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Are meta-ecosystems organized hierarchically? A model and test in rocky intertidal habitats

Are meta-ecosystems organized hierarchically? A model and test in rocky intertidal habitats

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Abstract. Ecosystems are shaped by processes occurring and interacting over multiple temporal and spatial scales. Theory suggests such complexity can be simplified by focusing on processes sharing the same scale as the pattern of interest. This scale-dependent approach to studying communities has been challenged by multiscale meta-ecosystem theory, which recognizes that systems are interconnected by the movement of "ecological subsidies" and suggests that cross-scale feedbacks between local and regional processes can be equally important for understanding community structure. We reconcile these two perspectives by developing and testing a hierarchical meta-ecosystem model. The model predicts local community responses to connectivity over multiple oceanographic spatial scales, defined as macro- (100s of km), meso- (10s of km), and local scale (100s of m). It assumes that local communities occur in distinct regions and that connectivity effects are strongest among local sites. Predictions are that if macroscale processes dominate, then regardless of mesoscale differences, (1) local communities will be similar, and (2) will be even more so with increased connectivity. With dominance of mesoscale (i.e., regional) processes, (3) local structure will be similar within but distinct between regions, and (4) with increased connectivity similar both within and among regions. With dominance of local-scale processes, (5) local communities will differ both within and among regions, and (6) with increased connectivity be similar within but not between regions. We tested the model by evaluating rocky intertidal community structure patterns with variation in ecological subsidies and environmental conditions at 13 sites spanning 725 km of the northern California Current system. External factors operating at meso- and local scales had strong effects, explaining 52% and 27% of the variance, respectively, in community structure. Sessile invertebrate and predator dominance was associated with weaker upwelling, higher phytoplankton abundance, and higher recruitment, and the opposite was true for macrophyte dominance. Overall, our results support the theory that meta-ecosystems are organized hierarchically, with environmental processes dominating at meso- to macroscales and ecological processes playing a more important role at local scales, but with important bidirectional cross-scale interactions.

Key words: *coastal ecosystems; ecological subsidies; ecosystem dynamics; meta-ecosystems; northern California Current large marine ecosystem; oceanographic conditions; relative importance; rocky intertidal communities; spatial scale; variation partitioning.*

INTRODUCTION

Natural ecosystems are inherently complex because they are shaped by ecological and environmental processes operating at multiple temporal and spatial scales. Current theory suggests that this complexity can be greatly reduced because ecosystem patterns and their underlying processes tend to share a common scale (Willis and Whittaker 2002, Pearson and Dawson 2003, McGill 2010). Hence, in order to understand an ecological pattern of interest, one can focus on the subset of processes that operate at the same scale and ignore the myriad of processes operating at different scales. An alternative to this intuitive, scale-dependent approach is multiscale theory, which attempts to explain ecological patterns as a product of the interaction between local and regional processes (Guichard 2005, Gotelli et al. 2010, Gouhier et al. 2010). Multiscale theory came to prominence relatively recently thanks to the recognition that most ecological systems (populations, communities, ecosystems) are open to some degree (Dayton and Tegner 1984, Wiens 1989, Menge and Olson 1990, Gilpin and Hanski 1991, Levin 1992, Loreau et al. 2003, Witman et al. 2004, Holyoak et al. 2005, Gouhier et al. 2010). This multiscale perspective suggests that communities are linked by the dispersal of multiple interacting species (termed meta-communities; Wilson 1992, Leibold et al. 2004) and can be further expanded to include the movement of propagules and

migrants, nutrients, and energy (termed meta-ecosystem; Loreau et al. 2003, Massol et al. 2011).

The ecological significance of this openness became particularly apparent following the work of Polis and colleagues (e.g., Polis and Hurd 1995, 1996, Polis et al. 1997, 1998), who coined the term "ecological" subsidies to refer to the flows of biomass, nutrients, and propagules across community and ecosystem boundaries, and also demonstrated the dramatic effects such flows could have on the dynamics of adjacent communities. Many studies have since shown the importance of ecological subsidies on the structure of communities linked by such flows (e.g., Menge et al. 1997a, 2003, 2004, Wallace et al. 1997, Nakano and Murakami 2001, Schindler and Scheuerell 2002, Dugan et al. 2003, Pace et al. 2004, Maron et al. 2006, Witman et al. 2010, Griffiths et al. 2013, Menge and Menge 2013, Vinueza et al. 2014). The spatial scales of these studies have varied, with some focused on the exchange of subsidies between adjacent systems at a single location (e.g., forest–stream; Wallace et al. 1997, Nakano and Murakami 2001; or lake–terrestrial; Pace et al. 2004, Soranno et al. 2014). Others have examined such exchanges at multiple locations, studying both site-scale subsidy transfer and how this varies among replicate sites linked in space through flows of ecological subsidies. Polis' classic study of within-site (desert island–ocean) exchanges and how these varied among multiple desert islands is an example, as are recent studies of benthic–pelagic material and propagule transfers within and among a large group of subtidal rock-wall habitats in the Galapagos Islands, Ecuador (Witman et al. 2010), and the influence of watershed and regional differences on phosphorus concentration in Midwestern and Northeastern United States lakes (Soranno et al. 2014).

This strong empirical evidence of spatial coupling between adjacent systems led Loreau et al. (2003, p. 673) to propose the meta-ecosystem concept, defined as "a set of ecosystems connected by spatial flows of energy, materials, and organisms across ecosystem boundaries," in order to forge a stronger conceptual link between community and ecosystem processes across spatial scales. Since then, Loreau, Holt, and colleagues have developed a conceptual body of work for meta-ecosystem theory (e.g., Holt 2004, Loreau and Holt 2004, Leroux and Loreau 2008, Gravel et al. 2010a, b, Massol et al. 2011). However, few empirical investigations of the influence of propagule and material exchanges on meta-ecosystems that span local to biogeographical scales are available. Our goal in this study is to develop a conceptual model of marine meta-ecosystem dynamics and to empirically test its predictions by determining the effect of cross-scale flows of ecological subsidies on local and regional ecosystem structure.

Coastal marine ecosystems are ideal for testing meta-ecosystem theory because spatial flows of organisms and materials exert a strong influence on population dynamics, community structure, and ecosystem functioning (e.g., Bustamante et al. 1995, Bustamante and Branch 1996, Menge et al. 2003, 2004, Nielsen and Navarrete 2004, Navarrete et al. 2005, Barth et al. 2007, Witman et al. 2010, Hessing-Lewis and Hacker 2013, Menge and Menge 2013, Vinueza et al. 2014). For example, in South Africa, productivity of benthic microalgae around the coast, from an upwelling-dominated west coast to a downwelling-dominated east coast spanning ~2000 km, was strongly associated with nutrient supply, which varied both locally and among upwelling regions (Bustamante et al. 1995). These trends are consistent with the hypothesis of an important influence of oceanographic conditions, but apart from the nutrient measurements, no other oceanographic data were collected. In another study, along a 900-km (6 latitudinal degrees) stretch of the central coast of Chile, a discontinuity in upwelling strength at about 32° S coincided with a sharp northward drop in recruitment rates of mussels, with consequent changes in predation rates, and a shift from top-down to bottom-up control (Navarrete et al. 2005). Here, regional-scale oceanographic variation was associated with between-region differences in ecological subsidies and species interaction strength.

These and similar investigations (e.g., Menge et al. 1997a, Witman et al. 2010, Menge and Menge 2013, Vinueza et al. 2014) suggest that rocky intertidal communities are likely to be influenced by meta-ecosystem processes. First, on a local-site scale, flows of propagules and materials occur reciprocally between benthic coastal communities (e.g., production of macrophyte detritus, waste products of invertebrates, larvae) and adjacent pelagic waters (e.g., provision of nutrients, retention and transport of larvae, delivery of phytoplankton- and macrophyte-derived detritus; e.g., Leslie et al. 2005, Morgan et al. 2009a, b, Bracken et al. 2012, Pfister et al. 2014). Second, the primary coastal habitats (e.g., rocky intertidal, kelp beds, estuaries, sandy beaches, coral reefs) are discontinuous along a coastline and are themselves linked by alongshore and cross-shelf currents that exchange materials and propagules. These currents typically have a complex spatio-temporal structure, with variability driven by a combination of coastal geomorphology, bottom topography, latitudinal gradients in climatic patterns, and large basin-scale climatic fluctuations (e.g., El Niño Southern Oscillation, Pacific Decadal Oscillation, North Pacific Gyre Oscillation; see Strub and James 1995, Graham and Largier 1997, Castelao and Barth 2005, Kirincich et al. 2005, Kosro 2005, Di Lorenzo et al. 2008, Menge and Menge 2013). Hence, coastal ocean conditions can alter connectivity within meta-ecosystems by imposing strong variation in the distribution of ecological subsidies, including flows of propagules, nutrients, and organic material across individual ecosystems.
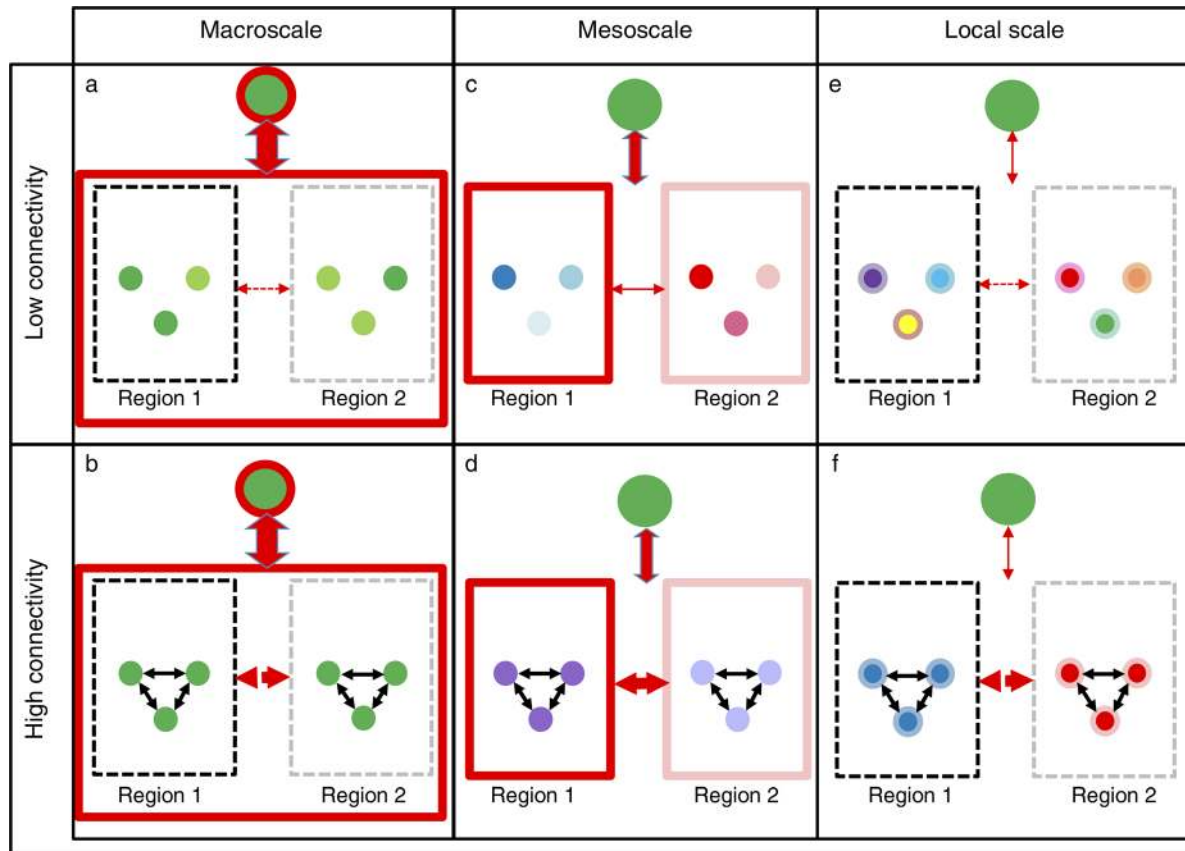
Fig. 1. General conceptual model of different meta-ecosystem configurations based on the relative strength of macro-, meso- (regional), and local-scale (site) flows of ecological subsidies (e.g., nutrients and propagules). Solid lines (around large circles or boxes) indicate the dominant scale of influence on community structure by a factor, while dashed lines indicate substantially reduced influence at that scale. Connectivity among sites (solid circles) is indicated by black two-headed arrows. Red arrows indicate flows of subsidies between macro- and mesoscales (vertical arrows) and between mesoscales (or regions; horizontal arrows). Thick arrows indicate strong flows, thin ones weak flows, and horizontal dashed red arrows indicate minimal to no impact of flows. When all sites share a common source of ecological subsidies (a and b), as shown by similar colors, local community structure will be similar both within and between regions and is macroscale driven. (a) Low connectivity will promote community dissimilarity (different colors) within regions, whereas (b) high connectivity will promote community similarity within and between regions. When sites located in different regions have distinct regional sources of subsidies, (c) community structure will be more dissimilar (colors are more different) between regions than within regions. Further, low (high) connectivity will promote ecosystem dissimilarity (similarity) both (c and d) within and between regions. When each site has a distinct local source of subsidies, community structure is expected to be (e) dissimilar between regions with low connectivity but (f) similar within regions and distinct between regions with high connectivity (site colors indicate relative differences).

A model of meta-ecosystem dynamics

That patterns in ecological systems are a result of processes operating and interacting across multiple scales in space and time has long been a central theme in ecology (e.g., Dayton and Tegner 1984, Wiens 1989, Menge and Olson 1990, Levin 1992, Schneider 2001). As noted by Levin (1992) and others, the amount of variability in a system is expected to increase as smaller scales are examined. One goal of this study is to test this prediction, and in particular, to empirically quantify the level of cross-scale interaction.

The complex spatiotemporal nature of environmental forcing and connectivity can lead to distinct meta-ecosystem predictions about spatial patterns of community structure (Fig. 1). Our model combines the orthogonal effects of the spatial scale of environmental drivers, including macro- (100s to 1000s of km), meso- (10s to 100s of km), and local (100s to 1000s of m) scales, and local connectivity, or the flow of propagules and materials, and ecological subsidies among local ecosystems (red arrows in Fig. 1). The model shows local ecosystems (trios of small circles in Fig. 1) nested within larger regions (rectangles in Fig. 1) differing in environmental conditions and representing mesoscale variation. Each of the six compartments (Fig. 1a–f) thus represents a meta-ecosystem, or collection of local ecosystems in the context of cross-scale environmental variation. Each panel reflects a set of predictions about how the structure of local-scale communities should vary in response to environmental drivers that

operate at macro- (Fig. 1a, b), meso- (Fig. 1c, d), and local (Fig. 1e, f) scales, and how these predictions are modified by differing levels of connectivity (rows in Fig. 1) through ecological subsidies. Note that the thickness of red horizontal arrows indicating connectivity between regions reflects the magnitude of connectivity, while the dashed (solid) arrows indicate a weak (strong) role of these links in determining local ecosystem structure. Here we distinguish between local ecosystems, or sites with biotic and abiotic components, and local communities, which refers just to the biotic components of local ecosystems. The model makes several predictions:

First, when environmental conditions are relatively homogeneous at the macroscale, so that all local ecosystems share a common or "global" pool of ecological subsidies, communities will be similar both within and among distinct geographical regions (Fig. 1a, b). In this case, increased connectivity among sites will promote increased community similarity within and between regions (Fig. 1b). Further, although the magnitude of subsidy flows among regions can vary, when system-wide flows dominate, regional inputs are irrelevant to community structure because they simply convey larger-scale inputs without substantial modification.

Second, when environmental conditions are spatially heterogeneous at the mesoscale and lead to distinct regional pools of ecological subsidies for local ecosystems, community structure will be less similar between regions than within regions (Fig. 1c). Under this scenario, increased connectivity among local ecosystems is also expected to promote community similarity both within and among regions (Fig. 1d; local systems are all shades of purple vs. shades of blue and red with low connectivity). In this case, however, the dominant influence is the among-region flows of subsidies.

Finally, when environmental conditions are spatially heterogeneous at local spatial scales so that each site possesses a distinct local pool of ecological subsidies (Fig. 1e, f; solid circles around each local system), community similarity will be low among local ecosystems both within the same region and among regions. Increased connectivity between sites will homogenize community similarity within a region, but not among regions.

Overall, the model suggests that environmental processes operating at and crossing macro-, meso-, and local scales can lead to distinct spatial patterns of variation in community structure within marine meta-ecosystems. It also suggests that connectivity among the local ecosystems due to material and propagule flows should increase homogeneity among local communities over that expected by local species interactions under the influence of varying environmental conditions alone. If this model is a reasonable approximation of how cross-scale processes interact and generate ecological patterns, then the scales at which heterogeneity among local ecosystems is observed may also provide insights into

the scales over which meta-ecosystem dynamics, and flows of materials and propagules, may occur.

Each compartment of the model in Fig. 1 reflects the "extreme" view that drivers (processes varying with spatial scale and connectivity) affect all components of local communities equally. In reality, however, we recognize that variability in life histories, species composition, and diversity will "blur" these models, and that the emergent model will likely be some combination of how drivers interact with complex local systems. That is, macro- meso-, and local scale environmental and biological factors are all likely to contribute to local community structure.

Application of meta-ecosystem theory to rocky intertidal ecosystems of the northern California Current large marine ecosystem (NCCLME)

We used the meta-ecosystem model and predictions to study meta-ecosystem dynamics within the California Current large marine ecosystem (CCLME), one of the most productive coastal regions in the world (Chavez and Mossié 2009). The focal system in our study was the rocky intertidal region of the northern CCLME (NCCLME), ranging from Bodega Bay in northern California, USA to just north of Depoe Bay, Oregon, USA (Fig. 2). This coastline is roughly linear, with two major headlands (Cape Blanco, Cape Mendocino) and a series of smaller, less prominent capes interspersed around these features. Rocky shores are typically interspersed among, and sometimes mingled with, sandy beaches. Sandy shores can sometimes extend many 10s of km, leading to nonuniform spacing of rocky habitats, and among the latter, only a subset consist of accessible, sloping shores appropriate for ecological research, and thus our choice of study sites.

We tested our model using data collected at (local scale) rocky intertidal sites (ecosystems) within the NCCLME (Fig. 2). The rocky intertidal habitats of the NCCLME have served as a research platform for studies aimed at understanding the linkages between rocky shores and the oceanographic conditions of the inner shelf, defined as the region from the shore to ~10 km offshore (e.g., PISCO studies). To assess variation at local (site), meso- (cape [regional]), and macroscales (the NCCLME meta-ecosystem), we investigated the relationship between oceanographic conditions, ecological subsidies, and patterns of community structure. Here, we define oceanographic conditions (or environmental variation) as strength of upwelling, water and air temperature, and shelf width; and ecological subsidies as nutrients, phytoplankton, and recruitment of invertebrates with pelagic dispersal (see *Methods* for details). Although identifications in our community surveys were done (as realistically possible) to the species level, for the sake of simplicity, we focus on three key ecological functional groups (sessile invertebrates, macrophytes, and their consumers) in the low intertidal zone. We sought to determine if oceanographic variability, occur-
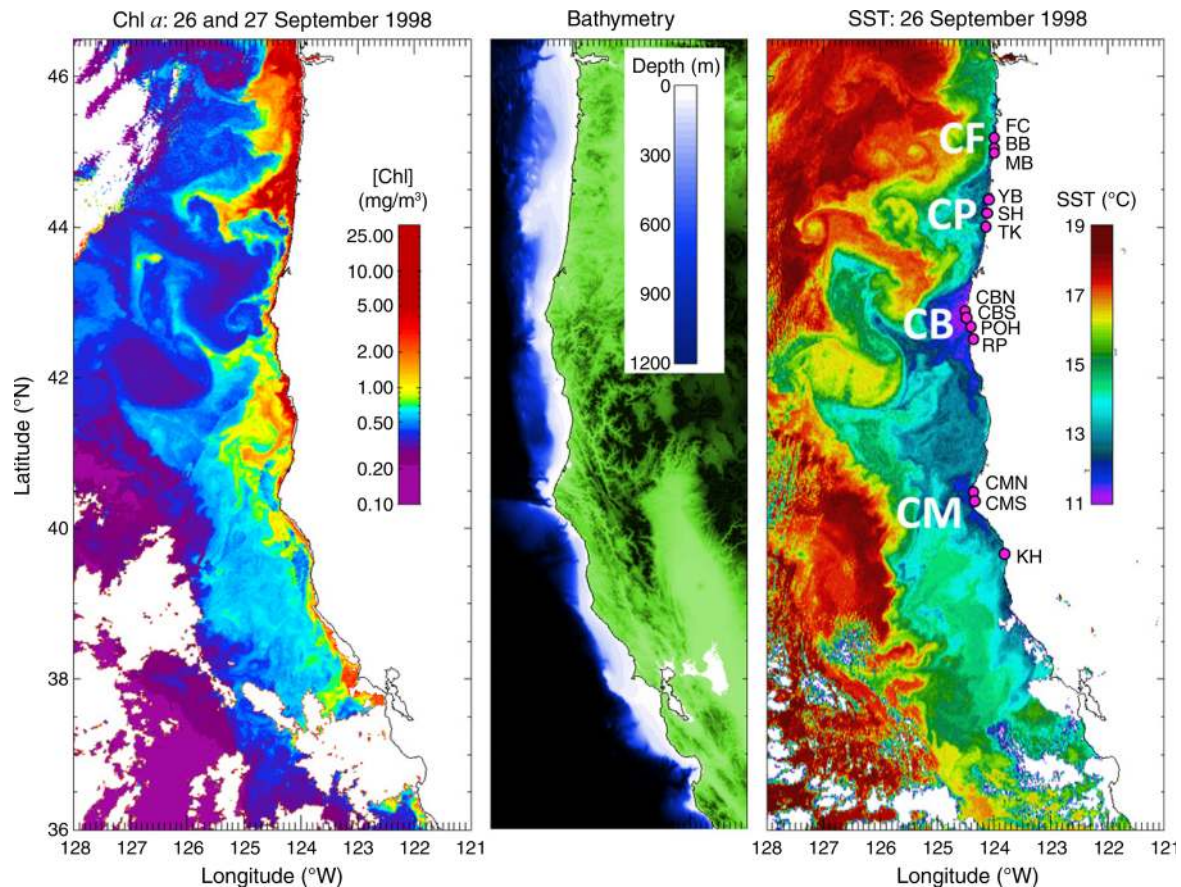
FIG. 2. Remotely sensed composite figures for ocean color (chl *a*; mg/m³), bathymetry, and sea surface temperature (SST) during a period of upwelling in the northern California Current large marine ecosystem (NCCLME) in September 1998. The latitudinal range shown, from just north of the Columbia River (Washington, USA) to the Big Sur coast of California, USA includes the study range, which spanned ~45° to 38° N. Locations of capes (CF, Cape Foulweather; CP, Cape Perpetua; CB, Cape Blanco; CM, Cape Mendocino) and sites (FC, Fogarty Creek; BB, Boiler Bay; MB, Manipulation Bay; YB, Yachats Beach; SH, Strawberry Hill; TK, Tokatee Klootchman; CBN, Cape Blanco North; CBS, Cape Blanco South; POH, Port Orford Head; RP, Rocky Point; CMN, Cape Mendocino North; CMS, Cape Mendocino South; KH, Kibesillah Hill) are shown in the right panel. Images were provided by Corinne James of the College of Oceanic and Atmospheric Sciences, Oregon State University, Corvallis, Oregon, USA.

ring mostly at macro- to mesoscales, was the primary driver of variation in local community structure, or if local processes were primary drivers of local community structure. Because collecting "mechanistic" data on connectivity (e.g., on larval, nutrient, or chlorophyll [chl] *a* transport) was not feasible, our analyses focus on within- and cross-scale spatial patterns of variation in community structure and their relationship to variation in oceanographic conditions and ecological subsidies as reflected in shore-based sensors and sampling.

Oceanographic setting: macro- and mesoscale patterns

A brief description of the oceanographic setting provides an important foundation for our studies. The CCLME is one of the most productive coastal regions in the world (Chavez and Mossié 2009). The California Current flows southward from the mouth of the Straits of Juan de Fuca through Baja California (Huyer 1983,

Hickey 1998, Checkley and Barth 2009). CCLME oceanographic structure varies with latitude in upwelling wind stress and sea surface temperature (SST), continental shelf width (which influences ocean currents), and other oceanographic and atmospheric factors (e.g., Fig. 2; see Strub et al. [1987], Largier et al. [2006], Checkley and Barth [2009] for details). Interactions among upwelling currents, coastal geomorphology, and bottom topography (including shelf width, canyons, banks, and headlands) in turn give rise to discontinuous latitudinal patterns in environmental conditions and ecological subsidies (Ebert and Russell 1988, Graham and Largier 1997, Broitman et al. 2008, Morgan et al. 2009a, b). For example, during upwelling, chl *a* concentration is often high, especially along the Oregon coast. Such blooms can extend well offshore, but discontinuously, with bands of narrow, coast-bound blooms between two broader regions of high phytoplankton concentration

(Fig. 2). South of Cape Blanco (~42.8° N), coastal blooms are briefer and generally narrower, but still vary discontinuously toward the San Francisco Bay area (~38° N). Patterns of SST map closely to the chl *a* pattern (Fig. 2). Upwelling centers (large areas of cold, upwelled water) off Cape Blanco (~42.84° N), Cape Mendocino (~40.50° N), and Point Arena (~38.95° N) also vary discontinuously, with the most intense centers south of the central Oregon coast (Fig. 2).

Bottom topography (e.g., shelf width and offshore banks) further contributes to the spatial organization of coastal oceanography (Castelao and Barth 2005, Largier et al. 2006, Kim and Barth 2011; Fig. 2). Continental shelf width (Fig. 2, center panel) varies in an undulating pattern from north to south, being wide just south of the Columbia River, at ~43.5–44° N near Heceta Bank, and toward the San Francisco Bay area and narrow in between (Fig. 2, center panel). The wider area of chl *a* and cool water at about 44° N occurs along a highly linear coast, suggesting that these features are driven by bottom topography, not coastline geomorphology alone (Castelao and Barth 2005, Kim and Barth 2011). Collectively, these patterns demonstrate macro- (1000s of km) and mesoscale (100s of km) heterogeneity in oceanographic and environmental conditions along the NCCLME meta-ecosystem, and thus represent the two larger spatial scales examined here. Do these inherent scales in physical conditions penetrate shoreward to influence local-scale coastal ecosystems?

Hypotheses and objectives

NCCLME rocky intertidal communities form a large marine meta-ecosystem network suitable for testing predictions of our conceptual model. From 2006 to 2010, we studied 13 local ecosystems nested in each of four capes (representing regions or mesoscales) in the NCCLME meta-ecosystem (macroscale; Fig. 2). Based on prior research (see *Introduction*), we collectively term these nested spatial scales (NCCLME, cape, and site within cape), along with shelf width and year, spatio-temporal variables. We also quantified a group of ecological subsidies (phytoplankton, nitrate, and barnacle and mussel recruitment) and environmental and oceanographic conditions (upwelling, and air and water temperature) to characterize local conditions and provide insights into connectivity. We used these observations to test a null and four alternative hypotheses. H_0; local community structure is independent of macro- and mesoscales of oceanographic variation and ecological subsidies (Fig. 1e). H_{A1}; local community structure is dependent on local oceanographic variation and inputs of ecological subsidies shared among local ecosystems (Fig. 1f). H_{A2}; local community structure is dependent on regional, or mesoscale, oceanographic variation in ecological subsidies (e.g., Fig. 1c or d, depending on the degree of connectivity). H_{A3}; local community structure is dependent on large, or macroscale, oceanographic variation in

ecological subsidies (e.g., Fig. 1a or b, depending on the degree of connectivity). H_{A4}; local community structure is dependent on a mix of cross-scale factors, but predominantly on ocean-driven variability.

To test these hypotheses, we had four specific objectives: (1) Quantify patterns of low intertidal community structure to examine their variability at different spatial and temporal scales, (2) establish the environmental context by summarizing macro- and mesoscale oceanographic and environmental patterns, and quantifying local-scale environmental conditions, (3) characterize the spatial patterns of apparent ecological subsidies of the inner shelf ocean, and (4) evaluate the relative contributions of local- (site), to meso- (region or cape) to macroscale (coastal, annual) environmental variability on community structure.

METHODS

Study sites

Study sites ranged across 725 km, from Cape Foulweather (CF) in the north to Cape Mendocino (CM) in the south (Fig. 2, Appendix A: Table A1). Our research was conducted on the most wave-exposed and accessible locations on gradually sloping rocky benches within each cape or region, and thus all were exposed to moderate wave action (Appendix B).

Site selection was driven by oceanographic spatial variability as described in the *Introduction*. Macroscale variation is expressed as that occurring within the NCCLME, and mesoscale variation is expressed as that associated with capes (Fig. 2). Within each cape, local site selection was driven by two factors in addition to being amenable to ecological research: (1) being central, or away from the edges of the oceanographic conditions associated with each cape, and (2) being accessible by foot. On CF and CM, the chosen sites were the only ones that fulfilled all criteria, while at Cape Perpetua (CP) and Cape Blanco (CB; see Plate 1), they were a subset of a slightly larger pool of acceptable locations. Three sites were chosen at all capes but CB, where POH (see Fig. 2 caption for site abbreviations) was included because it was observationally similar to CP sites, and could represent variation inherent to a region or cape, thus demonstrating possible links between larger and local scales.

Quantification of community structure

At all sites, we surveyed low intertidal zone (e.g., tidal height ± ~0.7 m) community structure in June and July 2006 and 2008–2010. We used a sector-quadrat method, which involves visual sampling in 10 haphazardly chosen 0.25-m² quadrats per each of two to three sectors per site (e.g., Menge et al. 2011*b*). Quadrats were subdivided into 25 10 × 10 cm squares, each of which included 4% of the total area enclosed by the frame. Visual estimates of total cover of each component in the quadrat were made by totaling the percentage of the quadrat occupied by each taxon across the 25 squares

(Dethier et al. 1993). Although our surveys were done at the species or near-species level, analyses focused on major functional groups of spatially dominant sessile invertebrates (e.g., barnacles and mussels), macrophytes (e.g., canopy and understory macroalgae and sea-grasses), and consumers (e.g., predators and herbivores).

Since the upwelling season is the time of highest biological activity, all analyses were conducted on summer (June and July) surveys. Our surveys also captured any impacts of wintertime disturbance, because resulting patches are easily identified in summer, although disturbance is minimal in the low intertidal zone (e.g., Menge et al. 2005). Prior research in this system has shown that, although community structure varies seasonally, such variation was due mostly to modest declines (increases) in macrophyte biomass in fall/winter (spring/summer; e.g., Turner 1983, 1985, Menge et al. 2005, Schoch et al. 2006).

Oceanographic and environmental measurements

To provide relevant physical oceanographic and environmental context for our local-scale ecological observations, we quantified upwelling, and air and water temperature. To match the biological sampling period, we used data from the upwelling season only, i.e., from April through September. To analyze the contribution of shelf width to variation in community structure and experimental results, we obtained data for 100 and 200-m isobaths at the site level from the ETOPO1 database. We obtained values of the Bakun upwelling index (cubic meters of upwelling water per second along each 100 m of coastline) for the years of our study (2006–2010) from NOAA, using values closest to 1° or less of the latitude of each site. We also deployed three replicate Pendant temperature loggers (Onset, Bourne, Massachusetts, USA), set to log at 5-min intervals, in the low intertidal at all sites. To fill in gaps when Pendants were inoperative, we supplemented the data from replicate TidBit loggers (Onset) deployed in low zones at most sites. A detiding program was used to separate air from water temperatures (e.g., Menge et al. 2008).

Ecological subsidy measurements

Following prior usage (e.g., Polis and Hurd 1996, Menge et al. 1997a, Massol et al. 2011), we define ecological subsidies to include nutrients (inorganic N, nitrate + nitrite [N + N]), phytoplankton (chl a), and recruitment of sessile invertebrates. Inorganic nitrogen was defined as an ecological subsidy because it is the primary limiting macronutrient in marine ecosystems, varies substantially with upwelling, fuels benthic primary production in the intertidal (e.g., Nielsen and Navarrete 2004), and underlies the phytoplankton supporting filter-feeding organisms (e.g., Bracken et al. 2012). Because the dominant intertidal invertebrates, barnacles and mussels, owe their population replenishment to recruitment of planktonic larvae potentially from different local sites (e.g., Barshis et al. 2011), we

also define recruitment as a subsidy to the system (e.g., Witman et al. 2010, Menge and Menge 2013).

Inorganic N.—Water samples for quantification of N + N were collected in triplicate, at each site at low tide, by dipping 250-mL opaque plastic bottles (high density polyethylene; HDPE) to ~30–50 cm depth while standing at the water's edge. Within 30 min of collection, samples were filtered in the field through pre-combusted (450°C for 4 h) 25-mm Whatman GF/F glass fiber filters (GE Healthcare Life Sciences, Pittsburgh, Pennsylvania, USA). Filtrates were collected in 20-mL acid-washed polyethylene vials, placed on ice, and transported back to the lab, where they were frozen for later analysis. In the lab, nitrate was reduced to nitrite via exposure to a cadmium copper column (Strickland and Parsons 1968) or spongy cadmium (Jones 1984). Concentration of N + N was determined spectrophotometrically following the formation of an azo dye from reaction with an acid sulfanilimide and N-(1-naphthyl) ethylenediamine dihydrochloride solution (Strickland and Parsons 1968).

Chlorophyll a.—We quantified phytoplankton abundance in the bottle samples (*Methods* in Menge et al. [1997b]) and chl a fluorescence. Annual and monthly mean chl a by site was calculated as the average of all sample means during the April–September upwelling season when most phytoplankton blooms occur. For example, earlier analyses have shown that on average, chl a is low in winter (2.5 ± 0.3 μg/L; $n = 29$ samples) compared to summer (14.3 ± 0.9 μg/L; $n = 379$ samples). We also deployed fluorometers (Wetlabs ECOFL, WET Labs, Philomath, Oregon, USA) at most sites for comparison with patterns documented by point-in-time bottle samples, and found that both methods reliably documented differences among capes and sites (Appendix B: Fig. B8).

Recruitment.—We quantified sessile invertebrate recruitment using well-established methods (e.g., Menge et al. 2009). Monthly deployments of five collectors (10 × 10 cm PVC plates covered with a nonskid surface for barnacles and plastic mesh pot scrubbers for mussels) were retrieved at each of the 13 sites (11 sites in 2006, 2007) and stored in a −10°C freezer for later counts. Barnacle and mussel recruits were counted under a dissecting microscope. Prior analysis (Menge et al. 2010) has shown that monthly recruitment of barnacles is positively correlated with abundance of cyprids (i.e., "settlers"; $P = 0.003$, $R^2 = 0.7$), suggesting that, although the total number of settlers is always greater than the number of recruits due to post-settlement mortality, recruitment provides a reasonable proxy for relative propagule input for barnacles. We assume the same is true for mussels, although we have not explicitly tested this assumption.

Data analysis

Analyses employed JMP v. 8.0.2.2 (SAS Institute, Cary, North Carolina, USA), SAS/STAT v. 9.2 (SAS

Institute), and R (R Development Core Team 2014). Data were transformed for final analysis, using ln-transformations (densities, counts, magnitudes, percent covers when the maximum value was <100%) and arcsine-transformations (proportions or percent cover when bounded at 100%). Data were checked visually for normality using probability plots and variance equality using plots of residuals against predicted values, and met these assumptions in most cases.

The statistical analyses employed depended on the objective. Community surveys were ultimately aimed at evaluating how the (1) integrated community and (2) its main functional components responded to the explanatory variables, so the analyses used multivariate approaches. First, to determine how functional components of the community varied across meso- to local scales and by year, we tested the effects of cape (mesoscale), year, cape × year, and site nested within cape (local scale) on abundance of barnacles, mussels, and canopy and understory macrophytes using nested multivariate analysis of variance (nMANOVA).

Next, to determine if ecological subsidies and environmental data varied on meso- or local scales, we evaluated the dominant scales of variation using nested three-way ANOVA. Using monthly averages from the upwelling season only (April through September) to estimate annual averages for 2006 to 2010, we tested for differences in upwelling season nitrate and phytoplankton abundance, barnacle and mussel recruitment, upwelling strength, air temperature, and water temperature. Factors were year, cape, and site nested within cape. These spatiotemporal factors were modeled as random effects to obtain variance components for each factor.

To generate a null expectation about how community structure might vary if driven solely by spatial proximity and arrangement along the coast, we used hierarchical cluster analysis of sites based on geographical distance. Similarly, to generate a null expectation about how community structure might vary if driven solely by environmental conditions, we used hierarchical cluster analysis based on Bray-Curtis dissimilarity between average environmental conditions at each site. The clustering pattern of community structure between sites was then compared to these two scenarios, which represent opposite ends of the spatial–environmental continuum.

We combined ecological and environmental data sets to relate community structure to the explanatory variables. Permutation-based MANOVA (PERMANO-VA) allowed assessment of the environmental–community structure relationship by considering the relative influence of local- vs. mesoscale factors on Bray-Curtis community (dis)similarity. We also used redundancy analysis (RDA), a form of constrained ordination that attempts to explain community structure using a linear combination of ecological subsidies and environmental conditions (Legendre and Legendre 1998). The multi-variate analyses were performed using the vegan package for R (Oksanen et al. 2013).

To complement these methods, we used path analysis (Li 1975, Sokal and Rohlf 1995, Grace and Bollen 2005, Grace et al. 2012) to explore linkages occurring among factors within each set of explanatory variables that affect community structure as well as between the sets of explanatory variables. For example, upwelling circulation is likely linked to shelf width (e.g., Castelao and Barth 2005, Botsford et al. 2006, Kim and Barth 2011), and upwelling can affect factors such as water temperature, nutrients, phytoplankton abundance, light attenuation (water clarity), and recruitment. In turn, these factors are likely to influence growth and/or abundance of macrophytes, sessile invertebrates, predators, and herbivores. Path analysis can be thought of as a series of multiple regressions linking variables based on an a priori model (Wootton 1994, Petraitis et al. 1996). By allowing variables to serve as both endogenous (response) and exogenous (explanatory) variables, path analysis can be used to quantify direct and indirect relationships via path coefficients. In our model, the path coefficients are standardized so they represent the predicted response in units of standard deviations (Grace and Bollen 2005). Using the SEM package in R (Fox et al. 2014), we used the classical likelihood approach to fit the model covariance matrix to the observed covariance matrix (e.g., Grace et al. 2012). Thus, our path analysis shares the same assumptions as general linear models, namely normality and independence of residuals, homoscedasticity, linear relationships between endogenous and exogenous variables, and lack of collinearity between variables. To adhere to these assumptions, all variables were square root- or $\log_{10}$-transformed as needed. Additionally, we computed the variance inflation factor (VIF) to ensure that multi-collinearity remained low (VIF < 5). We generated multiple alternative models to investigate different relationships between the variables in our data set based on prior understanding of functional group interactions and likely environmental influences. However, we present only the final model whose Akaike information criterion, corrected for small sample sizes (AIC_c), value was significantly lower than that of all other models (AIC weight >0.99).

RESULTS

Community structure

At the cape scale, low intertidal communities were macrophyte-dominated at CF, CB (except for POH), and CM (Fig. 3; canopy plus understory groups were always more abundant than sessile invertebrates). In contrast, at CP, the low zone was dominated by sessile invertebrates and understory algae (Fig. 3; Appendix B: Fig. B1). As expected, the exceptional site, POH, showed patterns that were consistently more similar to those at CP than CB, suggesting variation in structuring forces at the local scale in some cases.
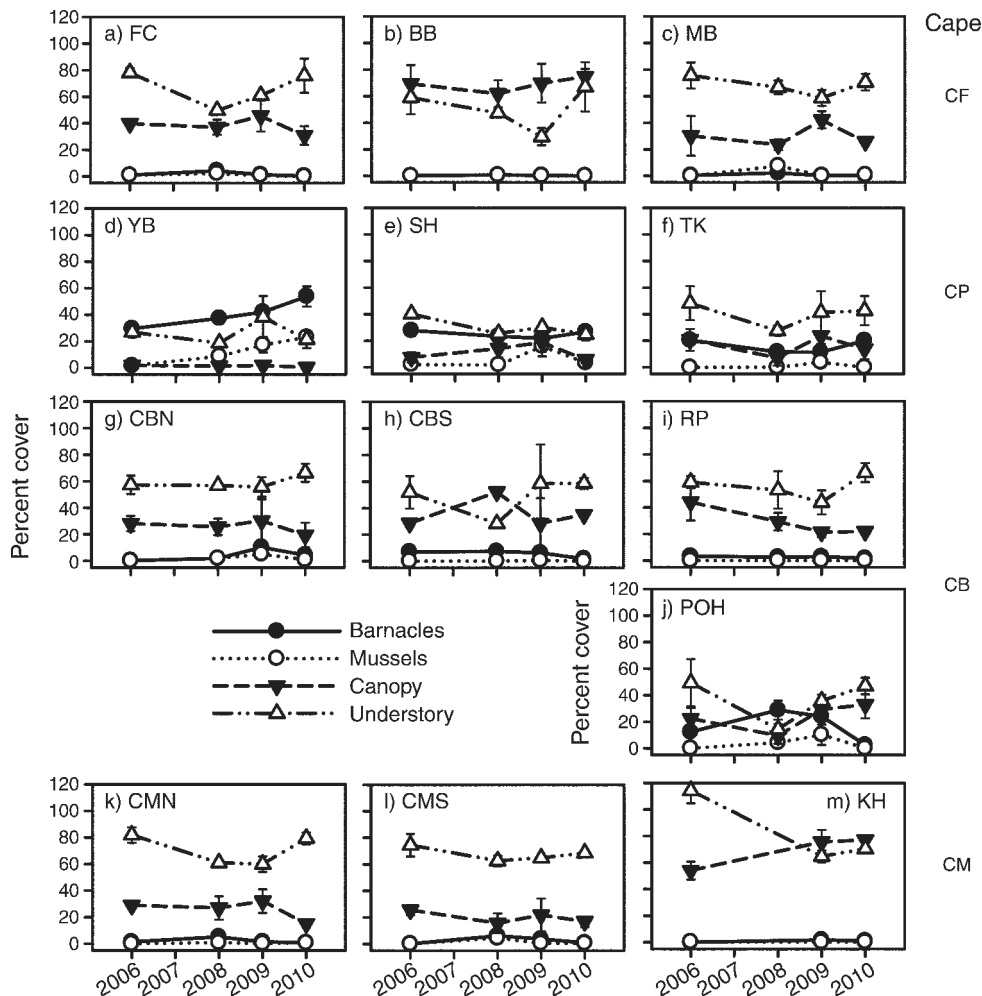
Fig. 3. Time series from 2006 to 2010 of abundance (mean percent cover ± SE) of major space occupiers (barnacles, mussels, canopy, understory) at all sites, nested within the four capes, arranged from north to south from top to bottom and from left to right within each cape. See Fig. 2 and Appendix A: Table A2 for details.

Community structure, defined as abundance of functional groups (barnacles, mussels, canopy and understory macrophytes) varied by cape, year (2006, 2009, and 2010), cape × year, and site nested within cape (Appendix A: Table A2A; Appendix B: Figs. B1 and B2; MANOVA, $P < 0.0001$ in all cases). In all years, structure at CF differed from that at CP and CB but not from CM (linear contrasts, cape × year interaction, $P < 0.05$). CP also differed from CB and CM, while CB differed from CM in 2006 and 2009 but not in 2010 (linear contrasts, cape × year interaction, $P < 0.05$). Among sites nested within capes, differences occurred in 10 of 15 comparisons, indicating considerable variability at the local (site) scale as well as at the mesoscale (regional) of capes (linear contrasts for site [cape], Appendix A: Table A2A).

Averaging abundances of these major functional groups across time clarifies the spatial patterns (Appendix B: Fig. B1; differences determined by linear contrasts). For sessile invertebrates at the cape scale, cover of barnacles, ranked highest to lowest, was CP > CB > CF = CM, while mussels were sparse at all capes but CP. Abundances at the site scales generally reflected patterns seen across capes, except that POH tended to have higher mussel cover than other CB sites.

Canopy and understory abundances of macrophytes were generally opposite in pattern to the sessile invertebrates (Appendix B: Fig. B3). At the cape scale, with the exception of canopy at CM, the general ranking was CM = CF > CB > CP. At the site scale, canopy cover was greatest at sites within CF (BB) and CM (KH), least abundant at YB within CP, but otherwise similar among sites. Understory cover varied among sites within capes (Appendix B: Fig. B1), but still generally followed the ranking listed. Analyses at the taxon level are given in Appendix B: Figs. B2 and B3. These analyses indicate that variation in abundance of

functional groups of sessile organisms, and in component taxa, occurs at local scales (among sites within cape and within sites through time) and mesoscales.

We performed cluster analyses to quantify the extent of these similarities and compare them to our expectation (Fig. 4). With exceptions, communities at sites tend to cluster within capes (Fig. 4; Appendix B: Figs. B1–B3). We found that while as expected, communities at CP and CB sites clustered together, sites at CF and CM were intermingled and hence even more closely similar than we expected (Fig. 4c). Interestingly, while FC and MB (CF sites) clustered with CMN and CMS (CM) sites, communities at neither BB, only a few hundred meters separated from FC and MB, nor KH, a site ~60 km from the other CM sites, clustered closely with their respective cape-mates, but rather with each other. On the other hand, clustering based on abiotic environmental conditions (Fig. 4b) indicates that BB and KH tend to cluster with the other sites in their capes, while sites at CB are split, with RP clustering with the CM sites and POH clustering with the CP sites. Hence, CM and CF sites were very similar overall, CB sites were next most similar to these, and CP sites were most different.

Environmental context

Shelf width.—Analysis of shelf width at both 100 and 200-m isobaths reveals variability at all scales, but primarily at the cape scale (Appendix B: Fig. B4). Sites within capes tend to have similar offshore shelf widths. Along the coast, the width of the continental shelf (distance to 200 m) varies from ~9 to 65 km. The differences between 100 and 200-m depths shows that the steepness of the shelf slope also varies, from steep at northern California sites to more gently sloping along the central Oregon coast.

Upwelling.—Upwelling varied at macro-, meso-, and interannual scales (Fig. 5a; Appendix A: Table A3). Upwelling varied by cape and among years, but spatial trends in upwelling remained constant over time (no cape × year interaction; Appendix A: Table A3). During 2006–2010, annual upwelling strength varied among years but with no obvious trend, and was generally stronger at southern than northern sites (Appendix B: Fig. B5). Site effects were not analyzed due to the coarseness of the Bakun index and its inability to resolve at the site scale.

Temperatures.—Surprisingly, neither average air nor average water temperature varied among capes, although both varied among years ($P < 0.0001$) and sites within capes ($P = 0.043$). However, air temperature coefficient of variation (CV) differed at local and mesoscales, while water temperature CV differed primarily at the local scale (Fig. 5b, c; Appendix B: Fig. B6). Air temperature CV varied with cape and year and among sites within capes, but not with cape × year (Appendix A: Table A3). Air temperatures tended to be similarly less variable from SH north and similarly more

variable from TK south, with the exception of POH (a CB site) and CMS (a CM site), which were ranked with the northern sites (Appendix B: Fig. B6). Water temperature CV differed among years and among sites nested within cape, but not among capes or cape × year (Appendix A: Table A3). Water temperature CV varied less among sites than did air temperature CV (Appendix B: Fig. B6).

Inorganic N.—Spatial variation in N + N occurred primarily at mesoscales and through time, but did not differ among sites nested within capes (Fig. 5d; Appendix A: Table A3; Appendix B: Fig. B7). In 2006 and 2007, N + N did not vary among sites, but did in 2008–2010. Despite temporal and cape-scale variation, spatial trends remained constant through time (Appendix A: Table A3).

Chlorophyll a.—Like nutrients, phytoplankton abundance varied spatially primarily at mesoscales (Fig. 5e; Appendix A: Table A3). This pattern was consistent between bottle and fluorescence sampling methods, suggesting that lower frequency point samples (bottles) captured the general pattern of variation in chl *a* concentration among sites as quantified by field fluorometry (e.g., Appendix B: Fig. B8). In both data sets, CF and CM had similarly low and CP and CB had similarly high chl *a* abundances. Phytoplankton abundance varied differentially with cape and year (Appendix A: Table A3; Appendix B: Fig. B9). Phytoplankton did not vary among sites nested within capes, but within CF, FC > MB (Appendix B: Fig. B9).

Recruitment.—Barnacle and mussel recruitment varied more at meso- than at local scales (Fig. 5f, g), although spatial and temporal patterns of recruitment showed some differences (Appendix B: Figs. B10 and B11; note different scales on ordinates). For example, both taxa varied at the cape scale, but only barnacle recruitment varied among years (Appendix A: Table A3). Among sites within capes, barnacle recruitment at CF did not differ ($P > 0.05$), but rank order within CP was YB > SH = TK, within CB was POH = CBS > CBN > RP, and within CM was CMS = CMN > KH (linear contrasts). Mussel recruitment also varied among sites within capes. Sites within CM did not differ, but rank order within CF was FC > BB = MB, CP was YB > SH > TK, and CB was POH = CBS, POH > CBN = RP, CBS = CBN, CBS > RP.

Variance components.—Most variation in environmental factors was attributable to the cape, or mesoscale (Fig. 5; Appendix A: Table A4). For upwelling, N + N, chl *a*, and barnacle mussel recruitment, the cape scale accounted for the majority of the variance not accounted for by time (Fig. 5). Time (year, year × cape) accounted for the majority of the variance in water temperature CV and N + N, while site within cape accounted for the majority of variance in air temperature CV and a substantial fraction of variance in barnacle recruitment.
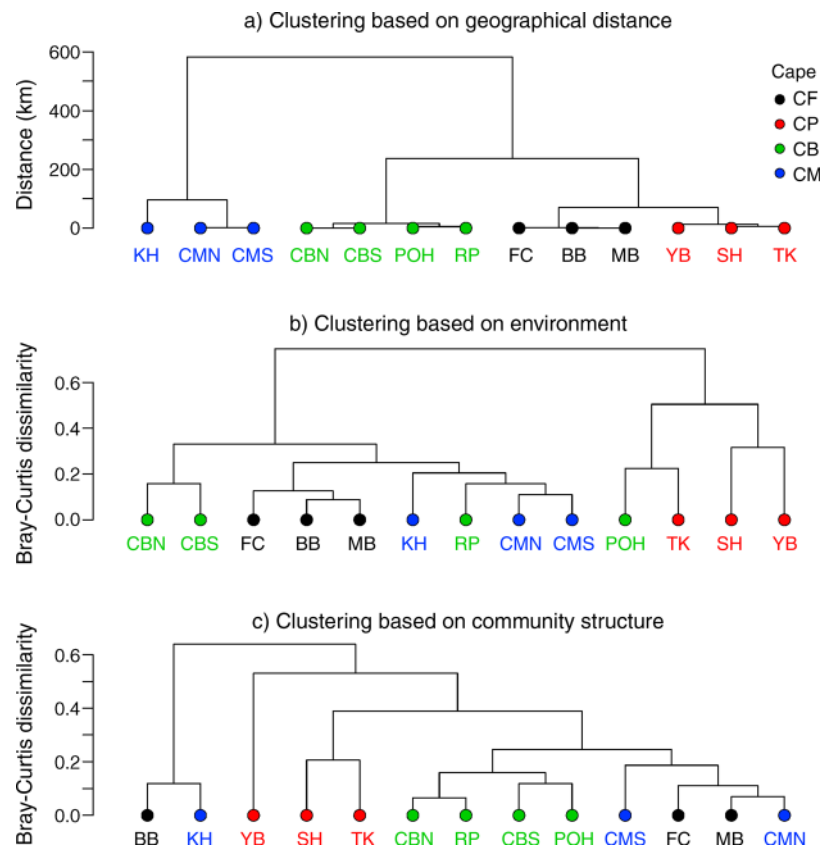
FIG. 4. Cluster analysis based on (a) geographical distance between sites, and Bray-Curtis dissimilarity between average and observed (b) environmental conditions and (c) community structure at all sites during the duration of the study. Sites are color coded by cape; Cape Foulweather (CF), Cape Perpetua (CP), Cape Blanco (CB), and Cape Mendocino (CM).

Relationship between community structure and environmental context

Association between oceanographic conditions, geographic location, ecological subsidies, and community structure.—Local-scale communities clustered into distinct groups at the cape scale, and varied with respect to their associations with ecological subsidies and environmental factors (Fig. 6; Appendix A: Table A5). Communities at sites on capes CF, CB, and CM (black circular, green diamond, and blue triangle symbols in Fig. 6) generally clustered together, with high overlap between CF and CM, and were generally dominated by abundant canopy, understory, and turf-forming algae. These communities and how they differed over time were also positively associated with upwelling, temperature, and nutrients, varying primarily along the vertical axis, RDA2 (Fig. 6). Communities at CP (red squares in Fig. 6) were quite distinct from the other three capes, and were dominated by abundant barnacles, mussels, and predators. These communities were associated with high levels of recruitment and chl *a*, and large shelf width, separating along the horizontal axis, RDA1. Herbivores did not cluster with any

cape, suggesting their abundance varied independently of geography.

The RDA axes differed in their relationships to subsidies and environmental factors (Fig. 6). CP-related patterns and factors tended to be most strongly and positively associated with RDA1, while environmental factors at other capes tended to be more associated with either positive (NO_3 and upwelling) or negative (air and water temperatures) values of RDA2, and functional groups were more associated with negative values of RDA1 (Fig. 6; Appendix A: Table A5).

PERMANOVA revealed that environmental factors, ecological subsidies, space, and time were all important contributors to community variance, but the majority of the variance in community structure due to external influences was associated with mesoscale variation, with local-scale variation being mostly associated with temperature (Fig. 7; Appendix A: Table A6). For example, upwelling and upwelling CV explained 22.7% of the variation, and combined environmental factors (upwelling and temperatures) explained 42.3% of the variance (Fig. 7; Appendix A: Table A6, sums of coefficients of determination). Ecological subsidies (N + N, phytoplankton, recruitment) accounted for 18.4%,
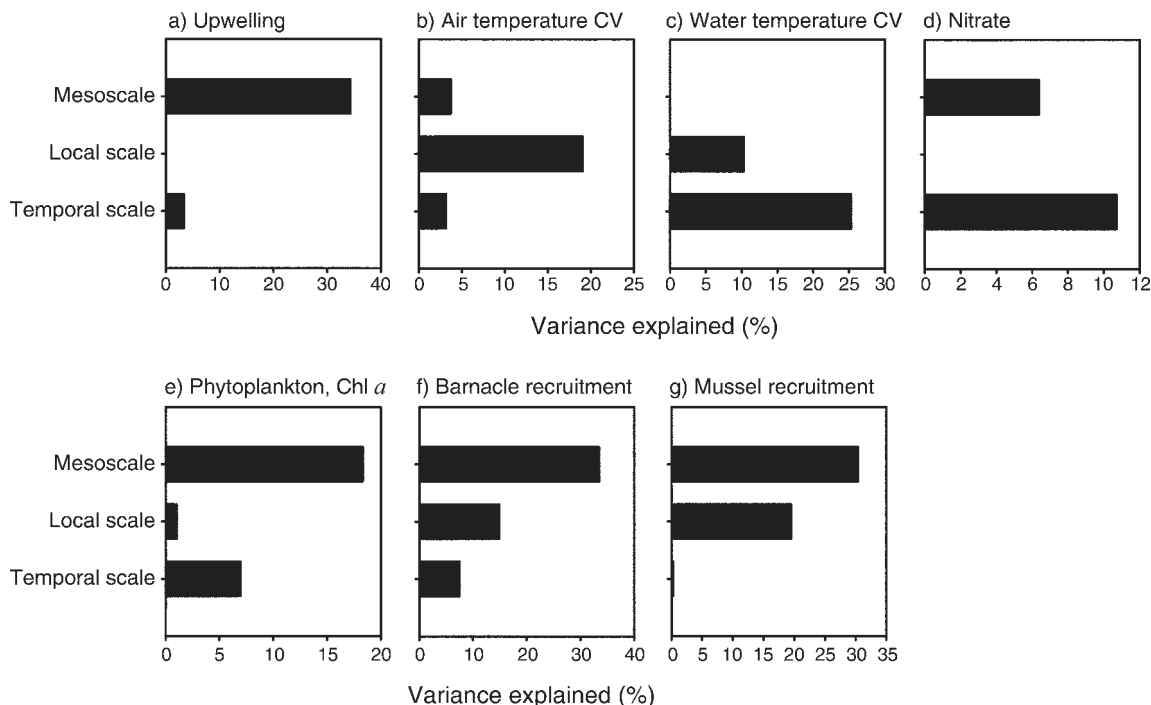
Fig. 5. Percentage of variance in environmental factors and ecological subsidies explained by spatial and temporal scales. Data are taken from Appendix A: Table A4.

space (capes, sites) accounted for 18.2%, and time (years) accounted for 16.7% of the variance. Hence, overall, mesoscale factors (environmental factors, subsidies, cape) accounted for 52.1% and local-scale factors (temperature, site) accounted for 26.8% of community variance.

Hierarchical scales: ocean to coast filtering.—The hierarchical flow from larger-scale variation in spatial and oceanographic factors such as shelf width and upwelling to local-scale patterns of community structure (at the functional group level) indicates a strong association between shelf width and community structure (Fig. 8; Appendix A: Table A7; Appendix B: Fig. B12). The path analysis links a wider, more gently sloping shelf with reduced upwelling, N + N, and canopy macroalgae, and with increased chl *a*, recruitment, and sessile invertebrates (Fig. 8). Increased upwelling was associated with increased N + N and invertebrates, and decreased recruitment; increased N + N was associated with increased chl *a*; and increased chl *a* was associated with increased sessile invertebrates and decreased algal turf. Increased sessile invertebrate abundance was associated with reduced canopy macrophytes and increased predator abundance, and increased canopy cover was also associated with increased algal turf. Interestingly, water temperature had a negative association with herbivore abundance, while N + N had a marginally positive influence of similar magnitude, suggesting that metabolic and energetic factors have an influence on herbivores (Fig. 8).

DISCUSSION

Historically, coastal ecologists explicitly or implicitly assumed that oceanographic variation was not expressed at the site scale, but that inputs of larvae, food for filter feeders, and nutrients for primary producers to coastal sites were products of a relatively homogeneous oceanic "bath." Thus, patterns seen onshore were thought to be a consequence of localized environmental stresses (e.g., thermal, wave, UV) and species interactions (e.g., Menge 1992). The discovery that coastal oceans were in fact highly heterogeneous, as perhaps most clearly revealed by the advent of satellite imagery (e.g., Strub et al. 1987), sparked a new track of research that increasingly incorporated a component of coupling between coastal habitats and the adjacent ocean (e.g., Underwood and Denley 1984, Gaines and Roughgarden 1985, Roughgarden et al. 1988, Bustamante et al. 1995, Menge et al. 1997*a*, Nielsen and Navarrete 2004, Blanchette et al. 2008, Broitman et al. 2008, Witman et al. 2010, Woodson et al. 2012, Menge and Menge 2013, Vinueza et al. 2014). Such studies hypothesized and/or revealed an important, sometimes dominant effect of large, oceanographic-scale processes on aspects of local-scale community structure and/or dynamics. Our goal here was to apply and assess the generalized concepts and theory of meta-ecosystem ecology by (1) proposing a specific model of marine meta-ecosystem dynamics, (2) testing it using a highly detailed and multifactorial, multi-scale data set, and thereby (3)
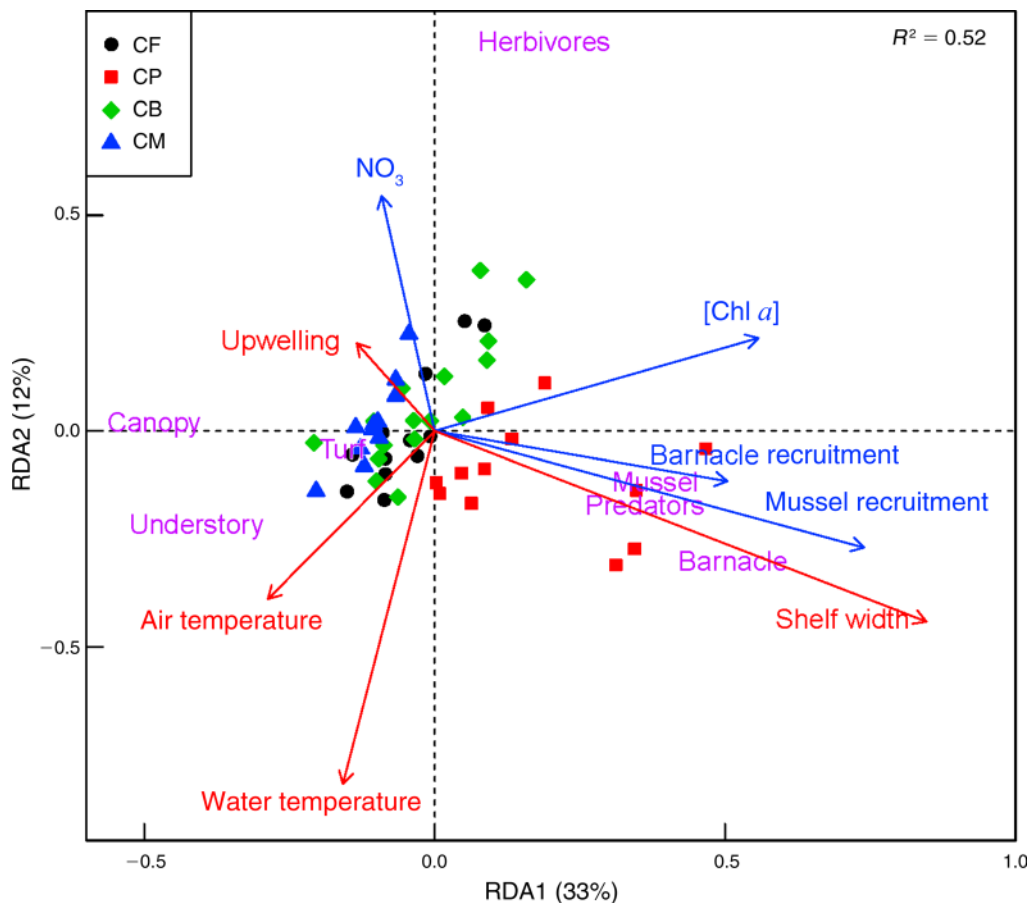
Fig. 6. Redundancy analysis (RDA) of community survey data. The vectors represent the contribution of oceanographic inputs (blue) and environmental conditions (red) to the RDA axes. The spatial variables were classified as local-, meso-, or macroscales based on their range using (semi)variograms. The pink text represents the species scores for the functional groups in the intertidal community. Each cape's site scores were plotted using a distinct symbol and color. Each site score represents a separate site × year combination, axis labels show percentage of variance explained by each RDA.

determining the relative importance of processes operating at local, regional, and coastal scales.

We initiated this research by asking several questions: Does variation in oceanographic and environmental conditions, and in ecological subsidies observed in coastal ecosystems, occurring at multiple scales in space and time, have an impact on local community structure? If so, which scales are most important? Are our results consistent with meta-ecosystem theory? We explore the extent to which our analyses answer these questions, and conclude by discussing the likely generality of our results, and how they advance the field of meta-ecosystem ecology.

Empirical patterns vs. model predictions

The models presented in Fig. 1 are meant to be general, and to outline alternative versions that are potentially broadly applicable to terrestrial, aquatic, and marine habitats. In Fig. 9, we assemble our results by factor and summarize how each varies with spatial scale.

The figure reflects the spatial arrangement of our study sites and capes from north to south (see Fig. 2).

The hierarchical aspect of our model (Fig. 1), and the idea that larger-scale oceanic drivers are filtered (e.g., by shelf contours, coastal geomorphology, river inputs, shelf steepness, submarine canyons, etc.) as they near the shore is supported by our analyses, and shown by the successive sets of scaled mean values to the right of the upwelling panels (Fig. 9). Shelf width clearly varies geographically, and this variation is associated with spatial differences in N + N, chl *a*, sessile invertebrate recruitment, and community structure (Fig. 9). The relatively invariant patterns of air and water temperature we documented are also reflected in Fig. 9.

Of the five hypotheses proposed in the *Introduction*, our results clearly reject the null hypothesis (H_0); i.e., independence of local community structure from oceanographic and ecological subsidy influences (Fig. 1e) was not supported. In addition to the biogeographic-scale variation to be expected in any coastal meta-ecosystem (e.g., Blanchette et al. 2008, 2009,
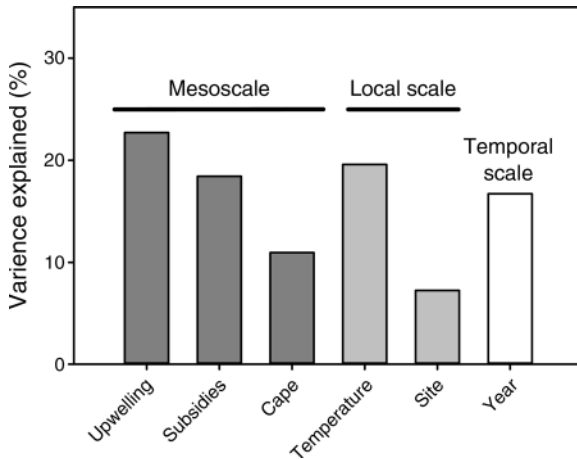
FIG. 7. Percentage of variance in community structure explained by environmental factors, ecological subsidies, space, and time, analyzed by PERMANOVA and arranged by scale. Data are taken from Appendix A: Table A6.

Wieters et al. 2009, Schiel 2011, Fenberg et al. 2014, Lathlean et al. 2014), local community structure clearly varied at local and regional (cape) scales, and this variation was strongly associated with variation in ecological subsidies across all scales considered. The simple observation that most variation in community structure as well as environmental conditions and inputs occurred at site and cape scales also rejects H_{A3}, that community structure is entirely macroscale driven. Because 52% of the variance was explained by mesoscale-linked variation and 27% was explained by local-scale variation (see Appendix B for discussion of

causes of local-scale variation in community structure), and environmental factors, ecological subsidies, and cape (regional space) accounted for more variance than did temperature and site (local space; Table 1, Fig. 8), we suggest that H_{A4} (community structure is driven by factors varying across scales, environmental factors dominating) is most strongly supported. This conclusion also indicates that variation in community structure is not simply a function of space, or latitude, but is most responsive to regional variation in subsidies and oceanography. Thus, the cluster analysis of community structure more closely resembles the clustering expected on the basis of both environmental similarity and spatial proximity (Fig. 4). The similarity of sites at the most widely separated capes emphasizes the strong impact of oceanography on community structure.

Our results suggest that the NCCLME coastal system reflects the range of scenarios encompassed in the general model of Fig. 1c. That is, oceanographic drivers at macro-, meso-, and local scales appear to be important determinants of meta-ecosystem structure. Path analysis (Fig. 8) clearly shows this hierarchical flow of factors. For example, N + N, larvae, and phytoplankton subsidies varied among sites within capes and between capes (Figs. 6, 9; Appendix B: Figs. B7–B11), indicating important influences of meso- and local scales on these inputs. The positive links from recruitment to sessile invertebrates and from sessile invertebrates to predators (Fig. 8) suggest that density of predators is driven by meso- to local-scale subsidies of prey recruits, and the resulting local-scale increase in abundance of sessile invertebrates. The stronger impact of predation at
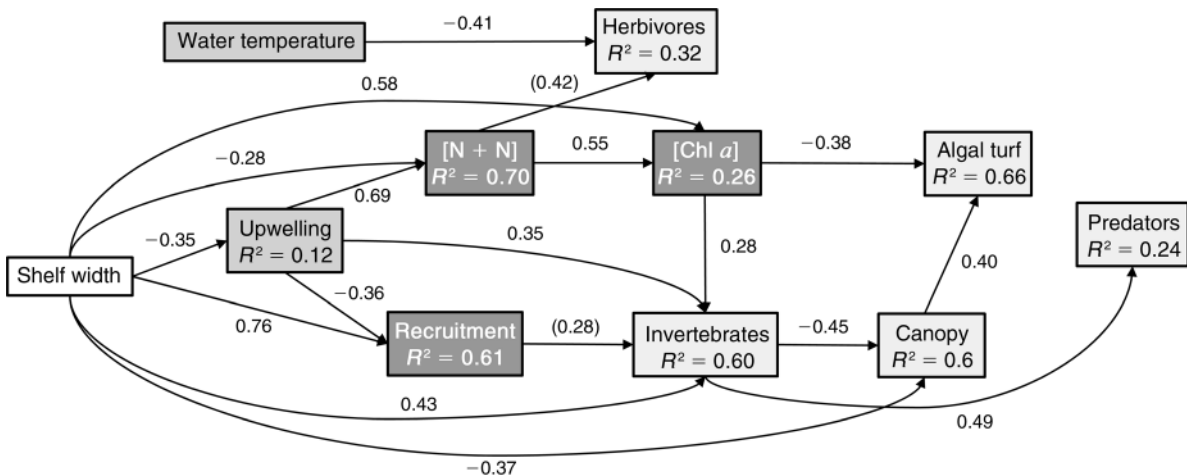

FIG. 8. Path analysis showing the flow of effects from larger to more local scales, through the intermediate set of environmental variables and ecological subsidies. Numbers by arrows are standardized path coefficients, which represent the predicted response in units of standard deviations. Coefficients significant at $P < 0.1$ are in parentheses; other coefficients are significant at $P < 0.05$. R^2 values represent the amount of variation in the endogenous (response) variable explained by all independent variables that point to it via arrows. Shades indicate the hierarchy through which effects flow, from shelf width (white) to upwelling (medium gray) to ecological subsidies (dark gray) to components of local community structure (light gray). Factors or links not shown were not significant at $P > 0.1$. Surprises are a lack of links from upwelling or shelf width to water temperature, and N + N to algal turf and canopy.
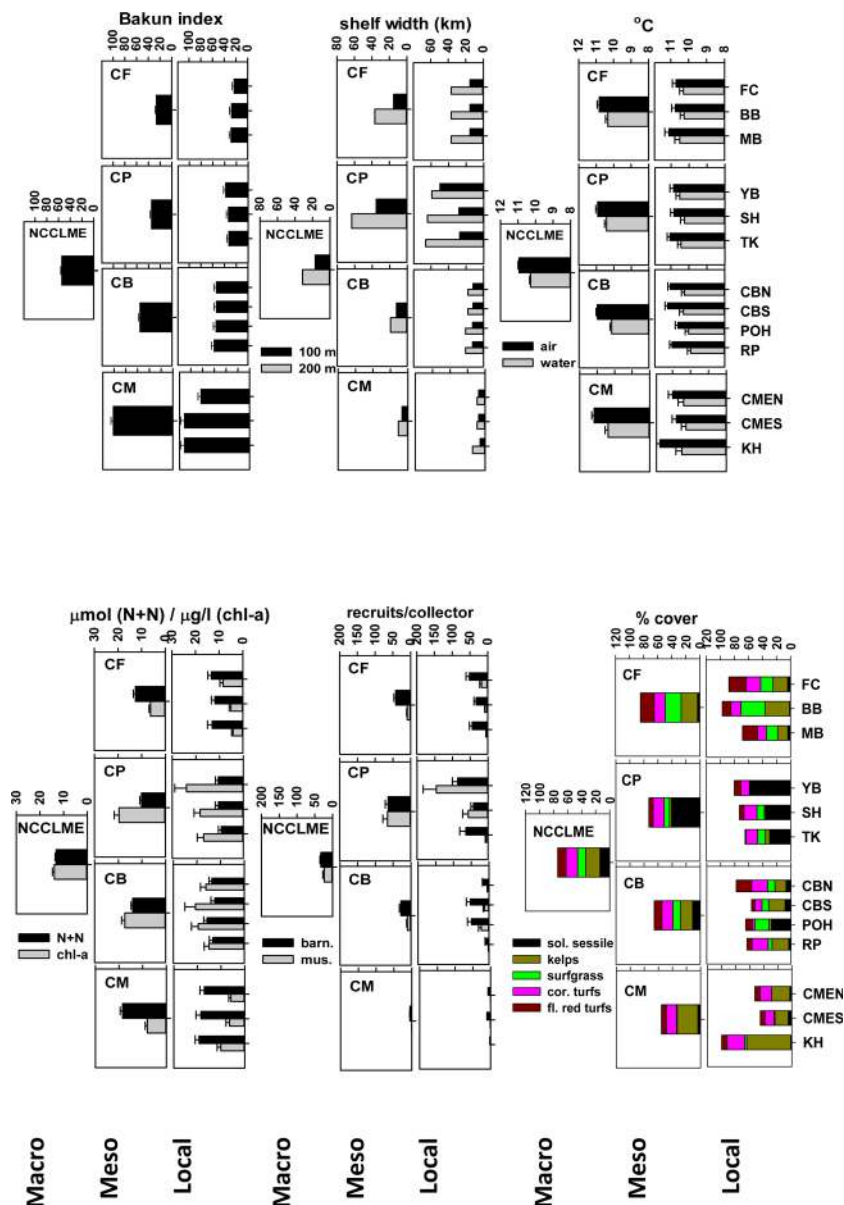
Fig. 9. Summary of results, showing mean (and SE, except for shelf width) values for environmental measures, subsidies, and community structure at onshore site (Local), cape (Meso), and NCCLME (Macro) scales. Capes and sites in sub-panels are arranged vertically from north to south to reflect their spatial arrangement. These figures are averaged across the 2006–2010 time span of the study. For shelf width, 100 and 200 m refer to depth; temperature is shown for air and seawater (water), both measured in situ; recruitment rate is shown for barnacles and mussels; community structure is shown as sum total of barnacle and mussel abundance (solitary sessile), total cover of erect coralline algae (cor. turfs), and total cover of non-calcified turfy red algae (fl. red turfs).

sites and capes of high prey inputs (e.g., Menge et al. 1997a, Menge 2000, Menge and Menge 2013) is consistent with the hypothesis that the strength of top-down effects depends on the magnitude of ecological subsidies (e.g., Oksanen et al. 1981, Leroux and Loreau 2008). Although our analysis was limited to the NCCLME, a recent study showed that factors varying at the entire CCLME scale, including nutrients, temperature, and upwelling regime were strongly linked to

biogeographic patterns of community structure in the Northeast Pacific (Fenberg et al. 2014). Thus, across all scales in this large marine ecosystem, oceanographic conditions and ecological subsidies played significant roles in structuring local communities.

Macrophytes vs. sessile invertebrates?

At the scale of functional groups, the most striking pattern in our data was the inverse relationship between

TABLE 1. Significant scales of variation (mesoscale, local scale, time) for oceanographic conditions, ecological subsidies, and space (variables) in relation to strength of association of each with overall community structure.

Variable	Mesoscale (cape)	Local scale (site)	Time (year)	Association with community structure
Continental shelf width	yes	yes	N/A	high
Upwelling	63.6	N/A	3.1	22.7
Air temperature	ns	19.1	3.2	17.7
Water temperature	ns	10.3	25.3	1.9
Nutrients (nitrate + nitrite)	6.4	ns	10.7	2.3
Phytoplankton	18.3	ns	6.9	6.9
Barnacle recruitment	33.5	14.9	7.5	4.5
Mussel recruitment	30.4	19.5	0.3	4.7
Geography (cape and site)	NA	NA	NA	18.2

Notes: Data are summed variance components for each cell taken from Appendix A: Tables A4 and A6, shown as percentage of variation. Nonsignificant factors ($P = 0.05$) are shown with ns, and N/A indicates the value could not be calculated or was not applicable. "Yes" and "high" indicate the strong association of shelf width with each scale and with community structure, respectively (Fig. 6; Appendix A: Table A5).

abundances of macrophytes and sessile invertebrates, which occurred most clearly at the cape scale. As noted, CM and CF, the most southern and northern capes respectively, were most similar (e.g., Figs. 3–4; Appendix B: Figs. B1–B3), because they have the highest abundances of macrophytes and the lowest abundances of sessile invertebrates. CB sites were similar to these capes, but had somewhat higher abundances of sessile invertebrates, and CP sites stand alone as unique because of high sessile invertebrate and low macrophyte cover, especially of canopy macrophytes.

What is the cause of these mesoscale differences? The evidence suggests that the position of CP in ordination space is associated with environmental factors such as shelf width, recruitment of mussels and barnacles, and phytoplankton (Fig. 6). These factors tend to be interdependent: wider shelves are associated with more retentive currents (Kirincich et al. 2005, Kim and Barth 2011), and thus higher recruitment and phytoplankton in the inner shelf. High recruitment may lead to high abundances of mussels and barnacles and thus strong competition for space with macrophytes (e.g., Paine 1974, Menge et al. 2011b), while high phytoplankton may shade and thereby inhibit intertidal kelp growth (Kavanaugh et al. 2009). However, these possible interpretations are not entirely satisfactory. For example, mussel recruitment at FC overlaps that at CP sites (Appendix B: Fig. B11), and phytoplankton abundance at CP and CB is similar (Appendix B: Figs. B8 and B9). Despite these differences, adult mussels are scarce in the low zone at FC, and canopy macrophytes are relatively abundant at CB. These exceptions suggest that other factors not considered here are in play, including interactions among functional groups (and species); their roles will be examined in a subsequent paper (Hacker et al., *unpublished data*). In addition, much is still unknown about the role of recruitment and the physiological responses of macrophytes at local to regional spatial scales. This is an area of research that lags behind that for sessile invertebrates and deserves considerable attention in the future.

An empirical perspective on meta-ecosystem theory

Theoretical research has generated a number of key predictions to help identify the position of a meta-ecosystem along the "openness" continuum (e.g., Holt 2004, Leroux and Loreau 2008, Gravel et al. 2010a, b). Leroux and Loreau (2008) developed a model that examined the relative importance of allochthonous and autochthonous inputs in a food-chain context, with external inputs supplementing internal flows at the levels of nutrients, plants, herbivores, and carnivores, but separately for each level. This model represents the limiting case whereby the local supply of nutrients and larval recruits is completely decoupled from local dynamics (Fig. 1a). Their model shows that (1) increasing external (allochthonous) inputs at any level increased the strength of trophic cascades or top-down effects, (2) inputs of external nutrients have only modest positive effects on plant abundance, and (3) effects of external inputs on primary consumers (herbivores) are weak when low and strong when high.

Although our model differs in several ways (we include inputs at several levels simultaneously, nutrient inputs are from the water, not soil), our results and others cited are generally consistent with these predictions. In support of prediction (1), the cape with the highest rates of allochthonous inputs and primary consumers (phytoplankton-feeding sessile invertebrates) is Cape Perpetua. CP sites have the highest rates of top-down effects, and the highest rates of growth and recruitment of sessile invertebrates (Appendix B: Figs. B10 and B11; Menge et al. 2004, 2008, 2011a, b, Broitman et al. 2008). Other capes and sites have lower rates of allochthonous inputs and weaker predation, slower invertebrate growth rates, and lower recruitment. In support of prediction (2), algal turf abundance was independent of N + N concentration (e.g., Fig. 9). Prediction (3) was supported in part by earlier research

PLATE 1. One of our rocky intertidal sites, Port Orford Head, Oregon, USA, with two researchers conducting community surveys (one of whom is Sally Hacker, a co-author on the paper), and the nearshore ocean, with Cape Blanco in the background. A dense phytoplankton bloom is the browner water nearshore, which is a main subsidy for the intertidal sessile invertebrates such as mussels (a band of which stretches from the pile of gear on the left to researcher John Schaefers, in orange) and barnacles. This linkage and its ecological importance is the basis for our study of meta-ecosystems across different spacial and temporal scales. Photo credit: B. A. Menge.

(Sanford and Menge 2001, Menge et al. 2008, Bracken et al. 2012); the primary external inputs affecting sessile invertebrates (herbivores/omnivores) were phytoplankton and detritus, and growth of sessile invertebrates increased with increasing phytoplankton and detritus inputs (but also temperature).

The validation of these independent model predictions is consistent with our result that local to macroscale oceanographic conditions mediating the supply of nutrients, phytoplankton, and larvae are critical determinants of community structure and ecosystem functioning in this rocky intertidal meta-ecosystem. Although nutrients, phytoplankton, and larvae are clearly transported by alongshore currents, it appears that determining the specific source and destination of these spatial subsidies (i.e., connectivity) is less important than identifying how local oceanographic conditions mediate their supply (see also Gouhier et al. 2013). The separate inputs of Leroux and Loreau's (2008) model, and simultaneous nature of subsidies in our system, suggest that further exploration of our predictions, with their potential for interactions and/or feedbacks, is warranted.

Comparison to other systems

Do similar influences occur in other habitats? One recent study (Hessing-Lewis and Hacker 2013) showed that differences in coastal upwelling regime could penetrate estuaries and influence the productivity of seagrasses and prevalence of macroalgal blooms, two important primary producers in the system. In the Galapagos subtidal, Witman et al. (2010) found that strong upwelling drove supplies of barnacle propagules, and that as a consequence of the effect of recruitment-driven high barnacle abundance, barnacle predators were abundant and exerted strong top-down control. In the Galapagos intertidal, Vinueza et al. (2014) also documented a strongly bottom-up-driven community, with nutrient inputs being maximal with the strongest upwelling, thereby supporting dense covers of macrophytes which in turn supported dense populations of herbivorous marine iguanas. With weak bottom-up inputs, grazing was the dominant interaction. In the Baltic Sea, rates of cod spillover from the main basin to the Gulf of Riga generate contrasting top-down/bottom-up regulation of Gulf of Riga trophic cascades (Casini et al. 2012). The semi-isolated Gulf of Riga lacks proper cod spawning habitat, and thus is a sink habitat for cod, which drives herring abundance down when common (e.g., 1978–1986), allowing them to rebound when absent (1988–2009), and leading to strong direct and indirect effects on zooplankton and phytoplankton, respectively.

Non-marine examples are also available. In Alaska, USA, lakes and rivers, sockeye salmon condition varied with rearing habitat productivity, not genetic stock

(Griffiths et al. 2013). Salmon that spawned in a more productive lake and swam to a less productive lake had poorer body condition than did those fish in the natal, more productive lake. In a meta-analysis of river meta-ecosystems from headwaters to estuaries, Battin et al. (2008) showed that downstream ecosystems and their microbial communities exploit energy that "escapes" upstream systems, suggesting that ecosystem metabolic efficiency relative to supply increases as individual ecosystems are aggregated in the (river) continuum. Realization of the power of such coordinated efforts and their increased capacity for scientific insights into the dynamics and structure of meta-ecosystems is growing (Carr et al. 2011, Duffy et al. 2013, Fraser et al. 2013, Heffernan et al. 2014), and the rate of understanding of the importance of cross-scale linkages is accelerating.

Our study was conducted in a region that experiences seasonally strong upwelling. Do our results provide any insight into coastal areas with weak upwelling influences? For example, western boundary current (WBC) systems likely will have downwelling as the average condition, with only localized areas of upwelling (e.g., Matano and Palma 2008). Because upwelling-dominated eastern boundary current (EBC) systems also experience downwelling, it seems likely that oceanographic variation will have important effects on WBC coastal ecosystems as well. Using the more general intermittent upwelling hypothesis model (Menge and Menge 2013), of which our models (Fig. 1) provide more detailed sets of predictions for the EBC half of upwelling–downwelling gradients, we speculate that downwelling-dominated coastal ecosystems (1) will exhibit patterns that are consistent with weaker bottom-up influences (e.g., lower recruitment rates, lower inputs of nutrients and phytoplankton, slower growth of sessile invertebrates, slower growth of algae), but that (2) localized and regional variability in community structure also will reflect coastal geomorphology (e.g., retention in gyres downstream of prevailing currents, small-scale upwelling, nutrient inputs from rivers).

Conclusion

Our results represent perhaps the most detailed attempt to quantitatively investigate the degree of correspondence between oceanographic forcing and biological responses in a coastal ecosystem at multiple spatial scales over several years. Our data are consistent with the hypothesis that oceanographic influences have an important impact on the structure and dynamics of coastal rocky intertidal communities across a large fraction of the NCCLME. We suggest that bottom-up factors are critical determinants of patterns at larger, coarser scales, such as the cape scale, and that species interactions, dispersal, local currents, and finer-scale coastal heterogeneity are important at more local, site scales. These results, and the insights gained from other studies, suggest that a focus on understanding patterns and dynamics at the meta-

ecosystem scale will lead to important and often counterintuitive insights into how such systems function, and why they vary spatially and temporally. We hope that this research inspires similar efforts in other systems, and suggest that such research will lead to major advances in our understanding of Earth's interconnected biological systems.

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