002), sea stars were functionally absent at east coast sites and abundant on the west coast (Figure 5).

At the functional group scale, between-site differences within regions were also observed at NZ (Appendix S2: Figure S9). Mussels were more dominant at NMB than at TMB, while barnacles were relatively sparse at NMB. Not shown in Appendix S2: Figure S9 was sand, which was present on all seven sample dates at NMB (mean cover ±1SE varied from 3.5% ± 2.1% to 34% ± 5%), 4 of 8 sample dates at TMB (4.2% ± 2.7% to 31.7% ± 3.9%), but never at east coast sites (and rarely at OR sites). Similarly, mussel and chthamaloid barnacle abundances were inversely related between east coast sites, with mussels more dominant at BT and chthamaloids more dominant at RR.

Limpet size structure

Although limpets were more abundant in OR, they were larger in NZ (Appendix S1: Table S2; Appendix S2: Figures S10–S12). In OR, three to five species of *Lottia* were abundant at each site, with only the small species *Lottia* spp. and *L. paradigitalis* occurring at all sites. Combining sizes across all species indicates that small species dominated size structure (bottom row, Appendix S2: Figure S10), with most limpets <15 mm in shell length and means between 3.3 and 10.8 mm (Appendix S2: Figure S12). In NZ, small species also occurred (e.g., *Notoacmea* sp., *Patelloida corticata*), but three *Cellana* species reached large sizes, with many limpets >15 mm in shell length (Appendix S2: Figure S11) and overall means ranging between 10.8 ± 0.41 and 20.7 ± 0.92 mm (Appendix S2: Figure S12). Two species (*Cellana radians* and *Notoacmea* sp.) occurred at all sites, and each site had two to six limpet species. The chiton *Sypharochiton pelliserpentis* was also common at most sites but never as abundant as limpets (e.g., densities on the lower shore ranged from 0.1 ± 0.07 to 4.1 ± 0.95 individuals/0.25 m^2).

Experiments: Community responses to disturbance

Summary of results

Photographic examples of results by site and treatment are shown in Figure 3. As detailed below, herbivores and predators each had distinct and interactive effects on community recovery in the experimental plots (Figure 6; Appendix S1: Table S6). In general, herbivore effects appeared first, usually by sample period 1 (when the green dash-dot [−H+P] line is higher than the black [+H+P] line; Figure 6), indicating that algae were typically the earliest colonists in the plots at most sites in herbivore exclusions. However, over the longer term, herbivory weakened as algal growth overwhelmed the herbivores (convergence of green and black lines over time) at all but downwelling-dominated NZ east coast sites (Figure 6i,j). Predation effects appeared more slowly than herbivore effects (the red dashed [+H−P] line lags the green dashed [−H+P] line), likely due to slower recruitment and growth of sessile invertebrates. Predation effects were strong at most OR sites and NMB and BT (Figure 6a–f,h,j; the red dashed [+H−P] line is above the black line) but weak at TMB and RR in NZ (red and black lines were close together) (Figure 6g–j). Consumer effects (−H−P dark yellow line vs. +H+P black line) varied mostly among sites. In OR, consumer effects were large at BB, moderate at FC and RP, and minimal at the other sites

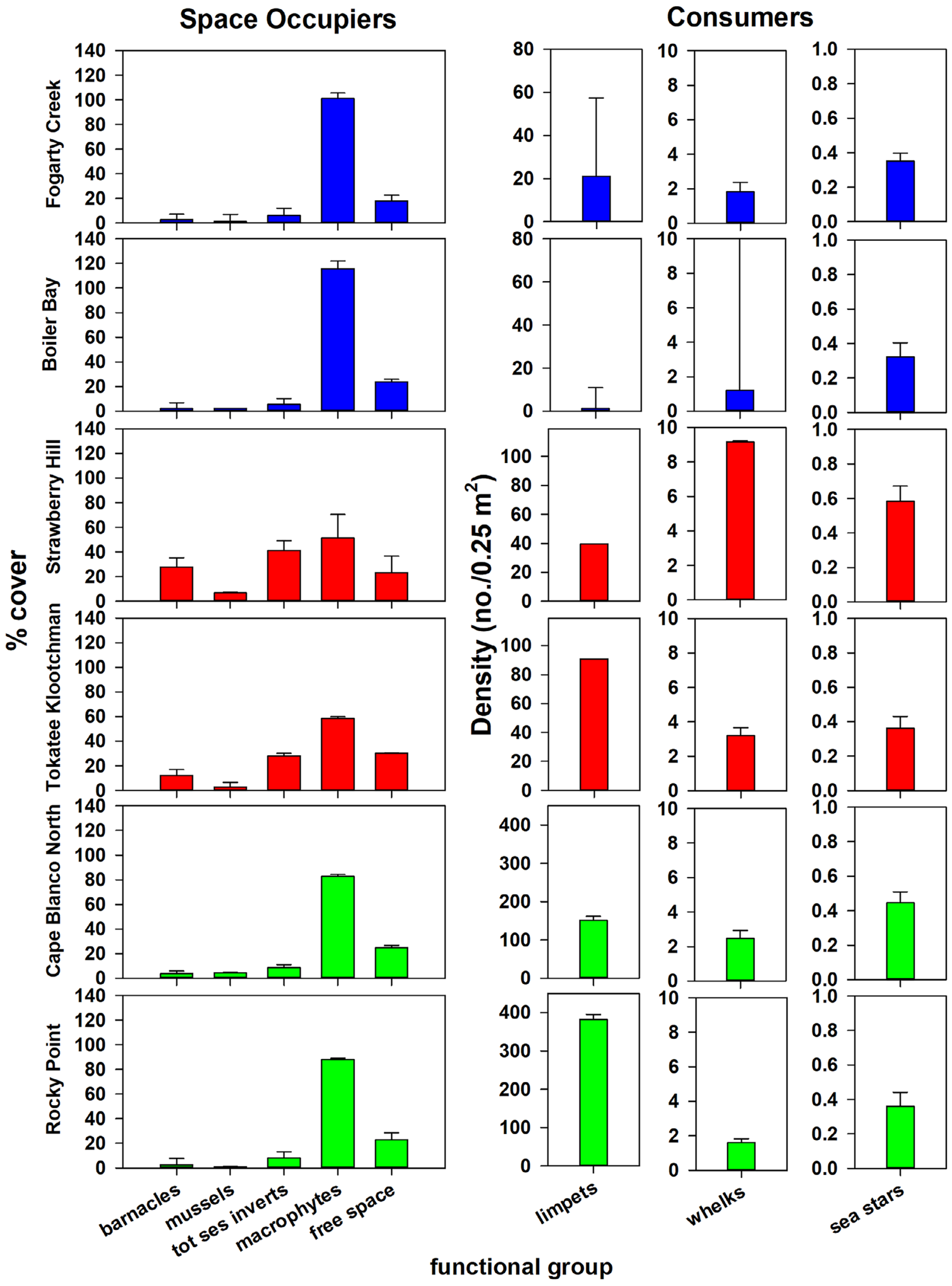

FIGURE 4 Patterns of abundance of major functional groups by site (names shown by *y*-axes) in three regions in Oregon. From north to south sites, are Fogarty Creek and Boiler Bay (in blue, northern region = Cape Foulweather), Strawberry Hill and Tokatee Klootchman (in red, central region = Cape Perpetua), and Cape Blanco North and Rocky Point (in green, southern region = Cape Blanco). Data are mean ± 1 SE.

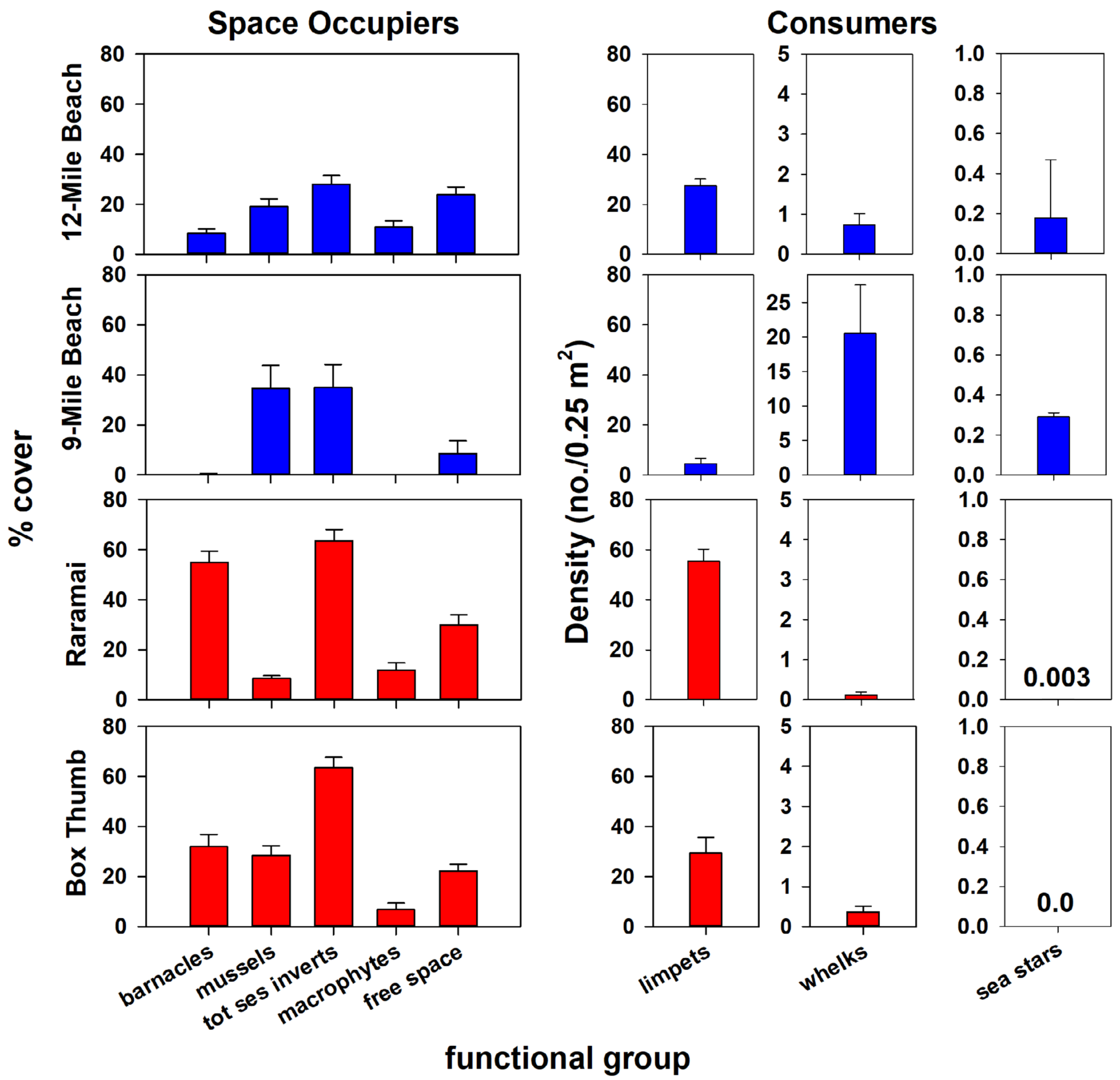

FIGURE 5 Patterns of abundance of major functional groups by site (names shown by *y*-axes) on west and east coasts of New Zealand. From north to south, sites are 12-Mile Beach and 9-Mile Beach (in blue; west coast) and Raramai and Box Thumb (in red, east coast). Data are mean ± 1 SE.

(Figure 6a–f). In NZ, consumer effects at NMB were like those at FC and RP and minimal at TMB, but almost identical to herbivore effects at RR and BT (Figure 6g–j).

Note that comparisons among time series allow inference on the importance of herbivory versus predation. Notably, black (+H+P) lines differ little from red lines (+H−P) at RR and BT, suggesting that predation is unimportant at these sites, while large differences between black (+H+P) versus yellow (−H−P) and green (−H+P) lines at these sites suggest high importance of herbivory. Below, we examine the details supporting these general points by summarizing how communities recovered (functional groups and overall structure) by geographic scale at site, regional, and LME scales.

Experiment trajectories: LME scale

When examining whole-community structure, herbivory and predation and their interaction were not significant as main effects, but except for the H × P interaction (1.9%), they accounted for similar % variance explained compared to other main effects (H = 7.7%, P = 3.7%; Table 2). However, both herbivory and predation had effects through multiple statistical interactions, with total variance associated with each = 35.5% and 23.0% for H and P respectively (Table 2; $p < 0.0001$ in both cases). In addition to site effects, variability in community development was also influenced by LME, region, and time, either as main effects or through multiple interactions (Table 2).

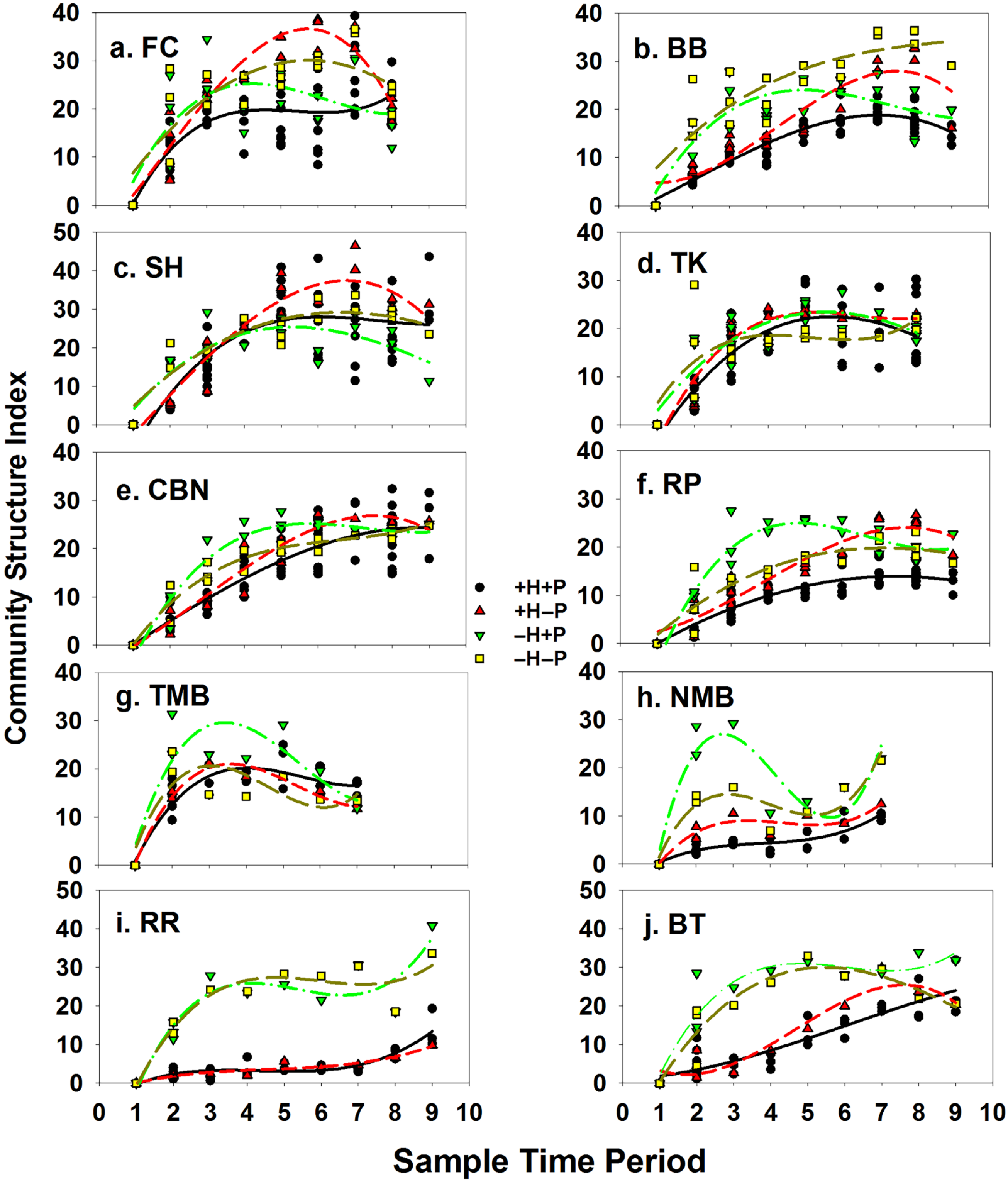

FIGURE 6 Changes in community structure by treatment in each site from sample periods 1–7/9. The difference between the black line (control, +H+P) and green, red, and dark yellow lines indicates the effects of each consumer group separately (green herbivory alone, −H+P; red-predation alone, +H−P) and together (dark yellow - herbivory plus predation, −H−P). From top to bottom, site pairs are from northern (a, b), central (c, d), and southern Oregon (e, f), and west (g, h) and east coasts (i, j) of New Zealand. BB, Boiler Bay; BT, Box Thumb; CBN, Cape Blanco North; FC, Fogarty Creek; NMB, Nine-Mile Beach; RP, Rocky Point; RR, Raramai; SH, Strawberry Hill; TK, Tokatee Klootchman; TMB, Twelve-Mile Beach.

Experiment trajectories: OR regional scale

Results varied among regions, between sites, through time, and with consumer presence (Appendix S1: Table S7). Main effects are subsumed by the many significant interactions, which indicate that the interaction between herbivores and predators varied by Site(Region) (Appendix S1: Table S7; Site(Region) × Herbivore × Predator interaction, $p = 0.0001$, 4.9% variance). Significant time effects occurred in the Site(Region) × Time × Predator interaction ($p = 0.0001$, 5.0% variance) with predator effects occurring at most times at all sites (Appendix S1: Table S7). Region differences interacted with time and herbivore effects (Region × Time × Herbivore interaction, $p = 0.0008$, 4.6% variance).

Experiment trajectories: OR top-down effects

In the early stages of each time series, herbivore and consumer exclusions (−H+P; green lines and symbols and −H−P; blue lines and symbols, respectively) followed similar traces, diverging from controls and predator exclusions (purple +H+P and red +H−P lines) (Figure 7). During these early stages, trajectories were associated with high covers of fast-growing algae (filamentous and bladed algae) (Figure 7; see Appendix S2: Figures S13–S15 for time series by site and taxon). In most cases, however, by about sample times 2 and 3 (hereafter T_2 and T_3), both herbivore and consumer treatments (green −H+P and blue −H−P lines) were less associated with algal dominance and more associated with barnacle or barnacle and mussel domination, suggesting that invertebrates began to dominate the macroalgae regardless of herbivore effects. From about T_3, consumer exclusions (−H−P; blue) diverged strongly away from herbivore exclusions (−H+P, green), that is, from algal dominance toward sessile invertebrate dominance, indicating that predator effects lagged those of herbivores.

Predator exclusions (+H−P; red lines and symbols) initially (T_2 and T_3) tracked changes in control plots (+H+P; purple), but trends varied between sites and among regions (Figure 7). For example, at FC, at T_2, turf-forming and bladed algae were abundant (Figure 7a), while at other sites, changes were slower with plots remaining in a state of bare rock or encrusting algae through T_2, and in some cases, T_3. In most cases, by T_4 and later, predator exclusions (+H−P; red) had become strongly sessile-invertebrate dominated, even at FC. In consumer exclusions (i.e., −H−P, blue), predation impacts emerged after the early bloom of ephemeral algae and, interestingly, appeared stronger than predation impacts when herbivores were present (+H−P; red), as suggested by the blue traces generally moving further to the right in 2D nMDS space (Figure 7).

Experiment trajectories: NZ regional scale

In NZ, results also varied between regions, through time, and between sites within regions, all as main effects (PERMANOVA; Appendix S1: Table S8). However, herbivore effects differed by region (Region × Herbivore $p = 0.043$, 10.0% of variance), between sites within region (Site(Region) × Herbivore $p = 0.0003$, 3.1% of variance), through time (Region × Time × Herbivore $p = 0.003$, 6.9% of variance), and interacting with predation (Site (Region) × Herbivore × Predator $p = 0.004$, 4.8% of variance). In comparison with OR, predation effects were weaker, varying with time (Time × Predator $p = 0.018$, 5% of variance), between sites (Site(Region) × Predator $p = 0.0008$, 4.2% of variance), and again, in interactions with herbivores.

Experiment trajectories: NZ top-down effects

In NZ, herbivore exclusions (Figure 8; −H+P; green) followed trajectories like those in OR: at most sites, ephemeral algae dominated early sample times to be replaced by later successional species. However, these later outcomes varied between coasts, and on the west coast, between sites (Figure 8a–d; Appendix S2: Figures S16 and S17). At TMB, algal dominance in herbivore exclusions persisted through T_5, then plots became mussel dominated (Figure 8a; −H+P green lines moved toward bottom right then top right). In NMB herbivore exclusions, chthamaloid barnacles and mussels dominated early, then communities moved toward algal dominance from T_4 to T_6, then back again toward chthamaloid dominance (Figure 8b; −H+P; green lines moved right, then up and left, then down). On the east coast, algal dominance persisted in herbivore exclusion plots throughout the experiment, with changes from shorter lived ephemerals toward longer lived algal turfs (Figure 8c,d; −H+P green lines moved right then upward). NZ consumer exclusion (−H−P; blue lines) trajectories were similar to herbivore exclusion plots (−H+P; green lines) except at NMB (Figure 8). At TMB, all 4 treatments initially moved toward algal and chthamaloid dominance, then moved in parallel to persistent mussel dominance, suggesting weak herbivory

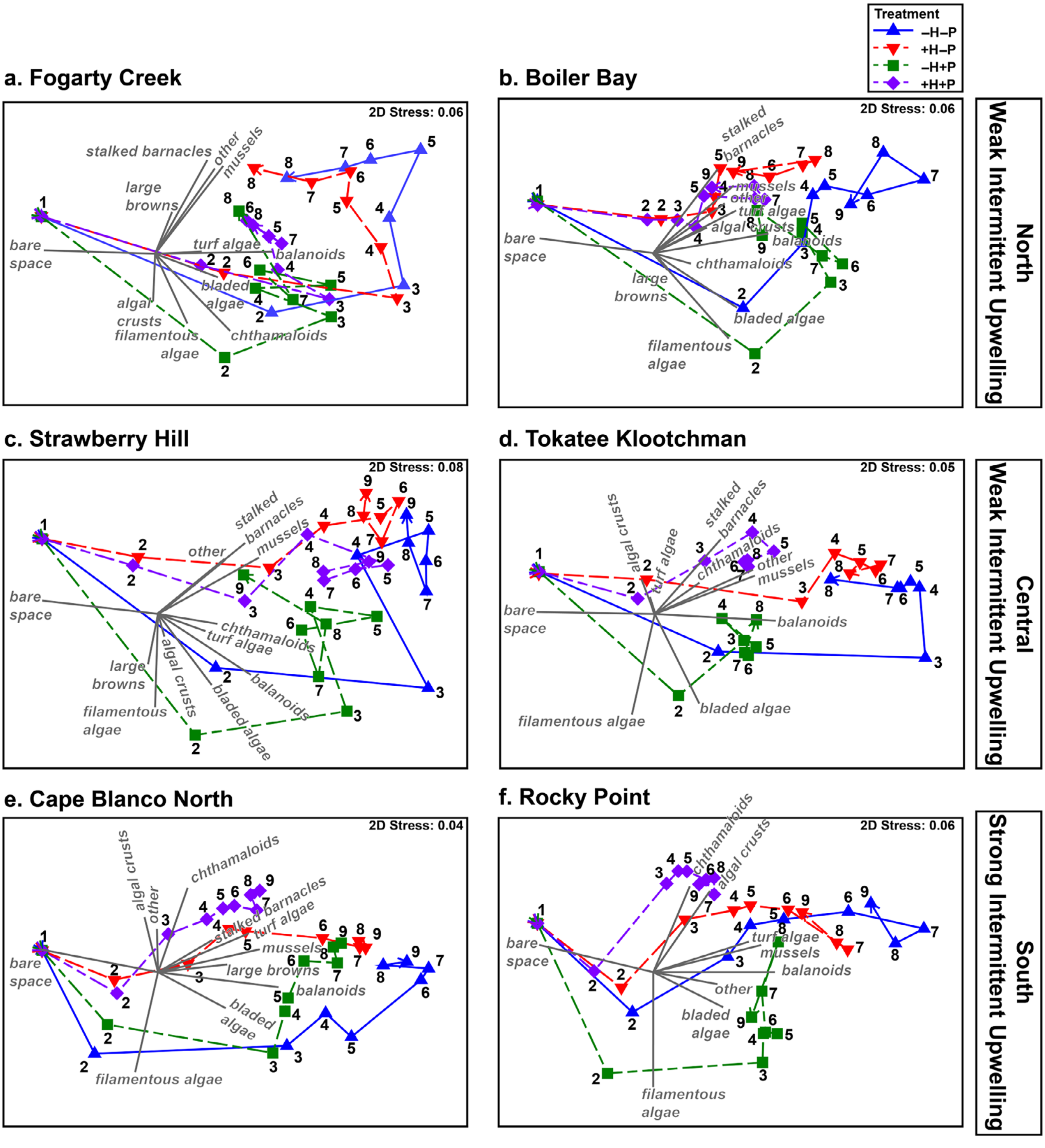

FIGURE 7 Non-metric multidimensional scaling plots of community change in Oregon northern region sites ([a] Fogarty Creek and [b] Boiler Bay), central region sites ([c] Strawberry Hill and [d] Tokatee Klootchman), and southern region sites ([e] Cape Blanco North and [f] Rocky Point) in H × P experiments by site and treatment. Rays show the direction of association of positive values of functional groups (see Appendix S1: Table S3 for group memberships). Numbers by symbols are sample times, T_i, $i = 1$ to 8 or 9; see Appendix S2: Figure S1 for details of sample dates.

and predation (Figure 8a; similar trajectories for all four treatments). Predator effects were also weak at east coast sites (Figure 8c,d; similar trajectories of +H−P; red with +H+P; purple lines), especially RR, which changed little from its initial state of bare rock (Figure 8c). At NMB, predator exclusions (+H−P; red)

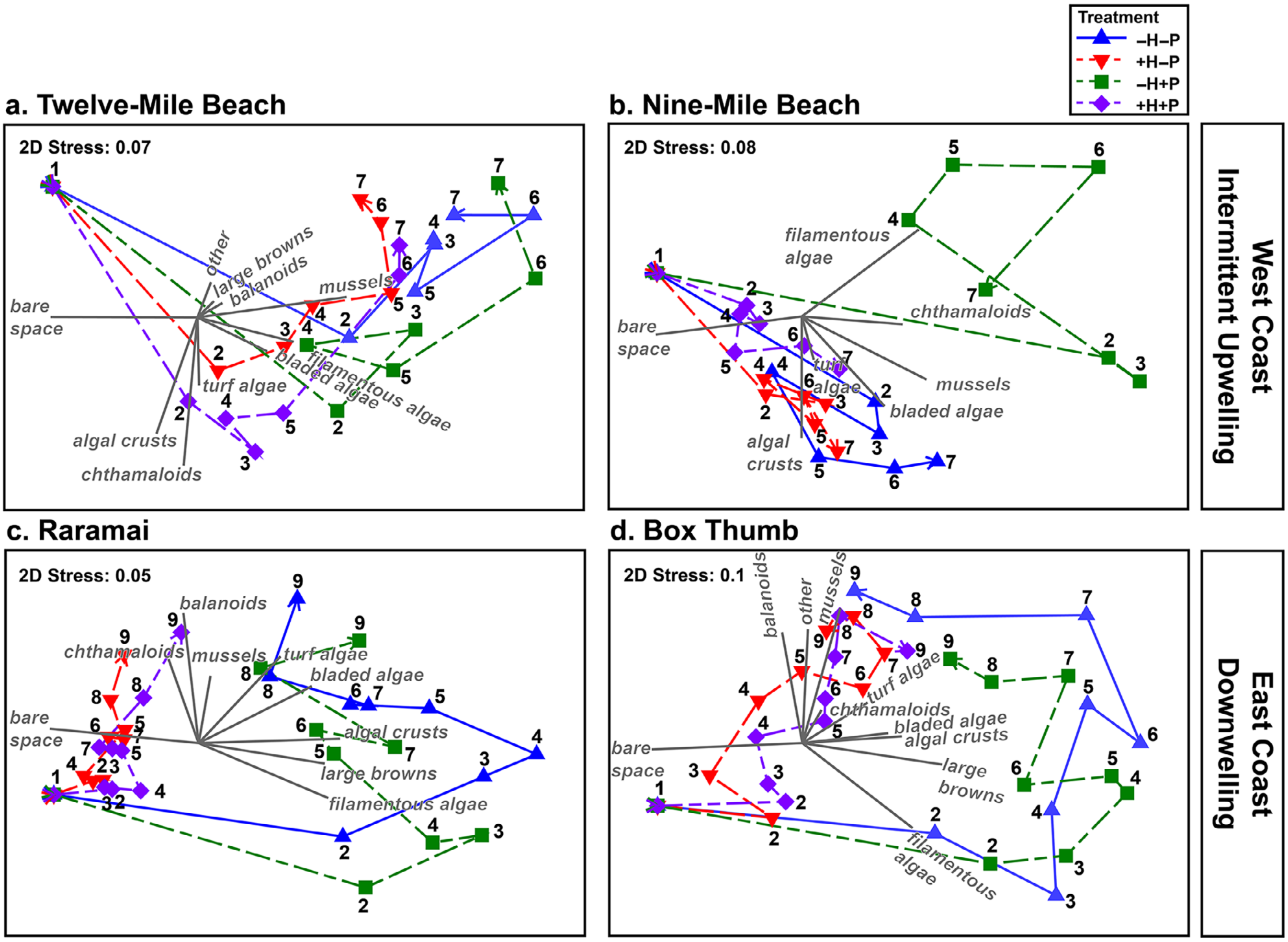

FIGURE 8 Non-metric multidimensional scaling plots of community change in New Zealand west coast ([a] Twelve-Mile Beach and [b] Nine-Mile Beach) and east coast sites ([c] Raramai and [d] Box Thumb) in H × P experiments by site and treatment. Rays show the direction of association of positive values of functional groups (see Appendix S1: Table S3 for group memberships). Numbers by symbols are sample times; see Appendix S2: Figure S1 for details of sample dates.

diverged minimally from controls (+H+P; purple) with a mix of algae and sessile invertebrates (Figure 8b).

Drivers of site differences

Upwelling was a primary differentiator between regions, with OR sites clustering at higher upwelling, NZ west coast sites at moderate upwelling, and NZ east coast sites at downwelling (Appendix S2: Figure S18; opposite *Upw*). NZ and OR sites were also separated by temperature, with warmer ISST to the left and cooler to the right (i.e., negatively correlated with upwelling, $p = 0.012$). Limpet density (*LimpDen*) and mussel recruitment (*MusRec*) separated central OR sites from northern and southern OR sites. NZ west coast sites were also distinguished by higher prey recruitment, a wider shelf than the east coast sites, while NZ east coast sites were associated with larger limpets.

Environmental factors related to consumer effects

All environmental factors contributed to variation in community structure across NZ and OR, accounting for 43.9% of the variance (distance-based linear model; Appendix S1: Table S9). In sequential tests, recruitment, especially of barnacles, loaded first, followed by upwelling strength and intermittency, shelf width, temperature, and limpet traits.

Associations between environmental factors and experimental results showed similar ordination patterns (nMDS) to those between environment and site (compare Figure 9 to Appendix S2: Figure S18). Results at OR sites were intermingled in both cases and fell in the direction of higher limpet density (*LimpDen*) and stronger upwelling (*Upw*). Results at NZ sites were more widely separated in 2D space, being distinguished on the west coast by high barnacle recruitment (*BarnRec*), wider

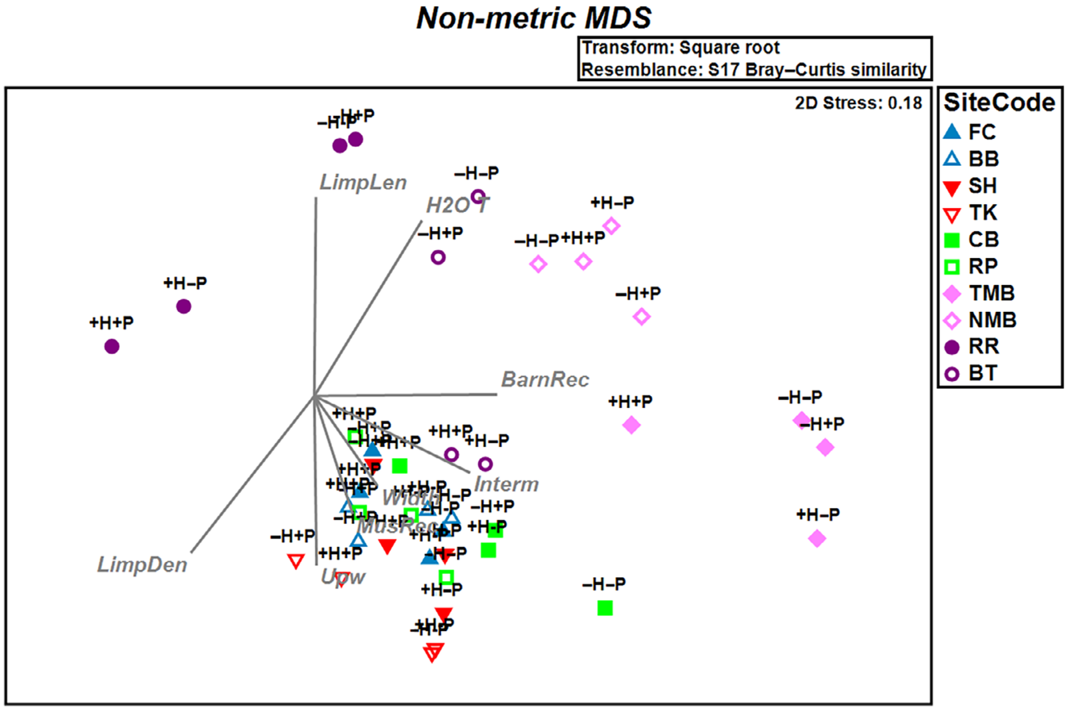

FIGURE 9 Non-metric multidimensional scaling showing the association between upwelling (strength = *Upw*, and intermittency = *Interm*), shelf width (*Width* at 100-m depth), prey recruitment (*BarnRec* and *MusRec*), limpet shell length (*LimpLen*) and abundance (*LimpDen*), and seawater temperature (H_2O *T*) related to treatments (+H+P = control, −H+P = herbivore effect, +H−P = predator effect, −H−P = consumer effect) experiments by site in Oregon (OR) (FC and BB in N-OR region, SH and TK in C-OR region, and CB and RP in S-OR region) and New Zealand (TMB and NMB in West region and RR and BT in East region). Ray direction is toward higher/stronger/warmer values of each factor. BB, Boiler Bay; BT, Box Thumb; CB, Cape Blanco; FC, Fogarty Creek; NMB, Nine-Mile Beach; RP, Rocky Point; RR, Raramai; SH, Strawberry Hill; TK, Tokatee Klootchman; TMB, Twelve-Mile Beach.

shelf (*Width*), and upwelling intermittency (*Interm*), and on the east coast by very low recruitment (to left and top, opposite to *BarnRec* and *MusRec*), large limpets (*LimpLen*), downwelling (opposite *Upw*), warmer water (H_2O T), and a narrow shelf (opposite *Width*). NZ treatments by site were also spaced well apart, with large differences at RR and BT between +H and −H treatments and between controls and all consumer treatments at TMB (Figure 9). NMB treatments were less different and spread in different directions. OR results, in contrast, were less spread out and overlapped.

Relative importance of spatial, temporal, and consumer effects

Using variance component estimates (Table 2), we estimated the relative importance (% variance explained) of the different variables affecting the outcome of the experiments from large to local scales (Figure 10; see Appendix S2: Figure S19 and Table 2 for variance components before standardizing by total variance explained by each factor at each spatial scale). At the LME scale (Figure 10a), herbivory emerged as accounting for the largest amount of variability in the full model (~20%) explained by a main effect. Variance explained by predation, overall, was about 9%, and the H × P interaction variance explained was about 3%. Space (LME, Region, and Site) variation explained was 8%–11%, and many of the impacts of main effects were through two-way interactions (Figure 10a).

In Regions within LMEs, spatial (region and site) variance explained was similar between OR and NZ. In OR, the relative importance of herbivory and predation was similar, but in NZ herbivory was more important than predation (Figure 10b). The H × P interaction was about six times greater in OR than in NZ but still accounted for a relatively small amount of variance (~5%). Among sites within Regions, in OR Site and Time accounted for more variation in Regions 1 and 3 than in Region 2, while importance of herbivory and predation were similar except in Region 2, where predation had about twice the impact of herbivory (Figure 10c). Herbivory × predation accounted for similar and small levels of variability among sites in OR (Figure 10c; variance explained = 3%–5%).

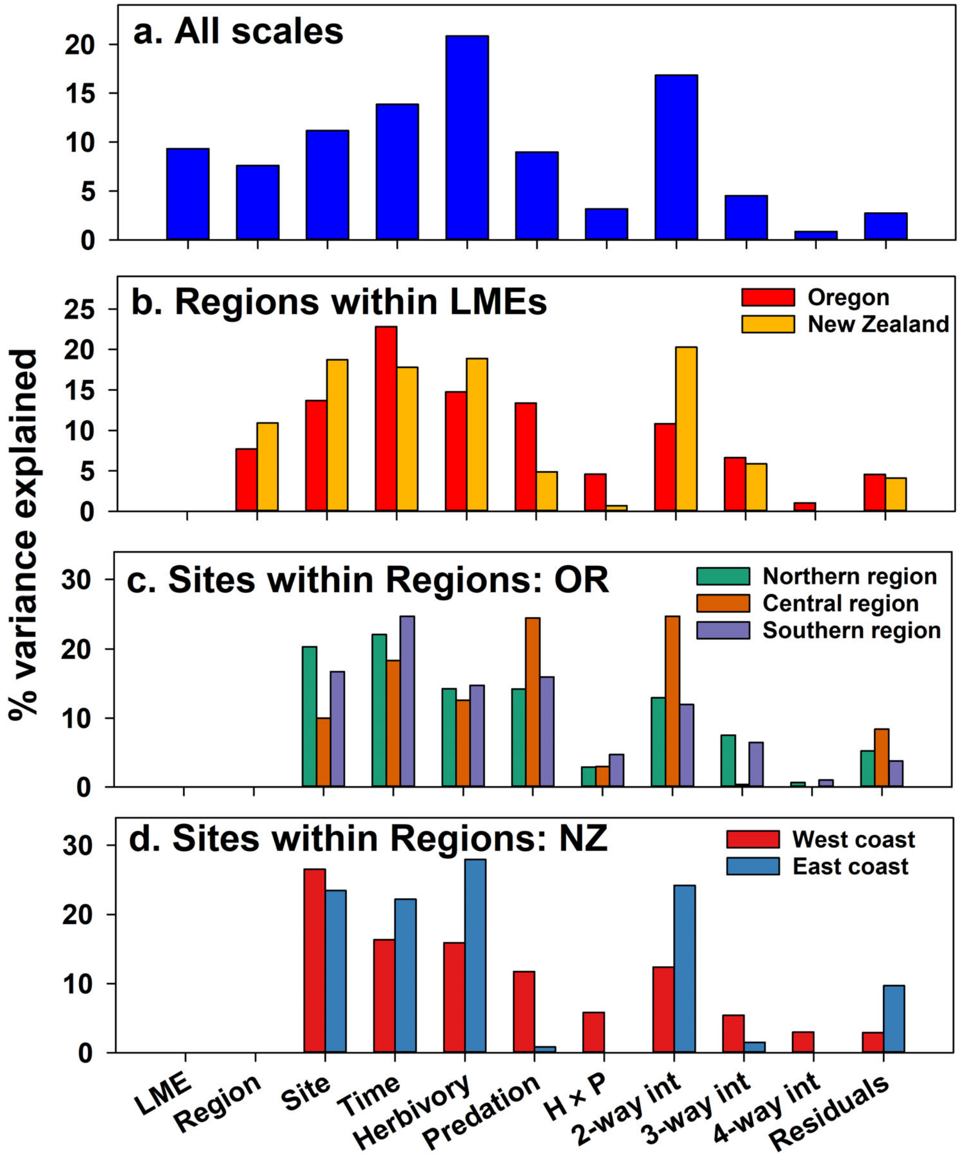

FIGURE 10 Relative importance (proportion of variance explained by each factor as a main effect + their occurrence in interactions in PERMANOVA analyses) of spatial scales, herbivory, and predation, and interactions for the entire dataset (Oregon [OR] and New Zealand [NZ] combined) (a), large marine ecosystems (LMEs) (b), Regions within OR (c), and Regions within NZ (d). Values were calculated by dividing the variance component for each factor by the sum of variance components × 100.

Finally, herbivory had a greater impact than did predation among sites within regions in NZ, especially on the east coast, where predation variance proportion explained <1% of the variability (Figure 10d). Site and Time variance explained was 16%–28%, and that for the H × P interaction on the west coast was about 6% on the west coast and 0% on the east coast.

When variance is simplified to each scale of space, time, and species interactions, time explained the most variability, but again, herbivory explained more variance than did predation (Appendix S2: Figure S20). LME and site explained more variance than did region.

Intermittent Upwelling Hypothesis versus Grazer-Weakening Hypothesis

Method One

Effect sizes of herbivores and predators based on vectors between controls and exclusion treatments varied with upwelling as predicted by the GWH and IUH, respectively (Figure 11; Appendix S1: Table S10a). Herbivore effects were strongest in downwelled regions (NZ East coast) and weakened with increasing upwelling (Figure 11b), while predator effects peaked with moderate (intermittent)

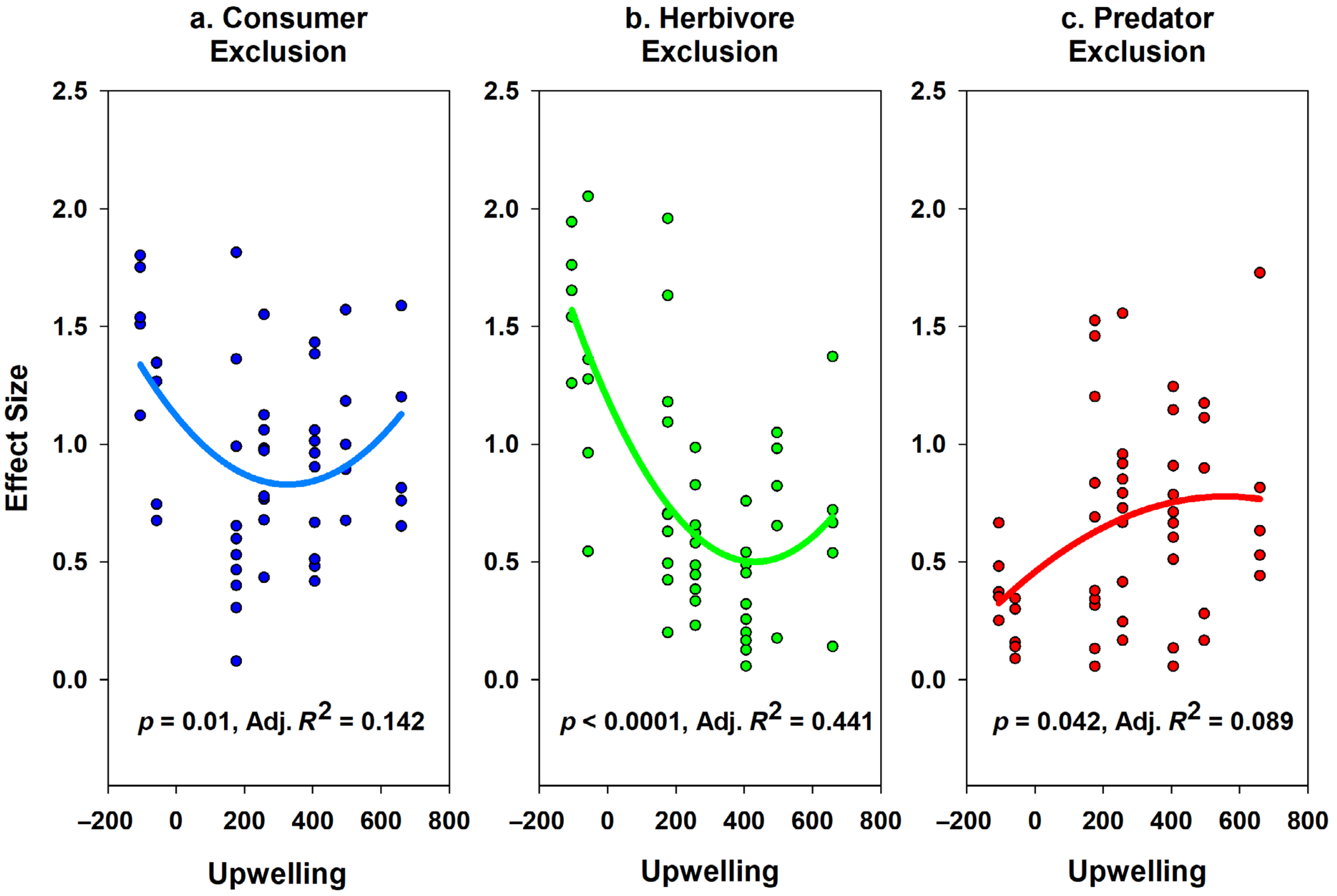

FIGURE 11 Effect sizes of consumers (a), herbivores (b), and predators (c) using Method One versus upwelling (Ekman cross-shelf transport component of Bakun index). See *Methods* for explanation of Method One calculation of effect size. *p*, *p*-value; adj. R^2, adjusted R^2.

upwelling (Figure 11c). Consumer exclusion was also parabolic, suggesting that herbivore effects outweighed predator effects (Figure 11a).

Method Two

As seen using Method One, herbivory and predation effect sizes based on the community index were consistent with the GWH and IUH, respectively (Figure 12; Appendix S1: Table S10b). As expected under the GWH, herbivory effects were strongest in downwelled, less productive regions (NZ east coast), weaker in more productive, intermittently upwelled regions (NZ west coast, OR northern and central regions), and moderate in the most productive region (OR southern region) (Figure 12a; Appendix S1: Table S10b). As was previously shown using an independent set of experiments (Menge & Menge, 2013), predation varied unimodally (but in this analysis, not significantly) with upwelling (Figure 12b; Appendix S1: Table S10b). Consumer effects (Figure 12c) were like those of herbivores alone, again suggesting herbivory was stronger than predation (i.e., in −H−P vs. +H+P treatments).

Metrics indicating acceleration or deceleration (i.e., the quadratic coefficients of the cubic regressions) varied oppositely to effect size metrics (slopes) when plotted against the upwelling index, but only the regression for herbivory was significant (Figure 12d–f; Appendix S1: Table S10b). That is, herbivore effects both increased and decelerated faster in downwelled regimes than in other upwelling regimes. The rapid deceleration of the curve likely reflects that macrophyte abundances reached high abundances faster in these treatments, and thus that percent cover reached an asymptote more quickly.

DISCUSSION

In the *Introduction*, we asked which model best explained sessile invertebrate-predator versus macrophyte–herbivore dynamics in these rocky intertidal subwebs: the IUH or the GWH? Our results support the hypothesis that MH subweb dynamics follow GWH predictions, while SIP subweb dynamics follow IUH predictions (Figure 1b). Besides predicting that herbivory effects decrease with increasing productivity, in marine systems at least, we note

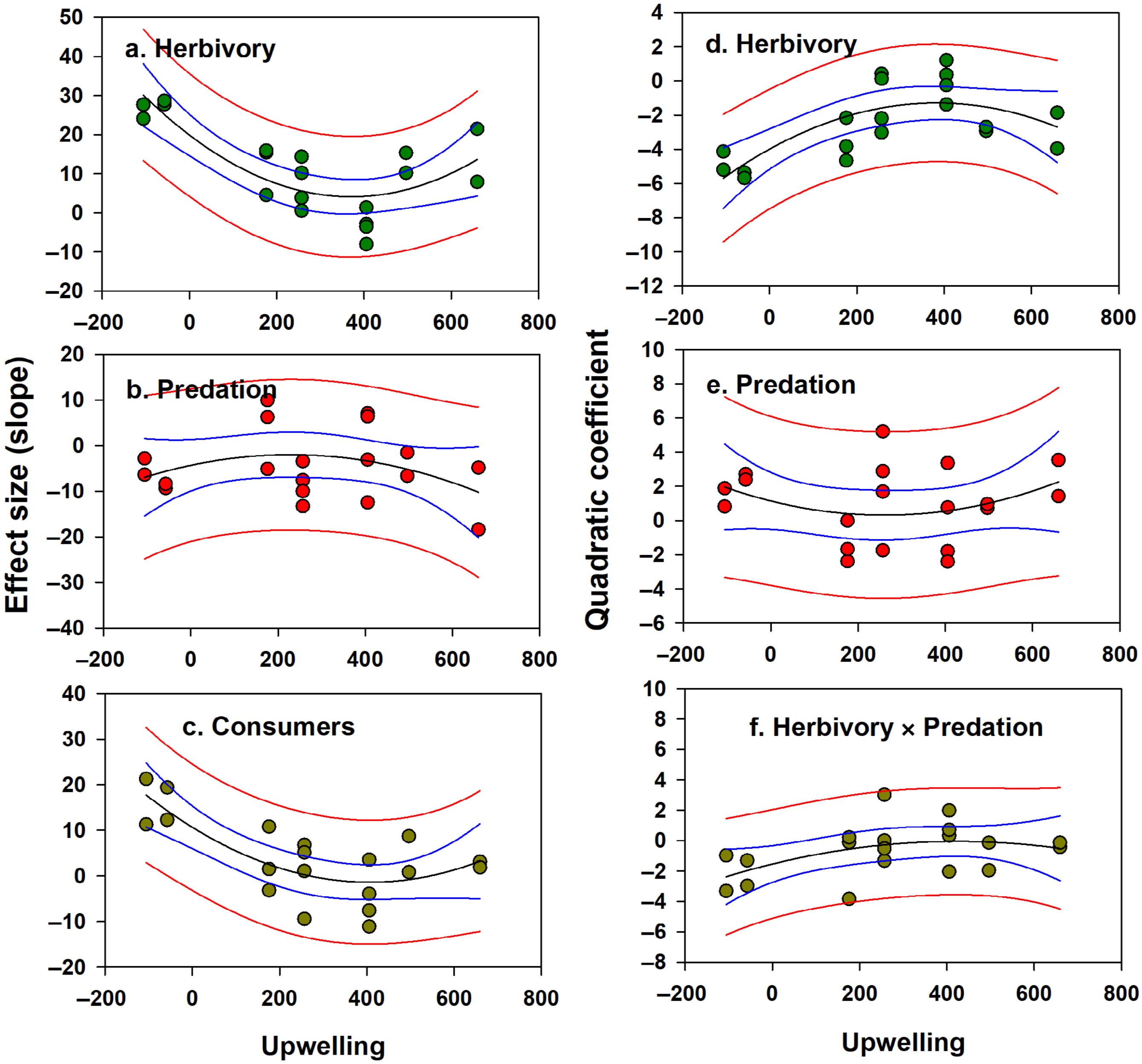

FIGURE 12 Method Two estimates of effect size and acceleration of response versus upwelling magnitude (Ekman cross-shelf transport component of Bakun index). Estimates are based on cubic regressions of community response through time in manipulations of herbivory, predation, and herbivory × predation. Effect size (a–c) on the community as measured by the slope of the cubic fit of the community response versus time rate of acceleration or deceleration of the community (d–f) as indicated by the quadratic coefficient of the community response. Red lines are 95% prediction intervals, and blue lines are 95% confidence intervals.

that two conditions must be met for the GWH model (Figure 1b) to apply to intertidal communities. First, upwelling should be positively related to nutrient inputs, and second, macrophyte productivity should increase with increasing nutrients. Increasing nutrients with upwelling is shown in Appendix S2: Figure S6a for the sites in this study. A more extensive geographical pattern is shown in Figure 13, indicating that for coastal habitats in OR, CA, and NZ, nutrients increase (nonlinearly) with upwelling.

Does macrophyte productivity increase along the same gradient? Although we do not have estimates of macrophyte productivity, total macrophyte cover estimated at 23 sites from northern CA, OR, and NZ increases with increasing upwelling, though the trend is only marginally significant (Figure 14; $p = 0.073$). When paired with the nonlinear curve between herbivore effect size and upwelling from this study (Figure 14), trends for macrophytes and herbivore effects are as predicted in Figure 1b. Thus, the basis of the difference between subwebs lies in contrasting effects of linked bottom-up forces. Nutrients were associated with generally increasing rates of macrophyte abundance with increasing upwelling, and phytoplankton underlies unimodal changes in sessile invertebrates with increasing upwelling (Figures 1 and 11–14; Menge & Menge, 2013).

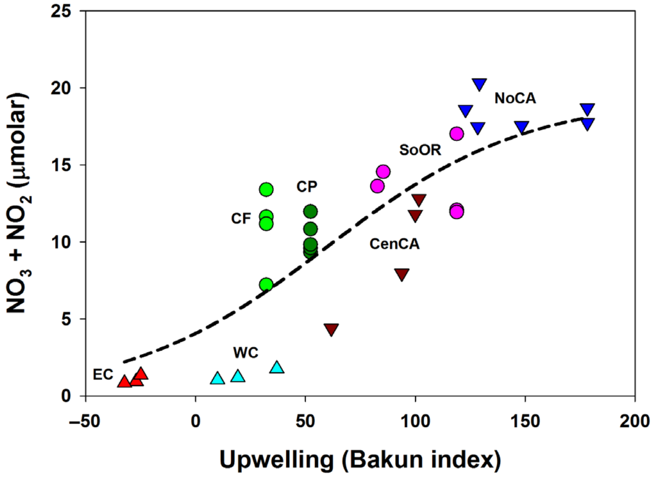

FIGURE 13 Nitrate + nitrite concentration versus the global Bakun upwelling index for sites from New Zealand (EC = east coast, WC = west coast), Oregon (CF, CP, SoOR = southern Oregon), northern CA (NoCA), and central CA (CenCA). See Figure 2 caption for site codes.

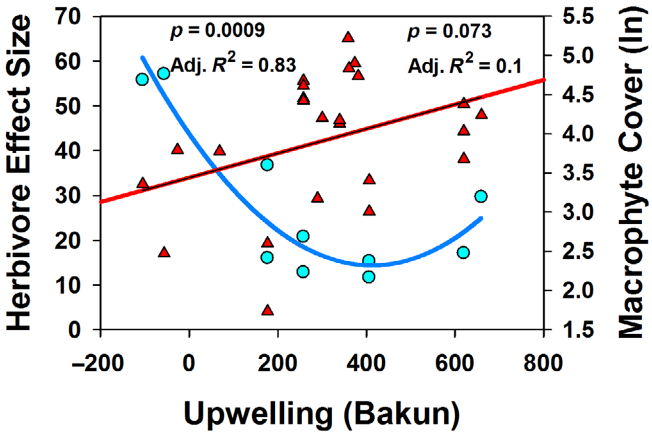

FIGURE 14 Overlay plots of herbivore effect size (blue and cyan) quantified as the difference in macrophyte cover in herbivore exclusions (−H+P) and in controls (+H+P) at the 10 Oregon (OR) and New Zealand (NZ) study sites and average macrophyte cover (red) (ln $(x + 1)$) at sites ($n = 23$) in OR, NZ, and northern CA versus upwelling (Ekman cross-shelf transport component of the Bakun upwelling index) for each site. The best fit model for the herbivore effect versus upwelling was quadratic (effect size = 43.81 − 0.143 [upwelling] + 0.0002 [upwelling]^2, $p = 0.0009$, adj. $R^2 = 0.83$). The best fit model for macrophyte cover versus upwelling was linear (cover = 3.44 + 0.0016 [upwelling], $p = 0.073$, adj. $R^2 = 0.10$).

We collect these results in a revised meta-ecosystem dynamics model (MEcoDynaMo; Figure 15). The curves proposed are meant to apply across large spatial scales, not to temporal changes at a site. At sites arrayed along downwelling to upwelling gradients, nutrient availability should be increasingly available (dashed green line plus

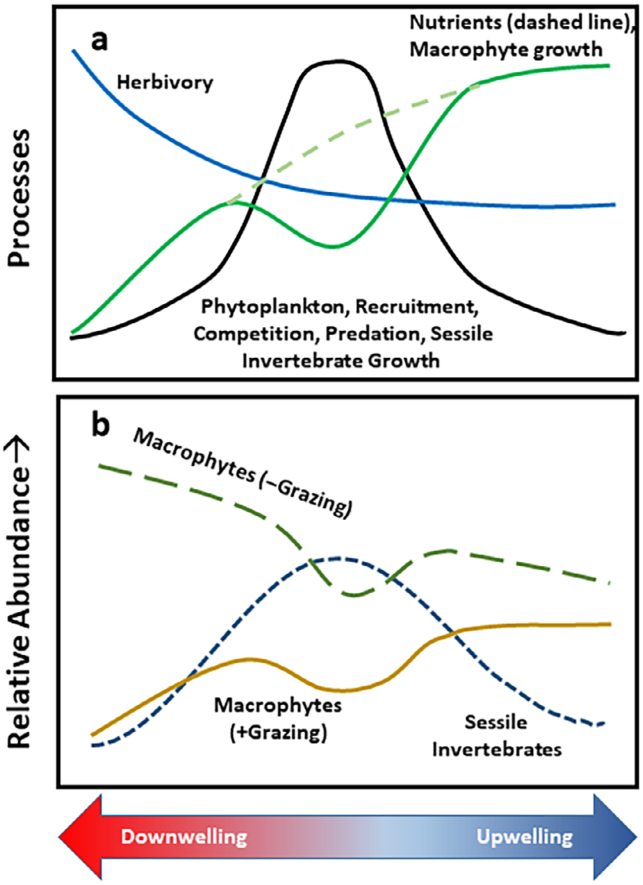

FIGURE 15 Meta-ecosystem dynamics model. (a) Model integrating sessile invertebrate-based and macrophyte-based subwebs into a revised Intermittent Upwelling Hypothesis (IUH) and (b) suggest how the abundance of these two groups will vary because of the processes in (a). The dip in macrophyte growth ([a] solid green line) and abundance ([b] dashed dark green and solid dark yellow lines) is driven by competition for light with phytoplankton and competition for space with sessile invertebrates. The predictions of the original IUH are shown as a solid black line in panel (a). Rates of herbivory are shown by the solid blue line in (a), and effects are suggested by the difference between the dashed dark green and solid dark yellow lines in (b). Sessile invertebrate (and phytoplankton) abundance varies unimodally (dashed dark blue line in [b]) because recruitment and growth are maximized with intermittent upwelling and minimized because of low rates of these processes with persistent upwelling or downwelling. The sessile invertebrate unimodal curve shape describes patterns of abundance in the presence and absence of predation, but in the absence of predation, the curve would be above and approximately parallel to the curve in the presence of predation. See Menge and Menge (2013) for details of the IUH.

solid green lines on the left and right sides of the panel; Figure 15a), and therefore macrophyte and phytoplankton productivity should increase. With intermittent upwelling (i.e., in the middle), macrophyte growth may be slower as a result of phytoplankton shading (e.g., Kavanaugh et al., 2009) and competition with increasingly abundant sessile invertebrates (green line; Figure 15a). With further increases in upwelling, phytoplankton blooms and sessile invertebrate abundance should decline (right half of Figure 15b), so macrophyte productivity should again increase (right half of Figure 15a), leading to abundance patterns shown in Figure 15b (solid dark yellow line). Our data on nutrients with increased upwelling (Figure 13; Appendix S2: Figure S6a) suggest that since nutrient availability levels off at intermediate to high intensities of upwelling, macrophyte productivity and abundance should also reach an asymptote (Figure 15a,b; solid green and dark yellow lines, respectively). As suggested by our data (Figures 11–13), the GWH, and the meta-analysis of Sellers et al. (2020), grazing rate should be strongest under low productivity (persistently downwelled sites) and decline as macrophyte productivity increases (Figure 15a; solid blue line). High herbivory at downwelling sites should strongly suppress macrophyte abundance (left side of Figure 15b; solid dark yellow line). But if herbivores are absent or excluded, macrophyte abundance should be a declining function of upwelling (Figure 15b; dashed green line). Herbivore–plant interaction consequences thus differ qualitatively from predator–sessile invertebrate interaction results, since the curve describing the latter (dashed blue line; Figure 15b) will have the same shape but just be displaced upward in the absence of predators.

Relative importance of predation and herbivory

We also asked, “What is the relative importance of predators vs. herbivores in controlling community structure?” Our analyses suggest that, at least in the context of this experiment, herbivory was overall the more important process (e.g., Figures 10a, 11, and 12; Appendix S2: Figures S19 and S20). Herbivory dominance was especially evident at the downwelled NZ east coast sites (Figure 10d). In OR, as in prior reports (Menge et al., 2016), predation was more important in the intermittently upwelled central region (Figure 10c). However, in northern and southern OR regions, herbivory and predation had similar importance (Figure 10c). In NZ, the between-coast difference in trophic structure (predators were scarce to absent at east coast sites, abundant on the west coast; Figure 5) is the obvious explanation for the near-zero effect of predation on the east coast. In contrast, predators are more abundant overall in OR and hyperabundant in the central region.

These data raise additional questions. First, given the higher predator abundance on the intermittently upwelled NZ west coast, especially of sea stars, and the lower density and smaller size of herbivores (Figure 5; one-way ANOVA on shell length, $F = 45.6$, $p < 0.0001$, east coast $= 15.33 \pm 0.19$ mm vs. west coast $= 13.45 \pm 0.19$ mm), why was not predation stronger? Our data suggest two likely answers: (1) At TMB, mussel recruitment was exceptionally high during this experiment (e.g., Appendix S2: Figure S7i), indicating that predators likely were temporarily swamped by prey abundance. This effect can be seen in Figure 3, which shows that at TMB, mussels occupied most-to-all space in all treatment combinations at this sample time. In our ~25 years of work in NZ, this swamping effect has occurred several times at this site (B. Menge, personal observations, 1994–2010). (2) At NMB, limpets were relatively sparse, whelks were exceptionally abundant (Figure 5), and sea stars were exceptionally large (288.9 ± 8.5 g wet mass at NMB vs. 126.1 ± 1.6 g at TMB), so we expected strong predation. However, as noted earlier, sand burial and scour were common at NMB, suggesting the possibility that prey recruitment was inhibited in all treatments by periodic burial.

Second, why were limpets larger and more abundant on the downwelling-dominated NZ east coast (see, e.g., MP, PC, and FC treatments in Appendix S2: Figure S3)? One possible explanation is the lack of sea star predation. Although *S. australis* consumes mostly mussels and barnacles, limpets and whelks are also eaten (including limpet species: *C. radians*, *Notoacmea* spp., *P. corticata*, *Siphonaria zelandica*, and whelks: *Haustrum lacunosa*, *H. albomarginatum*, and *Paratrophon patens*) (Menge et al., 1999; B. Menge, personal observations, 1994–2010). The virtual absence of *S. australis* at our east coast sites may thus allow limpets to grow to larger sizes/greater ages, and higher abundances. Other limpet predators, for example, oystercatchers (*Haematopus ostralegus finschi*, *H. unicolor*), occur on the NZ, but we have never seen them at our sites. We observed a trail of dead limpet shells suggestive of oystercatcher activity at BT, but only once in our dozens of trips to this site. In contrast, oystercatchers are common at most of our OR sites and prey heavily on limpets (Frank, 1982). Other alternatives, such as higher food abundance or reduced competition for food, seem unlikely given that nutrients and food (algal) availability are low on the east coast (Appendix S2: Figures S5, S6, and S9).

Third, why was herbivory more important in NZ than in OR (Figure 10b)? Besides the suggested minimal predation on limpets in NZ, especially on the east coast, limpets in NZ were ~3× larger than those in OR (Appendix S1: Table S2). For example, overall shell length across all species in NZ was 14.58 ± 0.14 mm ($n = 3328$) versus 5.76 ± 0.08 mm

($n = 1510$) in OR. The largest species in NZ was *Cellana denticulata* (28.98 ± 0.27 mm, $n = 243$ with *C. radians*, more widely distributed at 15.25 ± 0.27, $n = 564$) versus *Lottia pelta* in OR (10.78 ± 0.3 mm, $n = 180$). Since larger animals generally can eat a wider variety of, and larger, resources than smaller ones, the large limpets in NZ may be more effective grazers than the smaller ones in OR.

Fourth, why are *S. australis* absent from the NZ east coast? We suggest that exceptionally low prey recruitment (i.e., low food abundance) is a major factor (Appendix S2: Figure S8; also see Menge & Menge, 2013; Menge et al., 1999, 2003). Lack of larval dispersal to the east coast is another possibility, but given the millennia presumably available for the planktotrophic larvae of *S. australis* to reach these shores, it seems less likely. Although barnacle and mussel abundances at east coast sites can be substantial (Figure 4), the low rates of prey input result in a long time for such abundances to accumulate (Appendix S2: Figure S17), which may be insufficient to sustain populations of this voracious sea star. The importance of prey input rates is also suggested by the correspondence between *S. australis* body size (which decreases southward along the west coast) and prey inputs and growth rates (which also decrease southward on the west coast; Menge et al., 2003).

The NZ east coast sites seemingly present another paradox. These study sites tend to be dominated by sessile invertebrates (and bare space), but recruitment is very low, so why are barnacles and mussels dominant? Our experiments suggest that sessile invertebrate dominance is maintained by intense grazing. Herbivory suppresses macrophytes, allowing the covers of sessile invertebrates to slowly increase and cover much of the rock surface (Figure 5; Appendix S2: Figure S17). Note that this indirect effect is the opposite of that seen in systems like OR and Washington State (and at times the west coast of the NZ), where predation can control sessile invertebrate abundance (Menge et al., 1994; Paine, 1966, 1974), allowing macrophytes to dominate low intertidal space. The opposite pattern of low macrophyte abundance in NZ is consistent with the concept of strong top-down control in that at NZ east coast sites, grazers are functionally the top level in a two-trophic-level system (e.g., Menge, 2000; Menge & Sutherland, 1987; Oksanen et al., 1981).

A final point regarding the importance of herbivory in NZ is that, paradoxically, in the very low intertidal zone (i.e., below the low-mid zone studied here) at all our sites, macrophytes are moderately to very abundant (B. Menge, personal observations, 1994–2010). These macrophytes include the very large, kelp-like fucoid *Durvillaea* spp. as well as other larger algae (mostly fucoids). Does this contradict our conclusions about herbivory being strong to very strong in NZ? In particular, why are seaweeds abundant in the low zones of these areas, given the large and abundant limpets we observed? At least two hypotheses can be proposed as potential explanations. First, for unknown reasons, limpets, chitons, and other herbivores are sparse in these low intertidal macrophyte stands (B. Menge, personal observations, 1994–2010). Thus, very low-zone algae may have escaped control by grazers. Evidence consistent with this was provided by Taylor and Schiel (2010), who showed that herbivorous butterfish (*Odax pullus*) can decimate juvenile *Durvillaea antarctica* at sites on both the east and west coasts, but that survival is relatively high at wave-exposed sites such as those studied here. Second, many very low-zone algae may be unpalatable. Although butterfish readily consumed juvenile *D. antarctica*, other low-zone fucoids (e.g., *Cystophora* spp.) are likely defended chemically or morphologically against grazers (e.g., Steinberg, 1989; Van Alstyne, 1988). Investigation of this issue would be of great interest.

Role of omnivory

Another general question was, “Do the omnivory links between herbivores vs. sessile-invertebrate colonists and filter-feeders vs. algal spores affect community dynamics?” Omnivory is known to be more common than once thought (Arim & Marquet, 2004; Camus et al., 2008; Diehl, 1993; France, 2012; Polis, 1991; Yodzis, 1988) and, in theory, can be an important process in structuring communities (e.g., McCann & Hastings, 1997; Pillai et al., 2011). As suggested in Figure 1, molluscan grazer consumption of newly settled sessile invertebrates is a potential source of omnivory as is filtering of algal spores. However, the weak H × P interaction indicates such effects were of minor importance in explaining community variability (Figure 10; Appendix S2: Figure S19). The only treatment combination in which it accounted for even a modest percent variance was Site(Region (LME)) × Herbivory × Predation (3.9%; Table 2; Appendix S2: Figure S19). However, consistent with prior results (Dayton, 1971; Menge et al., 2010), at several sites, OR time series plots consistently showed an early peak of abundance of balanoid barnacles (mostly *Balanus glandula*) in herbivore exclusion treatments (i.e., −H+P and −H−P, sites BB, SH CBN; Appendix S2: Figures S13–S15l,p). As discussed previously, these peaks are most likely a consequence of excluding limpet bulldozing and/or incidental consumption of recent barnacle recruits. In contrast, in NZ despite the large sizes of limpets, such responses were minimal to absent. Exclusion of limpets (i.e., of bulldozing) might have caused the early peak of chthamaloid barnacles (*Chamaesipho columna*) seen at NMB (Appendix S2:

Figure S16l,p), but no such trend occurred at other NZ sites. At east coast sites, sessile invertebrate recruitment was very low (Appendix S2: Figure S7e,j), so detecting bulldozing effects likely would have been difficult.

Generality of results

How general are our results? Previously, we commented on the likelihood that the IUH applied more generally to other intertidal habitats (e.g., estuaries) (Menge & Menge, 2013). What about the MH subweb? Recent studies by Sellers et al. (2020, 2021) focused on how invertebrate grazer impacts on algal community structure varied in relation to the strength of upwelling, both globally in temperate systems and in the tropical East Pacific. Their global meta-analysis found that herbivory was consistently weaker in upwelling-dominated systems than in downwelling-dominated systems (Sellers et al., 2020). Thus, the meta-ecosystem dynamics model seems to apply broadly on temperate shores but needs further testing in other regions.

What about tropical shores? Classic wind-driven coastal upwelling largely fades out at lower latitudes, as do dense stands of noncrustose macrophytes (e.g., Lubchenco et al., 1984; Menge & Lubchenco, 1981; Menge et al., 1986). Thus, expectations are either that the dynamics suggested by the MEcoDynaMo model may not operate in these regions, or that tropical shores occur at the far left of Figures 14 and 15b. However, other upwelling mechanisms can operate in the tropics (e.g., Vinueza et al., 2014). For example, Sellers et al. (2021) investigated herbivory impacts along a ~300-km stretch of the Pacific coast of Panama. Here, due to seasonal shifts in trade winds, coastal upwelling occurred in the dry season but not in the wet season. Furthermore, due to regional orographic differences, upwelling varied seasonally, from stronger in the dry season and weaker in the wet season in the Gulf of Panama to weak in all seasons in the Gulf of Chiriqui to the west. Sellers et al. (2021) showed that the strength of herbivory varied seasonally with upwelling in the Gulf of Panama. Herbivory was stronger in the nonupwelled wet season and weaker in the upwelled dry season in the Gulf of Panama when noncrustose algal abundance increased, but in the nonupwelled Gulf of Chiriqui, it was consistently relatively strong. Thus, once again, upwelling appeared to be a key driver of variation in process rates and structure of an intertidal community.

What is the likelihood of seeing similar dynamics in subtidal kelp-, or coral-dominated systems? Globally, kelp beds occur in upwelled and nonupwelled, mostly temperate and polar environments (e.g., Krumhansl et al., 2016), so one might expect to detect an upwelling effect on kelp communities. However, kelp bed dynamics are extraordinarily complex (e.g., Dayton, 1985) and difficult to study experimentally, so conducting relevant studies would take a major, expensive, and intensively collaborative effort. Coral communities are mostly tropical and in low-nutrient, nonupwelled regions, so we suspect they are less influenced by ocean current regimes. Furthermore, the symbiotic nature of corals means they function as both primary producers and micro-predators, so their responses to changes in upwelling-driven nutrients versus phytoplankton may be more complex.

Relative effect of environmental conditions

Earlier studies suggested that oceanic conditions could account for ~50% of the variation in rates of ecological subsidies and species interactions (Menge & Menge, 2013) and in patterns of community structure and dynamics in the CA Current LME (Hacker et al., 2019; Menge et al., 2015). The present study aimed to determine effects and relative importance of herbivory, predation, time, and space in the context of oceanic conditions (upwelling and upwelling-dependent processes). We discussed above the relative importance of species interactions, which at the LME scale accounted for ~33% of the variance (Figure 10). Space and time collectively explained ~42% of the variance, with the remaining ~25% due to statistical interactions (21.4%) and residuals (2.8%). In OR, proportions of variance were similar (space/time = 44.2%, species interactions = 32.7%, statistical interactions = 18.5%, and residuals = 4.6), but in NZ, species interactions were a bit less important and statistical interactions more important (in the same order, 47.4%, 24.4%, 28.3%, and 4.1%). By region, OR central region (CP) and NZ east coast stood out, with space/time explaining 28.3% and 45.7%, and species interactions explaining 40% and 23%, respectively (vs. space/time ~42% and species interactions ~33% for all other regions). These numbers thus suggest that except for OR central region and NZ east coast, environment explained >40% of the variance compared to >30% for consumer effects. OR central region apparently had stronger biotic effects, and NZ east coast was more physically influenced.

Thus, in this experiment, environmental influences accounted for much of the variability observed in community development. That is, including the statistical interactive influences (which test joint effects of space/time × biotic interactions), the environment likely accounted for >50% of the variance in community development. This value is similar to the proportions seen as explaining community structure and rate processes in independent studies (Hacker et al., 2019; Menge & Menge, 2013; Menge et al., 2015).

The space component of these analyses (i.e., LME, Region, and Site) is clearly a reflection of upwelling region and shelf width, and how these influence ecological subsidies, and in turn, how these effects flow up through the food web to influence interactions. Consideration of these two environmental factors in detail helps to understand some odd results. For example, how could prey recruitment be so high at NZ west coast sites (Appendix S2: Figure S7) when phytoplankton (and nutrients) are so low in these areas (Appendix S2: Figures S5 and S6)? This pattern is puzzling, and an answer will require more detailed investigation into larval ecology and larval transport of the taxa involved (i.e., the mussels *M. galloprovincialis*, *P. canaliculus*, and *X. pulex*; the barnacle *C. columna*). Two factors associated with this pattern are a wide continental shelf and high upwelling intermittency on the NZ west coast (Appendix S1: Table S2), but the mechanism underlying the pattern awaits further research.

A still-unanswered question is why nutrients and phytoplankton abundance are so low on both NZ coasts, despite the intermittent upwelling regime on the west coast (Appendix S2: Figures S5 and S6). This was discussed in Menge and Menge (2013), where the possibility of micronutrient deficiency was raised, but to our knowledge, no further research has been conducted on this issue.

CONCLUSIONS

We conclude that the two subwebs that occur in many, if not most, intertidal ecosystems function differently from one another, and thus that the IUH applies only to the SIP subweb. The abundance-based version of the GWH appears more applicable to the MH subweb, and thus a more general model must include dynamics of both subwebs. We propose that the MEcoDynaMo model is such a model and that the underlying environmental factor linking the subwebs is upwelling. As our data suggest, a complete upwelling gradient, that is, downwelling to upwelling, generates variation in two linked metrics, nutrients and phytoplankton abundance. We propose that the nutrient component influences these systems in two ways: it supports phytoplankton and macrophyte assemblages, with the former being a primary determinant of sessile invertebrate dynamics (and thus higher trophic levels), and the latter being an important determinant of benthic herbivory. All these components interact to greater or lesser extents, producing the great complexity of intertidal communities. While we do not claim to have disentangled all this complexity, we believe that our studies provide a major step in this direction.

AUTHOR CONTRIBUTIONS

Bruce A. Menge designed the research, conducted research, managed and analyzed data, and wrote the paper; Sarah A. Gravem managed and analyzed data and edited the paper; Mae M. Noble conducted research, processed samples, oversaw collection of data, managed data, and edited the paper; Erin Richmond conducted research, processed samples, oversaw collection of data, managed data, and edited the paper.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Menge et al., 2023) are available from Dryad: https://doi.org/10.5061/dryad.3ffbg79p8.

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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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