

Dynamics of coastal meta-ecosystems: the intermittent upwelling hypothesis and a test in rocky intertidal regions

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Abstract. The intermittent upwelling hypothesis (IUH) predicts that the strength of ecological subsidies, organismal growth responses, and species interactions will vary unimodally along a gradient of upwelling from persistent downwelling to persistent upwelling, with maximal levels at an intermediate or “intermittent” state of upwelling. To test this model, we employed the comparative-experimental method to investigate these processes at 16–44 wave-exposed rocky intertidal sites in Oregon, California, and New Zealand, varying in average upwelling and/or downwelling during spring–summer. As predicted by the IUH, ecological subsidies (phytoplankton abundance, prey recruitment rates), prey responses (barnacle colonization, mussel growth), and species interactions (competition rate, predation rate and effects) were unimodally related to upwelling. On average, unimodal relationships with upwelling magnitude explained ~50% of the variance in the various processes, and unimodal and monotonic positive relationships against an index of intermittency explained ~37% of the variance. Regressions among the ecological subsidies and species interactions were used to infer potential ecological linkages that underpinned these patterns. Abundance of phytoplankton was associated with increases in rates of barnacle colonization, intensity of competition and predation, and predation effects, and rates of barnacle recruitment were associated with increases in mussel growth, barnacle colonization, and species interactions. Positive effects on interactions were also seen for rates of colonization, competition, predation, and predation effects. Several responses were saturating or exponential, suggestive of threshold effects. These results suggest that the IUH has geographic generality and are also consistent with earlier arguments that bottom-up effects and propagule subsidies are strongly linked to the dynamics of higher trophic levels, or top-down effects, as well as to nontrophic interactions. The ~50% of the variance not explained by upwelling is likely due to more regional-to-local influences on the processes examined, and future efforts should focus on incorporating such effects into the IUH.

Key words: *bottom-up; competition; ecological subsidies; intermittent upwelling hypothesis; Large Marine Ecosystems; meta-ecosystems; predation; productivity; recruitment; rocky intertidal; top-down; upwelling/downwelling regime.*

INTRODUCTION

The “meta-ecosystem” concept (Loreau et al. 2003, Holt 2004) explicitly attempts to incorporate a cross-scale perspective in understanding the dynamics of networks of ecosystems. Specifically, meta-ecosystems, defined as “sets of ecosystems linked by flows of energy, material

and organisms across ecosystem boundaries” (Loreau et al. 2003), have the potential to frame understanding of ecosystem dynamics at system-appropriate scales. For example, coastal marine systems globally have been classified into “Large Marine Ecosystems” (LMEs, e.g., Sherman 1991, Mann and Lazier 2006), spanning spatial scales of 1000s of kilometers along continental land masses. LMEs occur in regions of generally distinct oceanographic conditions, typically as determined by major currents. At the heart of the meta-ecosystem concept is the idea of spatially coupled systems. Although the spatial scale of such systems and the complexity of the communities they contain can be daunting, a growing

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body of knowledge indicates that flows of propagules, organisms, and materials linking adjacent ecosystems can be major determinants of ecosystem structure and dynamics (e.g., Bustamante et al. 1995, Polis and Hurd 1996, Menge et al. 1997a, Polis et al. 1997, Wallace et al. 1997, Nakano and Murakami 2001, Menge et al. 2003, 2004, Pace et al. 2004, Navarrete et al. 2005, Witman et al. 2010).

In our view, the issue of meta-ecosystem dynamics is arguably one of the largest problems facing community ecologists. The conceptual framework for meta-ecosystem dynamics remains inchoate, however, relative to other big ecological issues (but see Loreau et al. 2003, Holt 2004, Leroux and Loreau 2008, Gravel et al. 2010b). Here, we present a conceptual meta-ecosystem model for the dynamics of coastal ecosystems, and present evidence from recent research in rocky intertidal habitats across multiple spatial scales in two LMEs to evaluate the model.

Setting the stage: background

In the 1980s, the rising awareness of the potential importance of recruitment as a determinant of community pattern shifted research in coastal ecosystems from a primarily local focus to the incorporation of oceanographically influenced propagule connectivity among sites across larger spatial scales (Underwood and Denley 1984, Connell 1985, Gaines and Roughgarden 1985, Menge and Sutherland 1987). More recently, understanding of the role and influence of coastal oceans as suppliers of nutrients and food (e.g., detritus, phytoplankton) as well as propagules to coastal ecosystems has grown (e.g., Menge 1992, Bustamante et al. 1995, Menge et al. 1997a, 1999, 2003, 2004, Navarrete et al. 2005, Witman et al. 2010). Results from these studies firmly reject the null hypothesis of no influence of coastal oceanography on intertidal and subtidal systems.

What form might the alternative hypothesis (or hypotheses) take? That is, how does coastal oceanography influence coastal ecosystems? Two main issues are relevant to this question: (1) Which among several candidate oceanographic processes are the most influential drivers of variation in community structure and dynamics? (2) What are the mathematical relationships between these drivers and the response variables? For the first issue, in addition to waves (e.g., Bustamante and Branch 1996, Denny and Wethey 2001, Burrows et al. 2008, Rilov et al. 2008, McPhee-Shaw et al. 2011), variation in coastal systems or inputs to these systems has been linked to (e.g.) upwelling/downwelling regimes, temperature, river inputs, tidal flows, internal waves, larval behavior, and coastal geomorphology (Farrell et al. 1991, Connolly and Roughgarden 1999, Pineda 2000, Shanks et al. 2000, Navarrete et al. 2005, Shanks and Brink 2005, Broitman and Kinlan 2006, Porri et al. 2006, Broitman et al. 2008, Hawkins et al. 2009, Morgan et al. 2009a, b, Shanks 2009a, b; see *Discussion*). At present, however, we lack appropriate data sets to evaluate many

of these factors at the scale of meta-ecosystems. Specifically, to evaluate possible relationships to ecological processes along coastal gradients, we need site-based measures of the above and likely other factors, and their spatial and temporal variation. Although evaluating the influence of most potential drivers is not currently possible, we can examine the relationships of those few factors for which we do have extensive and reasonably fine-resolution data at scales that facilitate comparisons with community dynamics. Two of these factors are the upwelling/downwelling regime and temperature. Since upwelling/downwelling generate colder/warmer water temperatures, however, upwelling and temperature are confounded (e.g., regressions between average Bakun index and site average water temperature, or site coefficient of variation of water temperature, explain 51% and 52% of the variance, respectively, with $P < 0.0001$ in both cases). For these reasons we focus on upwelling regime as the independent variable (see *Discussion* for further justification of this choice).

Prior research suggests that upwelling, the flow of cold, nutrient-rich deep water to the surface photic zone via surface winds or currents, can have an important influence on coastal communities. For example, a model linking the upwelling regime to ecosystem dynamics on a coastal scale (Connolly and Roughgarden 1999) predicted how upwelling-driven variation in prey recruitment would influence the strength of predation. Field tests of their model were consistent with some model predictions, but not others (Menge et al. 2004). For example, as predicted, variation in recruitment of mussels and one barnacle species along the U.S. West Coast was far greater in a region of intermittent upwelling compared to a region of persistent upwelling (Broitman et al. 2008; see *Coastal oceanographic setting: Intra-seasonal variation and particle transport* for precise definitions of intermittent and persistent). In contrast, predation rates were similar in persistent and intermittent upwelling regimes, not greater in intermittent regimes, as predicted. The greatest variation in predation was seen at the among-site, within-regime scale, not the between-regime scale.

Evidence from other regions also varies in its consistency with the Connolly and Roughgarden (1999) model, but shows a strong linkage between coastal oceanographic regime and ecosystem dynamics. For example, in the Galápagos Archipelago, Witman et al. (2010) found that barnacle recruitment, growth, and productivity were higher, and predation rate was stronger, at intermediate and strongly upwelled sites compared to weakly upwelled sites. In South Africa, Bustamante et al. (1995) showed that an upwelling-related gradient in epilithic microalgal productivity (west to south to east coasts) was positively correlated with body size and biomass of herbivores (limpets), indicating strong spatial coupling between ocean-driven subsidies and a key consumer group at the coastal scale. In Chile, Navarrete et al. (2005) showed that a sharp

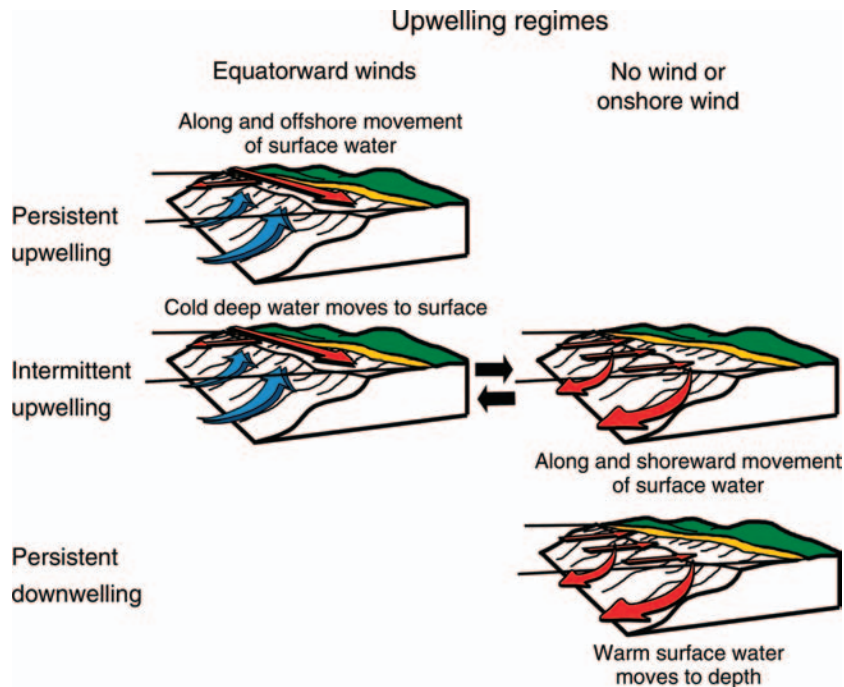


FIG. 1. Depiction of three upwelling regimes. Coastal upwelling occurs in eastern boundary upwelling systems when equatorward winds create a pressure gradient, propelling surface waters equatorward and offshore (top row, red arrows), bringing cold nutrient-rich water to the surface from depth (blue arrows). When upwelling is chronic, we refer to it as “persistent upwelling.” Downwelling is the opposite condition (bottom row): winds cease or reverse, allowing surface waters to relax coastward and poleward (red surface arrows). This shoreward flow increases surface pressure, forcing coastal waters to depth. When downwelling is chronic, we refer to it as “persistent downwelling.” When upwelling and downwelling alternate on a regular basis (e.g., ~3–14 days), we refer to it as “intermittent upwelling.” The diagrams are modified after Bakun (1990).

break in abundance and recruitment of mussels and barnacles occurred at the same latitude at which the upwelling regime shifted from weaker (higher recruitment and abundance) to stronger (lower recruitment and abundance). Thus, upwelling regime can link strongly with key aspects of coastal community dynamics and structure, but the collection of published studies are still too few to allow a strong, literature-based synthesis. In the next sections, we summarize coastal oceanographic patterns, propose a conceptual model that links coastal oceanography to community dynamics, outline the requirements needed in data sets that could evaluate the model, and present a test using our data sets.

Coastal oceanographic setting

Large-scale coastal ecosystems.—Our focus is on inner-shelf coastal marine ecosystems (i.e., from the shore seaward to ~60–100 m depth or to ~10 km offshore [Cudaback et al. 2005]) at the LME scale (e.g., Sherman 1991 and *available online*).⁶ Although there are 64 LMEs around the world, we have strong insights into the community and ecosystem dynamics of few of them. Among the best-studied coastal ecosystems are several within the Pacific and Atlantic Ocean basins. These basins are the locations of the world’s four major coastal

upwelling systems (California Current and Peru–Chile [=Humboldt] Current systems in the Pacific; Canary Current and Benguela Current systems in the Atlantic [Chavez and Mossié 2009]). In the northern hemisphere, the combination of the Coriolis effect and Ekman transport cause net movement of surface waters to the right of the wind direction, while in the southern hemisphere, these forces drive surface currents to the left of the wind direction (e.g., Huyer 1983, Colling et al. 2004, Largier et al. 2006, Morgan et al. 2012; also see Fig. 1). In summer, temperate coastlines on the west edge of land masses are paralleled by prevailing equatorward wind forcing and generally will be upwelling ecosystems (“eastern boundary upwelling systems” or EBUSes). The opposite condition, downwelling, results when winds are poleward along western edges of continents, or equatorward on eastern edges of continents (Matano and Palma 2008).

Coastal circulation model.—Although knowledge of the circulation dynamics of the inner shelf region remains limited, understanding of coastal circulation dynamics in adjacent mid- and outer-shelf regions has grown dramatically. Coastal currents have three components: alongshore, cross-shelf, and vertical. Alongshore currents are typically faster than cross-shelf currents (e.g., in models with varying depth and shelf width, ~2–6× faster [Botsford et al. 2006]), and thus

⁶ <http://www.lme.noaa.gov>

alongshore currents are a key mechanism linking different local ecosystems within a meta-ecosystem. The vertical dimension of coastal flows links surface to deep waters, with their differing magnitudes of light and nutrients, and is the key feature of upwelling/downwelling (Huyer 1983, Lentz 1994, Colling et al. 2004, Kirincich et al. 2005, Largier et al. 2006).

Building on this understanding of coastal circulation, Botsford et al. (2006) proposed the “mixed layer conveyor” (MLC) model. In cross-section, cross-shelf flows resemble a conveyor belt (Fig. 1). During upwelling, shelf water adjacent to the bottom flows upward and landward from depth to the surface, where it then flows seaward. During downwelling, the conveyor belt reverses, building pressure at the coast–surface interface, thus forcing water downward. The model assumes that passive particles, such as detritus, weakly swimming zooplankton, and phytoplankton will tend to be moved in the same manner. Surface-dwelling particles move away from the coast during upwelling and toward the coast during “relaxation” (cessation of wind) and downwelling (reversal of wind). Key factors influencing the extent to which nutrient-fueled phytoplankton growth is fully realized are shelf width and depth, or steepness of the shelf, and current speed (Botsford et al. 2006, Yokomizo et al. 2010). In general, the wider the shelf and the slower the current, the longer are nutrients available for phytoplankton production. The MLC model assumes that materials transported by cross-shelf currents beyond the shelf margin are lost to the coastal ecosystem (Botsford et al. 2006, Yokomizo et al. 2010).

Neither upwelling nor downwelling are constant; alternation between these two processes occurs seasonally or intra-seasonally on scales of days to weeks to months (Botsford et al. 2006, Kudela et al. 2008, Yokomizo et al. 2010). In upwelling systems, seasonal variation is characterized by summer upwelling and winter downwelling as average alongshore currents switch from southward to northward, respectively (Strub et al. 1987).

Intra-seasonal variation and particle transport.—Intra-seasonal variation also occurs during the spring–summer upwelling season due to short-term weather alterations (e.g., Barth et al. 2007). Intra-seasonal variation ranges from persistent, near-continuous upwelling to persistent, near-continuous downwelling (Fig. 1). The intermediate condition, where upwelling alternates with relaxation and downwelling on a frequent basis, is termed “intermittent upwelling” (Wing et al. 1995b, Kudela et al. 2008; see also Fig. 1). Examples of the distribution of upwelling/downwelling at sites located in such regimes are shown in Fig. 2.

The potential ecological consequences of each regime type vary with shelf width and wind and/or current speed (Botsford et al. 2003, 2006). During persistent upwelling, surface flows move equatorward alongshore and seaward offshore nearly continuously, leading to potentially rapid transit times for near-surface particles

(e.g., phytoplankton, larvae) and thus loss to the shelf ecosystem (Botsford et al. 2006, Largier et al. 2006, Keister et al. 2009, Morgan et al. 2012). During upwelling, near-bottom larvae may be transported upward and shoreward, and thus may recruit, but if they remain caught in the conveyor belt current, they are likely to be swept off the shelf. Although nutrients are high in the inner shelf during persistent upwelling, the phytoplankton blooms they fuel take 2–3 days to begin, and thus also tend to be swept equatorward and seaward off the shelf. Hence, in contrast to previous views, strong upwelling can be associated with low, not high productivity over the shelf (Botsford et al. 2006, Largier et al. 2006, Kudela et al. 2008).

During persistent downwelling, flows should favor cross-shelf transit of particles toward coastal habitats (Fig. 1), but two factors mitigate against high abundances of phytoplankton or larvae moving shoreward. First, without upwelling, surface waters will remain nutrient poor, and the zooplankton-supporting phytoplankton blooms will not occur. Persistent downwelling should also reduce the production of larvae by adults due to a lack of subsidies. Second, downwelling flows should also prevent coastally produced propagules from moving to offshore areas, at least in the surface layer. Even if such propagules ride the seaward bottom current and then swim upward to reach offshore feeding grounds, the lack of phytoplankton blooms seems likely to lead to high mortality.

The intermediate condition of alternation between upwelling and downwelling (Fig. 1), particularly when it occurs on temporal scales of a few days to about two weeks, should retain high phytoplankton and propagule densities on the shelf, especially over wider shelf regions (Botsford et al. 2006, Largier et al. 2006). Phytoplankton blooms are stimulated by upwelling bouts of 3–10 days. Although these blooms would tend to move seaward during upwelling, relaxation or reversal should retain the entrained materials, including propagules, or return them shoreward and poleward. Larvae can require days to weeks in the plankton to feed and reach metamorphosis, so the frequent seaward and shoreward movements, perhaps assisted by upward and downward swimming (Shanks and Brink 2005), could retain them close to shore, thereby favoring higher recruitment.

Intermittent upwelling hypothesis

The intermittent upwelling hypothesis (IUH) proposes that rates of ecological subsidies (bottom-up effects and recruitment), prey responses, and species interactions vary with the upwelling regime. The IUH builds on the MLC model of Botsford et al. (2006; see also Yokomizo et al. 2010), by (1) linking mid- to outer-shelf (e.g., >10 km from shore) coastal oceanographic dynamics, as described by the MLC, to the dynamics of inner shelf coastal meta-ecosystems (<10 km from shore), and (2) adds predictions about rate processes in benthic ecosystems. We report here results of the first

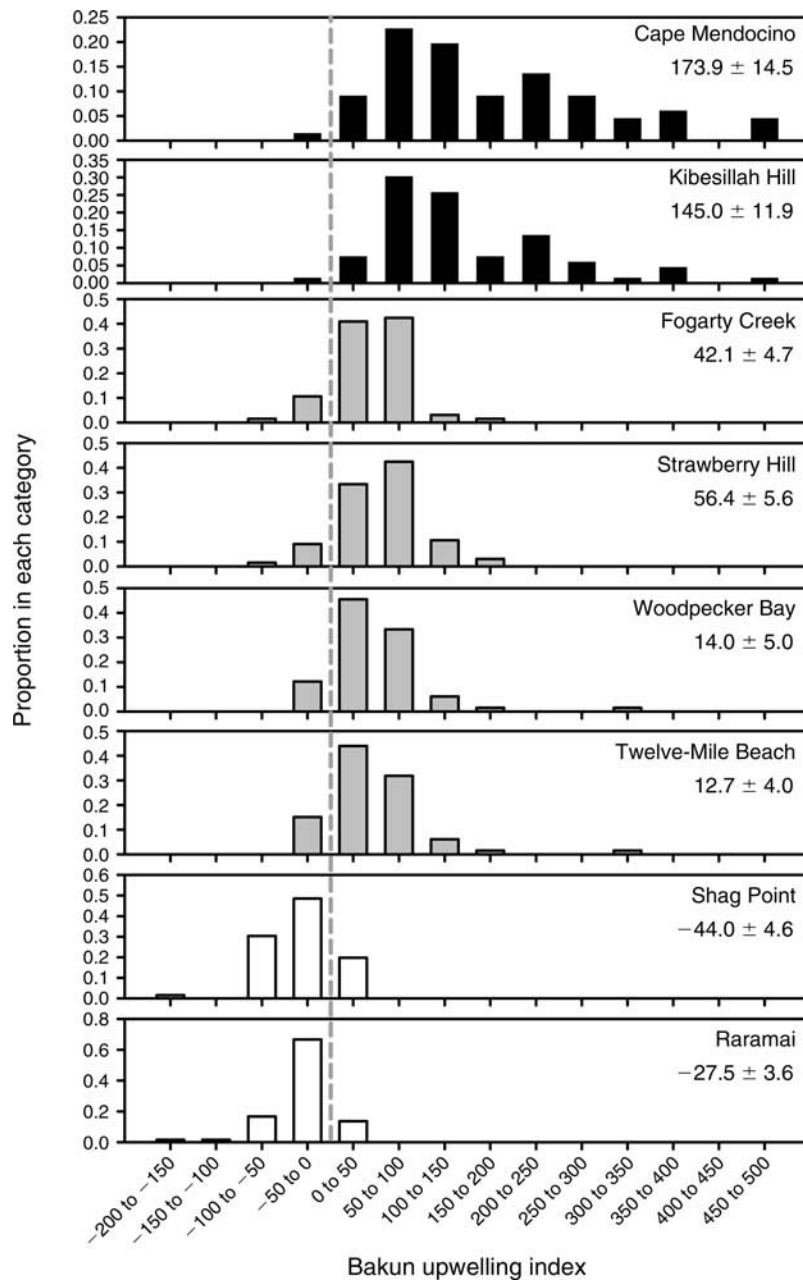


FIG. 2. Illustrations of upwelling regimes: frequencies of upwelling and downwelling at selected sites in Oregon (Fogarty Creek, Strawberry Hill), northern California (Cape Mendocino, Kibesillah Hill), and New Zealand (Woodpecker Bay, Twelve-mile Beach, Shag Point, and Raramai). Sites are arranged from top to bottom by upwelling regime: black indicates persistent upwelling, gray indicates intermittent upwelling, and white indicates persistent downwelling. The numerical values in each graph are mean upwelling ± SE.

step in this modeling procedure, i.e., the relationship between upwelling regime and meta-ecosystem patterns and processes.

An upwelling regime has several possible metrics. Here we focus on two of these, the average *magnitude*, and the *intermittency*, or the tendency to switch between upwelling and downwelling (precisely defined below). The IUH model predictions differ with the metric. First,

as the average *magnitude* of upwelling increases from net downwelling to net zero to net upwelling (Fig. 3A), the model predicts that key ecological dynamics and processes in inner shelf coastal communities will vary unimodally (see also Botsford et al. 2006: Fig. 10). Second, as the *intermittency* of upwelling increases, the model predicts monotonic (though not necessarily linear) increases (Fig. 3B).

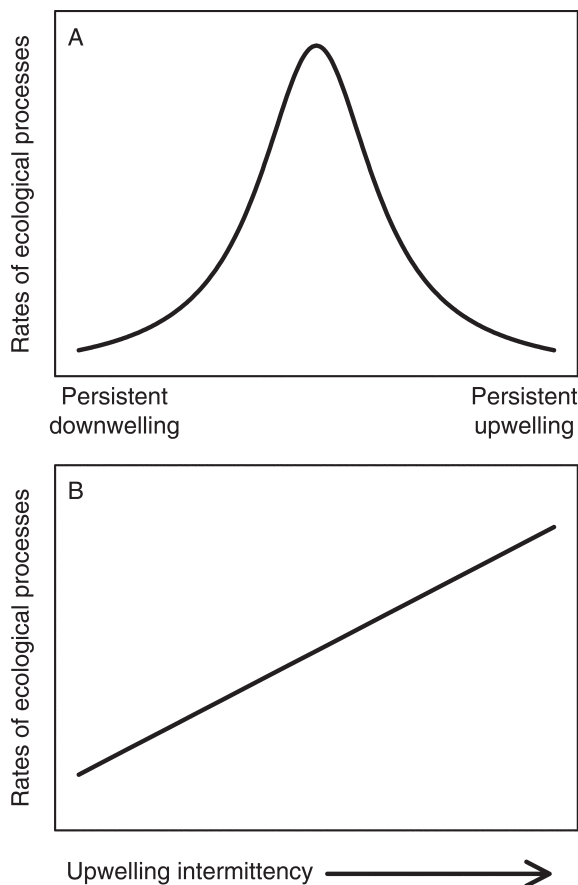


FIG. 3. Intermittent Upwelling Hypothesis (IUH). (A) Rates of ecological subsidies (inputs of phytoplankton = food for filter feeders, recruitment of sessile invertebrates), prey responses (colonization rates, growth rates), and species interactions (predation rate, predation impact, competition rate, facilitation rate) are predicted to vary unimodally along a gradient of persistent downwelling to persistent upwelling. (B) Rates of ecological subsidies, growth of sessile invertebrates, and species interactions are predicted to increase linearly along a gradient of increasing upwelling intermittency (from minimal switching to the opposite regime [upwelling to downwelling or vice versa] to frequent switching between upwelling and downwelling). See *Coastal oceanographic setting* and later sections for further explanation.

Model predictions and underlying mechanisms.—Predictions of the model and mechanisms underlying them arise from the current dynamics patterns summarized previously.

1. *Ecological subsidies (phytoplankton, recruitment of barnacles and mussels).*—Because upwelling provides the nutrients that fuel phytoplankton blooms but sweeps phytoplankton offshore, we predict that plankton abundance varies unimodally with upwelling magnitude and increase monotonically with upwelling intermittency. Similarly, upwelling fuels plankton-feeding larvae (meroplankton) by stimulating phytoplankton blooms but sweeps larvae offshore, so we predict that prey recruitment varies unimodally with upwelling magnitude

and increases monotonically with upwelling intermittency. (It is important to distinguish among (1) settlement, or the arrival of larvae to the adult habitat, (2) recruitment, or the survival of settlers for up to a month, and (3) colonization, or the persistence of recruits for several months (e.g., Connell 1985, Gouhier et al. 2011, Menge et al. 2011a), which depends on growth to visually detectable size. Because of the different time scales involved, and the increased likelihood of post-settlement and post-recruitment processes having an effect, these processes are not considered synonymous.)

2. *Prey responses (barnacle colonization rate, mussel growth rate).*—To a first approximation, growth rates of filter-feeding invertebrates should track the abundance of particles in the water (see *Ecological subsidies* and *Discussion*). Phytoplankton appear to be better nutritionally than is macrophyte-derived or terrigenous detritus (e.g., Coe and Fox 1942, Newell and Shumway 1993, Bracken et al. 2012), so we predict that prey growth rates will exhibit similar relationships with upwelling as phytoplankton. Predictions for *colonization rates* of sessile organisms derive from, and are identical to, recruitment predictions.

3. *Species interactions (competition, facilitation, predation, effect of predation on prey colonization, effect of predation on final prey abundance).*—Predictions for *competition rates* among sessile organisms follow recruitment and growth arguments because recruitment and growth are the primary drivers of resource use. These predictions may not hold under strong predation, since predation commonly varies inversely with competition (e.g., Menge and Sutherland 1976, 1987, Bruno et al. 2003), but if predators are absent or removed, these predictions should apply. Similarly, *facilitation* of mussels by barnacles (e.g., Menge 1976, Berlow 1997, Menge et al. 2011b) should depend primarily on barnacle recruitment and colonization. Although predation often weakens and even blocks this interaction by keeping sessile invertebrates scarce, under some conditions facilitation can occur even in the presence of strong predation (e.g., Menge et al. 2011b). We thus predict stronger facilitation under intermittent upwelling conditions. Finally, *predation* depends primarily on prey input and bottom-up considerations, so we predict low rates and impacts of predation at the extremes of the downwelling-to-upwelling gradient but high predation rates and impacts at sites with intermittent upwelling.

Test of the model

Although the idea for the IUH model was empirically generated, the model is meant to apply to coastal LMEs generally. However, the ecological data needed to test such a model are still limited. Although processes such as recruitment, competition, facilitation, and predation have been studied in coastal ecosystems worldwide, methods typically vary among researchers and investigations, and usually do not allow estimation of (e.g.)

species interaction strengths, or per-site rates of recruitment. To reduce variation introduced by differences in methodology and other factors, the strongest test of such a model would require data from studies that have used identical or at least very similar methods, as presented here. Our approach employed the comparative-experimental method. This method attacks the issue of how to apply experimental approaches across large spatial scales (e.g., Menge et al. 1994, 2002, McPeck 1998, Navarrete et al. 2005, Paine 2010) by carrying out identically designed experiments at multiple locations along an environmental gradient. By quantifying key processes and conditions along the gradient, one can infer or identify mechanism (e.g., Dayton 1971, Menge 1976, Menge et al. 2004, Navarrete et al. 2005).

The research we report was conducted in the 1990s and 2000s in the middle and lower intertidal regions of rocky shores in Oregon, California, and New Zealand's South Island. This habitat is generally characterized by dominance of space by mussels, barnacles, and macrophytes, although free space can be extensive at certain sites. These studies had a goal of assembling a database that could be used to test the IUH model. To capture the full range of persistent downwelling to persistent upwelling, studies were conducted in two LMEs, the California Current Large Marine Ecosystem (CCLME) and the New Zealand Shelf Large Marine Ecosystem (NZSLME). See Appendix A for comparisons of the biota of these systems and Appendix B for a map and coordinates of study sites.

Studies on the Oregon–California coast were conducted to capture the intermittent-to-persistent upwelling end of the gradient (e.g., Menge 1992, 2000a, Menge et al. 1994, 1997a, b, 2004, Connolly et al. 2001, Barth et al. 2007, Broitman et al. 2008, Krenz et al. 2011). The CCLME is an Eastern Boundary Upwelling System, and no region along its coast is characterized by persistent downwelling. To capture this portion of the gradient, and another region of intermittent upwelling, we looked to New Zealand. A preliminary study (Menge et al. 1999) indicated that the east coast of the South Island of New Zealand was dominated by persistent downwelling and the west coast by weakly intermittent upwelling (e.g., Fig. 2), so we designed and carried out identical experiments at sites on each coast. Use of studies from LMEs so far apart might be questioned because of the near total lack of any shared species (the mussel *Mytilus galloprovincialis* is the only one, to our knowledge, and this is an introduced species) and the presumably independent evolutionary histories of these regions. However, the two ecosystems exhibit remarkable convergence in terms of higher-level taxonomic composition and functional groups (Appendix A: text and Table A1). First, both have similar types of consumers, herbivores (limpets, chitons, grazing snails), and predators (whelks, sea stars, crabs, fish, birds) (see Morton and Miller 1968, Morris et al. 1980, Menge et al. 2003, 2004, Schiel 2011). Second, ecological interactions are comparable in type

and effect (Appendix A; see also Paine 1971, 1974, Marsh 1986a, b, Menge et al. 1999, 2003, Rilov and Schiel 2006a, b, 2011, Novak 2010 for examples from a much larger literature). Third, both have similar zonation patterns, with macrophytes usually dominating the low intertidal zone, and mussels and/or barnacles common in the mid-intertidal zone. High zones are more divergent, with barnacles and macroalgae sharing space on the U.S. West Coast, and barnacles and mussels being predominant in New Zealand (e.g., Menge et al. 1999, 2003, Allison 2004, Blanchette et al. 2008, 2009).

The systems are physically similar as well. First, tidal ranges are similar (3–4 m). Second, although sea water temperatures tend to be warmer in New Zealand (means between $\sim 14^\circ$ and 17°C , range 11° – 19°C [Menge et al. 1999, 2007]) than in Oregon (means between $\sim 11^\circ$ and 14°C , range 7° – 18°C [Helmuth et al. 2006; B. A. Menge unpublished data]), there is overlap in both means and ranges. Third, though they are in different hemispheres, both regions span similar latitudes (Appendix B: Table B1; 34° – 45°N for CCLME and 42° – 45°S for NZSLME), and have similar temperate maritime climates. All these similarities were the prime reasons why we chose New Zealand as our complementary study region.

Although it could be argued that differences in composition still may introduce variation in the extent to which combined data fit the IUH model, we suggest that this possibility does not invalidate our approach. It simply adds additional factors to the set summarized earlier that could introduce variation into the fit of ecological data to upwelling regimes. In fact, our approach is a conservative one. By not including these factors in our analysis, tests of the model are made even stiffer, since these sources of variation are not explicitly included.

Below, we present an approach to testing the predictions of the IUH. First, we describe how we quantified upwelling regimes and upwelling intermittency. Second, we explain the procedures used to quantify ecological subsidies, prey responses to subsidies, and species interaction strength. Third, we summarize the methods of analysis. Fourth, we present our analyses of the relationships between upwelling and intermittency vs. ecological subsidies, prey responses, and species interactions.

METHODS

Quantification of upwelling regimes.—To quantify upwelling, we obtained Bakun upwelling index data from the Pacific Fisheries Environmental Laboratory (PFEL) Live Access Server (*available online*).⁷ This index reflects the water flux (cubic meters per second per 100 m of coastline) seaward (upwelling; positive values) or shoreward (downwelling; negative values). The PFEL server can generate upwelling data for any site around the world at 0.5° intervals (averaged over 3° pixels centered over the latitude and longitude entered into the server) after inputting the latitude, longitude, and

⁷ <http://pfel.noaa.gov>

coastal angle (in degrees from North). Data were downloaded at two temporal scales, monthly averages from 1995–2005 (represents the period of most intense field studies) for calculations of average Bakun upwelling at the site scale, and six-hourly values for use in generating upwelling intermittency. Site locations, names, and the nearest upwelling location are shown in Appendix B: Table B1, Fig. B1). Because biological processes (growth, recruitment, activity) are minimal in winter, we limited our estimates to data from the “upwelling season” in each region (~April–September in the CCLME, ~October–March in the NZSLME).

To our knowledge no index of upwelling “intermittency” exists, so we created one to reflect three components of “intermittency” that seemed most relevant to coastal oceans. These are (1) magnitude, (2) duration, and (3) frequency. First, in terms of the amount of water movement, we define sites switching between strong upwelling and strong downwelling as more intermittent than sites switching between weak upwelling and weak downwelling (Appendix B: Fig. B2A, B). Second, we define sites with upwelling and downwelling bouts of similar duration as more intermittent than sites with alternating short downwelling and long upwelling events, or vice versa (Appendix B: Fig. B2C, D). Third, we define regimes with high-frequency switches (e.g., on a weekly scale, with alternating weeks of upwelling-favorable and downwelling-favorable winds) as being more intermittent than regimes with low-frequency switches (e.g., on a monthly scale; Appendix B: Fig. B2E, F).

The intermittency calculation was a three-step process. Because of time lags between the surface winds and the generation of Ekman transport, and between Ekman transport and phytoplankton blooms, the “0” value of the Bakun index (which is based on wind speed) is not the ecologically relevant threshold between upwelling and downwelling. Therefore, the first step in our intermittency calculation was defining the ecologically relevant upwelling/downwelling threshold for each data set. We estimated this threshold empirically as the mean Bakun magnitude value at which each response variable peaked (the parameter in Appendix B: Table B3), reasoning that this was the best information we had on the value of this threshold. We then subtracted this threshold value from all values to redefine the threshold as 0.

Second, for a given time interval, say 20 days, we calculated the “limiting” water flux by taking the minimum of the sum of the upwelling data points (Bakun indices above the above-defined threshold) and the absolute value of the sum of the downwelling data points (below the above-defined threshold; Appendix B: Fig. B3A). Each sum reflects the ecologically relevant water flux onto or off shore over that time period, capturing the first component of intermittency described previously. Taking the minimum of these two sums infers that the intermittency is limited by either upwelling or downwelling, in the same way that ecological processes can be

limited by one factor over another. We did this for every possible time interval of this length during the upwelling season, which graphically looks like a sliding window, and normalized this to calculate a value for this time interval (Appendix B: Fig. B3B).

Third, we calculated the limiting average water flux at time intervals ranging from three days (the minimum time needed to generate upwelling [e.g., Kirincich et al. 2005, Botsford et al. 2006]) to the entire upwelling season, then summed across all such time intervals (Appendix B: Fig. B3C). This captures the temporal dynamics of intermittency; e.g., the limiting water fluxes will be greater at short time intervals for weekly oscillations compared to monthly oscillations. These calculations were based on data from 1989 to 2011, which encompassed the full time span of our recruitment studies. Note that the different threshold for each response variable generates different sets of intermittency indices for each response variable. Also, since they are based on the same basic data set, these two measures (magnitude and intermittency) are not independent, nor were they intended to be; we conducted separate model-fitting analyses with each measure. The goal was simply to see if different ways of characterizing upwelling regime provided different or additional insight.

Ecological data sets.—Comparative-experimental studies were carried out at 16 sites in the CCLME and at seven sites in the NZSLME (Appendix B: Tables B1, B2, Fig. B1). Some measurements such as phytoplankton abundance, recruitment, and mussel growth were also taken at an additional 19 sites in the CCLME and two sites in the NZSLME (Appendix B: Table B2). Using identical methodologies, we quantified phytoplankton abundance, mussel and barnacle recruitment, barnacle colonization rates, mussel growth rates, competition rates, facilitation rates, predation rates, and predation effects (Appendix B: Table B2). There were 5–8 replicates per site for all factors except phytoplankton, for which there were 3–5 replicates. For recruitment and phytoplankton, only data from May through October (CCLME) or October through March (NZSLME; i.e., abundances that occurred during the upwelling season) were used.

Phytoplankton abundance was quantified by taking bottle samples during low tide at each site, at varying time intervals, but at least monthly. Methods of collection and sample processing have been detailed elsewhere (e.g., Menge et al. 1997b, Leslie et al. 2005, Barth et al. 2007). Briefly, 200-mL opaque ODCP acid-washed bottles were dipped to ~0.5 m from the shore at low tide, and refilled four times, with the final fill constituting the sample collected for analysis. Samples were filtered in the field, taken to the laboratory, and estimates of chlorophyll *a* (hereafter, chl *a*) were obtained (in micrograms per liter) using a fluorometer (model TD-700, Turner Designs, Sunnyvale, California, USA). Most chl *a* was contributed by phytoplankton, and inspection under a microscope showed that most of this was diatoms. Analyses not included here show that

chl *a* in bottle samples is correlated with field fluorometric data ($r = 0.81$, $P < 0.0001$, $n = 1029$; K. Nielsen and B. A. Menge, *unpublished data*), and thus bottle samples capture patterns of abundance of phytoplankton reasonably well.

Recruitment was quantified approximately at monthly intervals and was standardized to rates per day. Mussel recruitment used ovoid mesh ball collectors (Tuffies) and barnacle recruitment used 10×10 cm PVC plate collectors coated with a uniform textured surface (e.g., Menge et al. 1999, 2003, 2010, Navarrete et al. 2005). Replicates were placed in gaps in mussel beds (or at three of the NZSLME sites, where mussels would be) in the mid-intertidal zone. Barnacles recruiting in the CCLME were primarily *Balanus glandula* (see Plate 1) and *Chthamalus dalli*, and those recruiting in the NZSLME were *Epopella plicata*, *Chamaesipho columna*, and *C. brunnea*. Mussels recruiting in the CCLME were *Mytilus californianus* and *M. trossulus*, and those recruiting in the NZSLME were mostly *M. galloprovincialis*, *Perna canaliculus*, and *Xenostrobus pulex*. For our analyses, we lumped across taxa using total barnacles, total mussels, and total prey (barnacles + mussels).

Mussel growth was quantified using previously described methods (e.g., Menge 1992, Blanchette et al. 2007, Menge et al. 2008). In spring, mussels ~ 40 mm in length were collected from a single site, notched at the posterior edge (site of fastest shell accretion during growth), allowed to recover in the laboratory for two weeks, and then returned to the field. Translocation involved placing them in groups of 30–50 (5–8 replicates/site), ventral side down in the mid-intertidal zone, covering them with plastic mesh, and securing the mesh to the rock using lag screws driven into predrilled holes in the rock. Cages were loosened after two and four weeks to allow the mussels to attach more firmly, and were removed after six weeks. Mussels were collected the following year and measurements were taken of total length, length of the growth increment, and wet and dry mass of shell and tissue. Growth is expressed as micrometers per day per initial length. The mussel species used in the CCLME was *M. californianus*, and that used in the NZSLME was the ecological analogue, *P. canaliculus* (e.g., see Paine 1971).

Predation rates were quantified by transplanting locally collected mussels into the low intertidal zone (i.e., the primary foraging zone for sea stars and whelks) using the same protocol as that used for growth, and following their survival after removal of the mesh used to hold them in place while they were reattaching (e.g., Menge 1992, Menge et al. 2003, 2004, 2011b). Treatments in this experiment were exclusions (no predator access to transplanted mussels; surrounded by a fence or cage), and exposed to predators (partial fence). Mortality rates were corrected for control mussel mortality, and expressed as mussels killed per day. See Appendix A: Table A1 for a list of the predator taxa occurring in each region.

Predation impacts on prey (mussel and barnacle) colonization, predation impacts on final prey abundance, competition rates between the dominant sessile organisms (mussels and barnacles), and colonization rates of barnacles were determined by establishing predator exclusion experiments. We used results from these experiments to determine rates of total (barnacles plus mussels) prey increase, total prey abundance at the end of the experiment, rates of overgrowth of barnacles by mussels in predator exclusions, and rates of increase of barnacles during the colonization phase of the experiment, respectively (e.g., Dayton 1971, Menge 1976, 2003; Appendix C: Fig. C1). This method of estimating rates is identical to methods used in calculation of interaction strength (e.g., Navarrete and Menge 1996, Berlow et al. 1999, Menge et al. 2004).

Plots initially were cleared of all biota except for encrusting algae and randomly assigned to one of three treatments. Marked plots (+predators, –mesh) tested rates of prey colonization in the presence of predators with no potential experimental artifact. Partial fences or two-sided cages (+predators, +mesh) tested rates of colonization in the presence of predators with mesh present; comparison to marked plots tested the effect of mesh. Complete fences or cages (–predators, +mesh) tested rates of colonization in the absence of predation from sea stars and whelks; comparison to partial enclosures and marked plots tests the effect of predation. In this analysis, abundances of prey in partial enclosures and marked plots did not differ, so we used the difference between exclusions and partial enclosures (hereafter termed “controls”) as our measure of predation effect. Plots were photographed monthly, or in winter, as often as stormy conditions allowed. At NZSLME sites, plots were initially photographed monthly, then less often (every 2–6 months), as we observed that colonization and growth rates and predator reinvasion rates were slow at most sites. Two to three separate runs of these experiments were carried out at sites in the CCLME and NZSLME; we considered each run to be a replicate (see Appendix B: Table B2). We examined predation effects at two stages of each experiment, during the colonization or prey increase phase, and at the final stage after the experiment had run its course (Appendix C: Fig. C1; experiment length ranged from one to three years depending on the pace of changes occurring at each site). The criterion for deciding whether or not an experiment was in its final stages was when abundances of prey in all treatments had reached relatively stable abundances for two to three consecutive sampling periods. Predation effect on colonization was quantified as the difference between the slope of total prey increase in predator absent (exclusions) and the predator present (controls) treatment (Appendix C: Fig. C1). Total predation effect over the duration of the experiment was quantified as the difference between final prey

abundances in exclusions and controls (Appendix C: Fig. C1).

In exclusion cages, a common result was initial colonization by barnacles followed by mussel settlement on barnacles, which are a primary facilitator of mussel recruits (e.g., Menge 1976, Navarrete and Castilla 1990, Berlow 1997, Menge et al. 2011*b*). The rates of change in prey abundance in the predator exclusions varied among sites and regions. Hence, we used the mussel–barnacle interaction to estimate the rates of colonization of barnacles, of competitive overgrowth, and facilitation of mussels by barnacles (Appendix C: Fig. C1). To quantify barnacle colonization rates, we calculated the slope of increase in percentage cover of barnacles during the colonization phase, defined as the period in days from initial clearance (no colonists) to maximum barnacle abundance. To quantify the site-specific rate at which mussels outcompeted barnacles (defined as the rate at which mussels overgrew the barnacles), we determined the slope of the decline of barnacle abundance after peak abundance was reached and mussel colonization stopped further increases in barnacle abundance, which usually began at ~50–60% total prey cover. Where colonization was so low that competition did not occur, rates of competition were defined as zero. Colonization and overgrowth rates are expressed as increases and decreases, respectively, in percentage cover per day. Finally, we used the slope of the linear regression between barnacle abundance (independent variable) and mussel abundance (dependent variable) during the colonization phase, previously defined, as an indication of the strength of facilitation of mussels by barnacles. A low slope should occur where barnacle facilitation of mussel colonization was slow, and a high slope should occur where facilitation was rapid. Note again that all these changes are those occurring in cages, in the absence of predation.

Data analysis.—In our analyses, we calculated site-level means for subsidies and predation rate experiments, and site by experiment means for predation effect, facilitation, and competition experiments. Averaging in this way masks temporal variation in the response variables. We justify this by noting that, although processes such as recruitment, phytoplankton blooms, and predation can exhibit among-year (as well as short-term) variation, among-site differences tended to be consistent. That is, high/low phytoplankton/recruitment/predation sites tended to be high/low through time (e.g., see Menge et al. 2008, 2009, 2011*a, b*), so averaging across time should reflect among-site differences. The exception to this is mussel growth, in which among-site differences disappeared over a 15-year period (Menge et al. 2008), but these changes were observed at only a subset of four sites along the Oregon coast. We do not mean to dismiss temporal change as unimportant, but believe that for the purposes of this analysis, simplifying our analysis by using site averages is a reasonable approach.

All analyses relating the response variables to upwelling were done using JMP v. 8.0 (SAS 2008) and the statistics module in Sigmaplot (v. 11.0; SYSTAT 2008). For all relationships between upwelling regime (Bakun upwelling index, in cubic meters per second per 100 m of coastline, or the intermittency index) and response variables (ecological subsidies, prey responses, species interactions), we calculated one to several regressions in each of three categories to evaluate predictions of the IUH. “Intercept” models tested the hypothesis of slope = 0, indicating no relationship. Monotonically increasing functions (linear, exponential growth, power, exponential rise to a maximum, hyperbola) tested the hypothesis of a positive relationship. “Peak” models (Gaussian, Modified Gaussian, Lorentzian, lognormal) tested the hypothesis that the relationship was unimodal. Similar analyses were done for regressions among the response variables to gain insight into likely mechanisms underlying the regressions with upwelling regime. We calculated regression sets for each comparison using the nonlinear regression library available in Sigmaplot v. 11. We then used AIC_c (corrected Akaike Information Criterion) to determine the best-fit monotonic and peak models for comparison to the intercept model (e.g., Quinn and Keough 2002; Appendix B: Tables B3–B6). We also used AIC_c to calculate w_i , or relative model weighting. For calculation of w_i we consider the best fit monotonic, the best-fit peak, and the intercept models as “the set” to facilitate interpretation of our hypothesis testing. Response variable data were transformed using $\ln(x + 1)$ (chl *a*, recruitment, mussel growth, predation rate) or arcsine transformations (colonization rate, predation effect, competition rate, facilitation rate) prior to analysis. In a few experiments ($n = 2–4$), barnacle recruitment failed at sites where it was normally moderate to high (e.g., Cape Blanco in 2007, Twelve-Mile Beach and Woodpecker Bay in 2002). We omitted these cases from the final analyses. Details of these analyses are in Appendix B: Tables B3–B6.

To explore the relationships among the various response variables and gain insight into the actual mechanisms underlying their relationships to upwelling, we examined regressions among the ecological subsidies and species interactions using the same approach as above. In most cases, independent variables were those measures that occurred on lower trophic levels (e.g., chl *a* was used as the independent variable for recruitment, competition, mussel growth, colonization, facilitation, and predation). For regressions involving recruitment comparisons, we assumed mussels were dependent on barnacles (because of the facilitation mentioned previously).

The measures of chl *a*, recruitment, mussel growth, and predation rate are all independent, as are each component of the suite of measures taken from the predation effect experiments (colonization, competition, facilitation, effects of predation on total prey colonization, and on final prey abundance) when analyzed

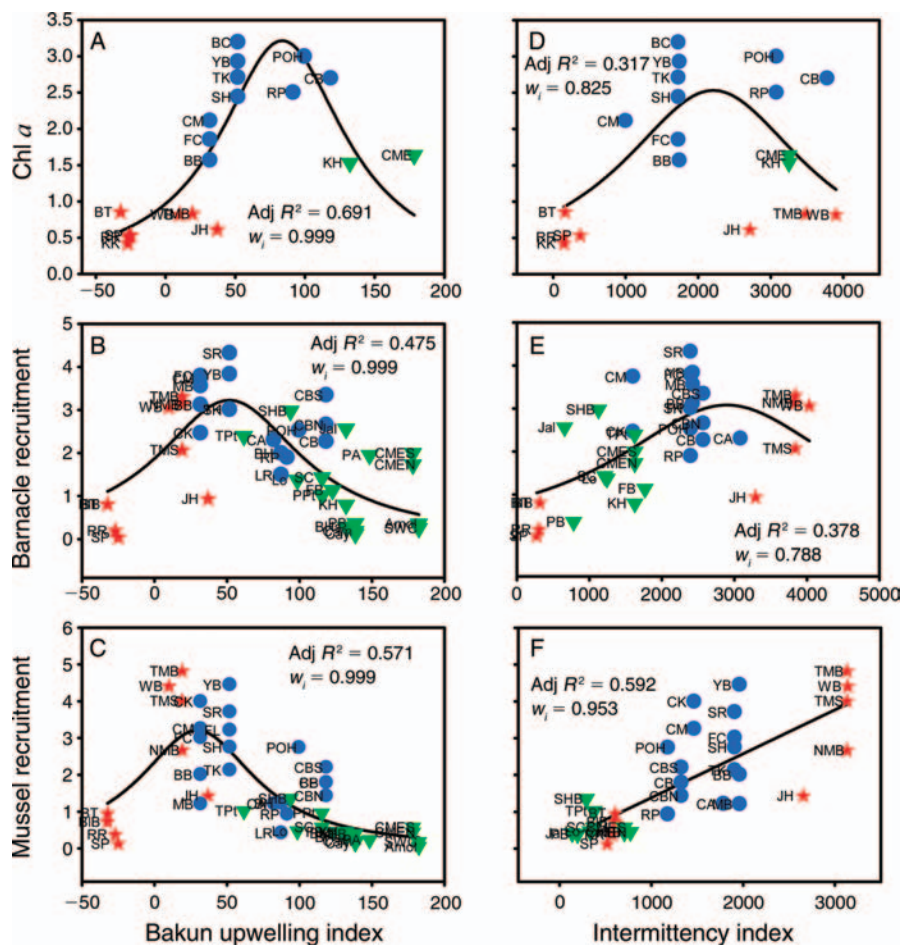


FIG. 4. Patterns of variation in ecological subsidies as a function of upwelling (Bakun index) and upwelling intermittency from sites in Oregon, California, and New Zealand. Symbols indicate Oregon (blue circles), California (green triangles), and New Zealand (red stars) and include site abbreviations to the left of each symbol (see Appendix B: Table B1). Regression statistics are shown in Appendix B: Table B3. Significance level used here and in all following figures was $P = 0.05$. $Adj R^2$ is adjusted R^2 , and w_i is relative model weighting (see *Methods*). (A, D) Phytoplankton abundance (ln[chlorophyll *a*] measured in $\mu\text{g/L}$). Each symbol represents the mean annual chlorophyll *a* abundance per site averaged across the upwelling season for samples taken between 1993 (USWC) or 1999 (SINZ) and 2005 (SINZ) or 2008 (USWC). (B, E) Barnacle recruitment (ln[recruits/d]). (C, F) Mussel recruitment (ln[recruits/d]). See *Methods* for further details.

separately with the first three measures mentioned. Within the predation effects experiments, measures of effects consider different phases of the course of the experiment (early vs. late), and look at differences between cages and controls, but are not completely independent. Colonization, facilitation, and competition are all based on cage results only, with colonization and facilitation analyzing early phases of the results and competition analyzing late phases of the results.

RESULTS

Ecological subsidies and upwelling regime.—As predicted, abundance of phytoplankton and recruitment rates of sessile invertebrates (barnacles, mussels) were all highest at sites of intermediate upwelling intensity (Fig. 4A, B, C). Specifically, chl *a* abundance (a proxy for phytoplankton, which is a primary food for larvae and

filter-feeding invertebrates such as mussels and barnacles), was best fit by a unimodal relationship with the Bakun index, explaining 69.1% of the variance in this basic ecological subsidy. Similar relationships were observed for recruitment rates of barnacles (47.5% of the variance) and mussels (57.1%). Weight (w_i) of all unimodal models was 0.999, and the likelihood that each model was better than monotonic or intercept models (likelihood of best fit ratio $w_{i\text{max}}/w_{i\text{model}}$) ranged from $96\times$ (a multiple of 96) to 2.5×10^6 times (Appendix B: Table B3).

For all subsidies, the persistent downwelling end of the scale is anchored by sites on the east coast of the South Island of New Zealand (=SINZ: Box Thumb, Shag Point, Raramai, Boulder Bay, Kaikoura), while the persistent upwelling end is anchored by sites in northern and central California (Cape Mendocino

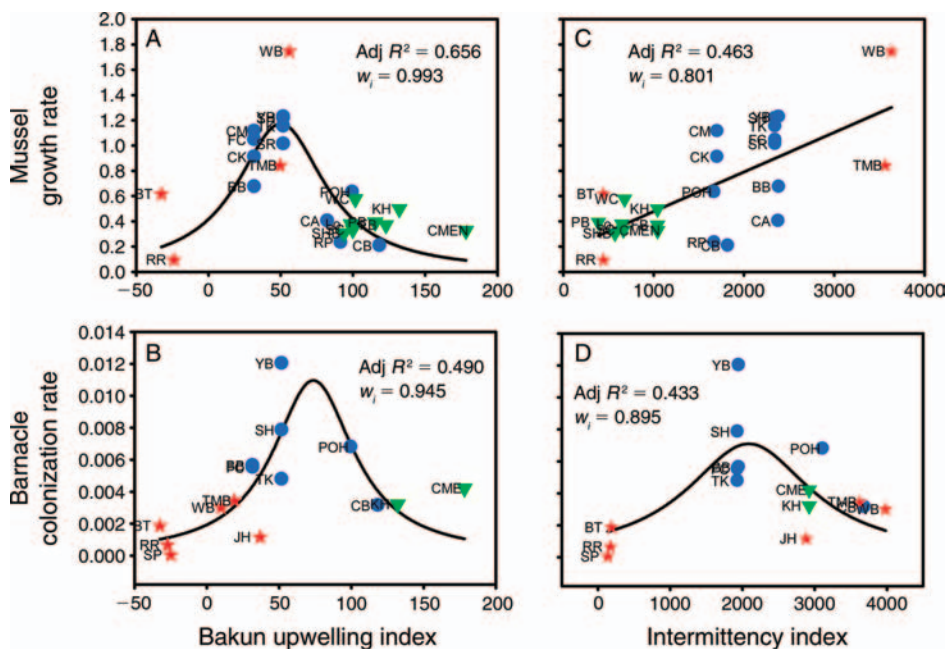


FIG. 5. Prey responses to subsidies in relation to upwelling and intermittency. Patterns of variation in mussel growth rate ($\text{mm}\cdot\text{d}^{-1}\cdot\text{initial length}^{-1}\times 1000$) and barnacle colonization rate as a function of (A, B) upwelling (Bakun index) and (C, D) upwelling intermittency from sites in Oregon, California, and New Zealand. See Fig. 4 caption for further explanation.

North and South, Kibesillah Hill, Andrew Molera, Stillwater Cove, Cambria, Cayucos; Fig. 4A, B, C). Sites of intermittent upwelling include both those on the west coast of SINZ and along the Oregon coast (Fig. 4A, B, C). The overlap between sites in the different regions suggests that these different systems are responding similarly to similar oceanographic regimes.

The relationship between intermittency and the ecological subsidies was unimodal for chl *a* and barnacle recruitment (Fig. 4D, E), and monotonic (linear) for mussel recruitment (Fig. 4F), explaining 32%, 38%, and 59% of the variance, respectively. These analyses suggest that from most to least intermittent, site ranks were west coast of SINZ > Oregon > California > east coast of SINZ (Fig. 4D–F). The intermittency vs. mussel recruitment linear model was strong (model weight was 0.953, likelihood ratio $w_{i\text{max}}/w_{i\text{model}}$ was 20.2 \times vs. the unimodal model and $2.4 \times 10^6 \times$ vs. intercept model), as was the intermittency vs. chl *a* (unimodal $w_i = 0.825$, likelihood ratio $w_{i\text{max}}/w_{i\text{model}}$ was 11.8 \times for the linear model). However, intermittency vs. the barnacle recruitment (unimodal $w_i = 0.788$) relationship was less well distinguished from the linear alternative (likelihood ratio $w_{i\text{max}}/w_{i\text{model}} = 3.7 \times$, respectively; Appendix B: Tables B3, B5). Using the rule of thumb that a “confidence set” of models would include all those within 10% of $w_{i\text{max}}$ (Burnham and Anderson 2002), the intercept ($w_i = 0.105$) and linear ($w_i = 0.211$) models cannot be dismissed as plausible alternatives for intermittency vs. chl *a* and barnacle recruitment, respectively.

Prey responses and upwelling regime.—Mussel growth rates and barnacle colonization rate both varied unimodally with upwelling intensity (Fig. 5A, B), with 65.6% and 49.0% of the variance explained, respectively, and w_i was high in both cases (0.993 and 0.945). Likelihood ratios $w_{i\text{max}}/w_{i\text{model}}$ ranged upward from 27.2 \times for these unimodal models. Mussel growth rate increased linearly with intermittency, but barnacle colonization rate varied unimodally with intermittency, explaining 46.3% and 43.3% of the variance, respectively (Fig. 5C, D). Model weight w_i was 0.801 for intermittency vs. mussel growth, and 0.895 for barnacle colonization rate. Using the 10% rule of thumb, the unimodal model cannot be ruled out for intermittency vs. mussel growth rate (Appendix B: Tables B3, B5).

Species interactions and upwelling regime.—Except for barnacle facilitation of mussels, unimodal relationships were also observed between upwelling magnitude and all species interactions, explaining 54.8%, 71.4%, 39.4%, and 27.0% of the variance in predation rate (Fig. 6A), predation effect on prey colonization (Fig. 6B), predation effect on final prey abundance (Fig. 6C), and competition between barnacles and mussels (Fig. 6D), respectively. Facilitation rate was unrelated to upwelling (data not shown, $P > 0.05$). Model weights w_i were all high, ≥ 0.955 . Likelihood of best fit ratios for species interaction vs. upwelling intensity relationships were $\geq 34 \times$ (Appendix B: Tables B3, B5), and in each case the confidence set included only the unimodal model.

One of four species interactions increased with intermittency models (predation effect on final abun-

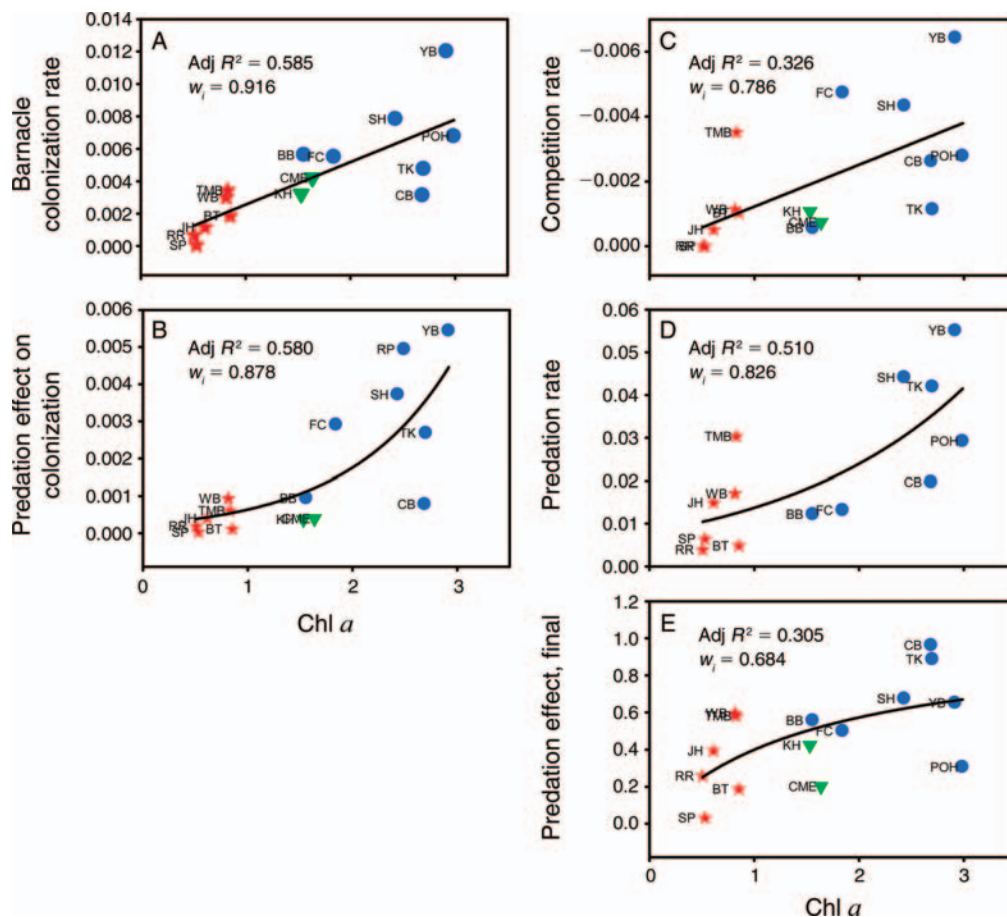


FIG. 7. Relationships between chlorophyll *a* (ln-transformed) and five variables: (A) barnacle colonization, (B) effect of predation on prey colonization rate, (C) competition rate, (D) predation rate, and (E) effect of predation over the entire experiment. See Fig. 4 caption and Figs. 4–6 for labeling explanation and units of change for each response variable, respectively.

vs. predation rate (unimodal) and competition (linear) were not excluded from the confidence set (Appendix B: Tables B3, B5).

Mechanisms underlying the relationships.—Prior evidence suggests that phytoplankton abundance may be an important determinant of rates occurring at higher trophic levels (e.g., Menge et al. 2008, 2009). That is, bottom-up effects seem to be a likely factor influencing some of these unimodal or linear relationships between ecological subsidies or species interactions and chl *a*. Our analyses are consistent with this idea; barnacle colonization rate, competition rate, predation rate, and the effect of predation on prey colonization and final prey abundance all increase with increasing chl *a* (Fig. 7A–E). These relationships explain between 30.5% and 58.5% of the variance, and model weights w_i range from 0.684 to 0.916. However, the confidence set excludes the unimodal model only for chl *a* vs. barnacle colonization (Appendix B: Table B5), as reflected also by the low $w_{i\text{max}}/w_{i\text{model}}$ ratios (minimum was 3.2 \times ; Appendix B: Table B4). Generally, the higher the bottom-up input of phytoplankton, the higher the success of barnacle

colonization, and the more intense were predation and competition. Geographically, the SINZ downwelling sites are always the closest sites to the origin of the graphs (lowest chl *a* and lowest rates), followed by SINZ intermittent sites, the northern California persistent upwelling sites, and the Oregon sites, two of which overlap with the northern California sites (Fig. 7).

Increases in barnacle recruitment were related to increases in mussel recruitment (Fig. 8A; variance explained was 59.8%), mussel growth rates (Fig. 8B; 40.4%), colonization rate of barnacles in cages (Fig. 8C; 31.1%), facilitation rate (Fig. 8D; 29.3%), competition intensity (Fig. 8E; 39.3%), and the effect of predation on prey colonization (Fig. 8F; 33.0%). Model weights ranged from 0.515 to 0.904, and in all cases the alternative model was included in the confidence set, as reflected by relatively low $w_{i\text{max}}/w_{i\text{model}}$ ratios (Appendix B: Tables B4, B5). Based on their similar responses to large-scale oceanography (Broitman et al. 2008), a positive relationship between barnacle and mussel recruitment was expected (Fig. 8A). Colonization of cages by barnacles and facilitation rates would also be

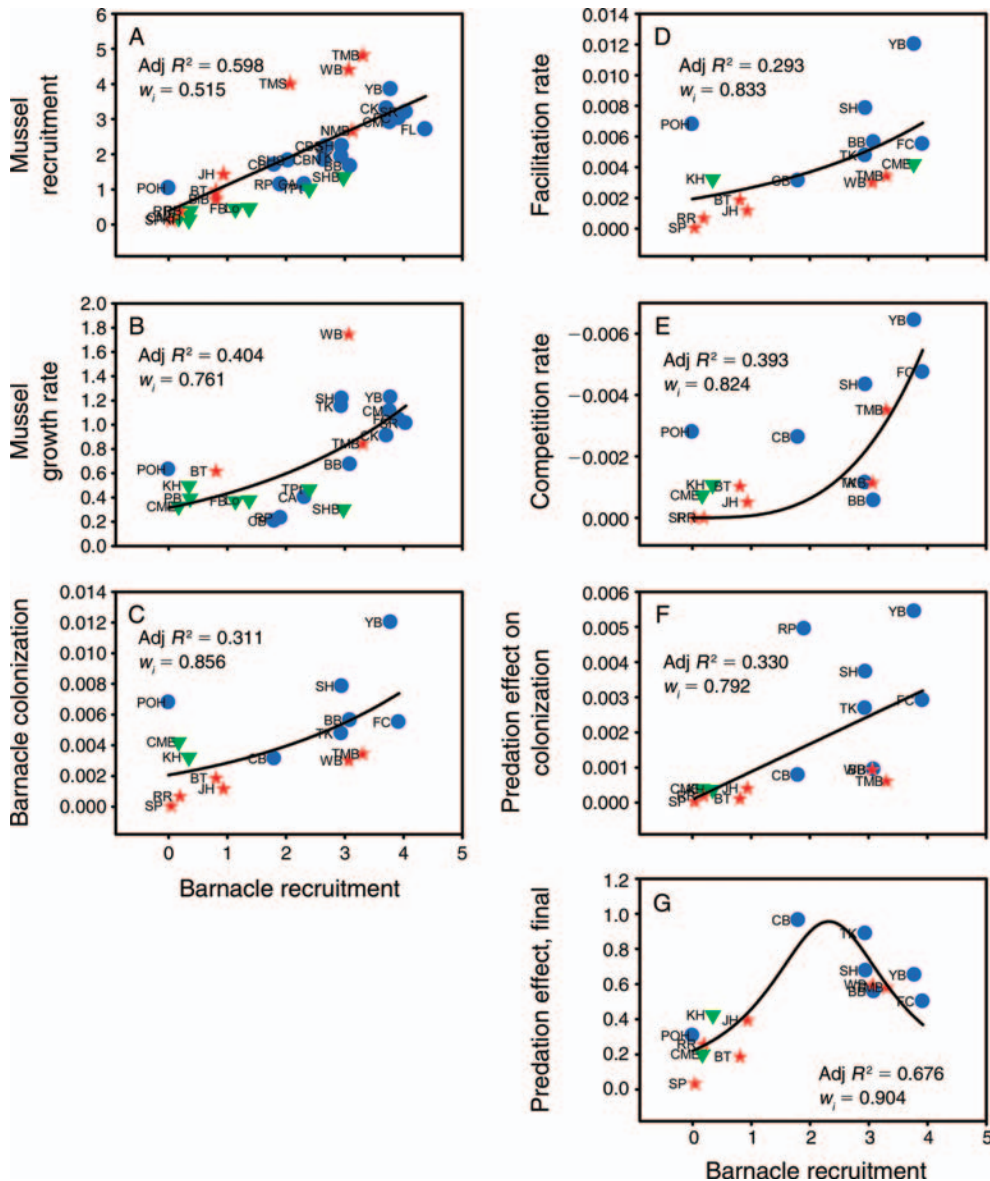


FIG. 8. Relationship between barnacle recruitment rate (ln-transformed) and seven variables: (A) mussel recruitment rate, (B) mussel growth rate, (C) colonization rate of barnacles, (D) facilitation rate of mussels by barnacles (measured as percent cover/d), (E) competition rate, (F) effect of predation on prey colonization rate, and (G) effect of predation over the entire experiment. See Fig. 4 caption and Figs. 4–6 for labeling explanation and units of change for each response variable, respectively.

expected to increase with input of barnacle recruits (Fig. 8C, D). Competition rate was low at low to moderate rates of barnacle recruitment, but intensified at higher rates of barnacle recruitment, suggesting that a threshold rate of recruitment is necessary before adult abundance becomes sufficiently high for competition to occur (Fig. 8E). Also as expected, the effect of predation on colonization increased with increased barnacle recruitment (Fig. 8F). Barnacle recruitment was unimodally related to the effect of predation on final abundance (Fig. 8G; 67.6% of the variance explained), and this was the strongest fit among all the response

variables, suggesting that the greatest impact of predation occurred at intermediate rates of barnacle recruitment. The surprising result, the monotonic relationship between barnacle recruitment and mussel growth (Fig. 8B), will be considered in the *Discussion*.

Increasing mussel recruitment was related linearly to variation in mussel growth rate (Fig. 9A; 62.6% of the variance explained), and unimodally to barnacle colonization rate, competition intensity, effect of predation on colonization, and on final prey abundance (Fig. 9B–E; 32.15%, 59.5%, 30.2%, and 45.9% of the variance explained, respectively). Model weights w_i ranged from

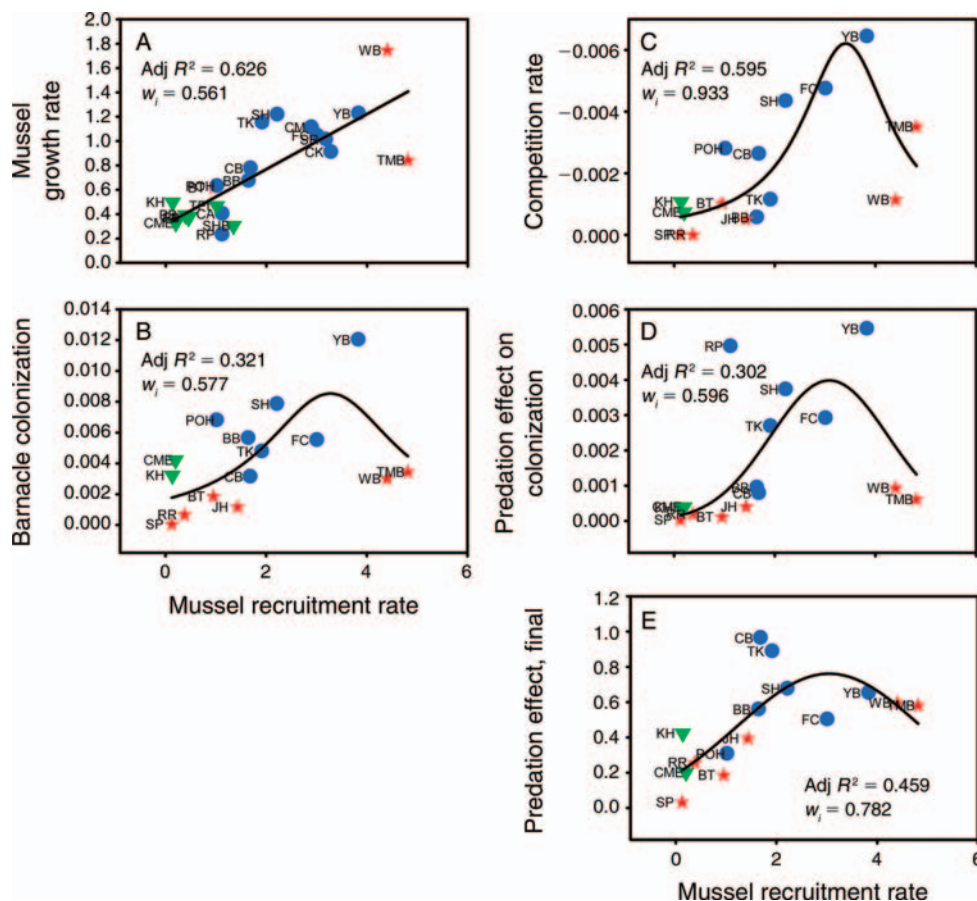


FIG. 9. Relationships between mussel recruitment (ln-transformed) and five variables: (A) mussel growth rate, (B) barnacle colonization rate, (C) competition rate, (D) predation effect on colonization, and (E) predation effect on final prey abundance. See Fig. 4 caption and Figs. 4–6 for labeling explanation and units of change for each response variable, respectively.

0.561 to 0.933. The confidence set excluded the next-best alternative model only for mussel recruitment vs. competition rate (likelihood ratio $w_{i\max}/w_{i\text{model}} = 15.2\times$, but $1.2\times$, $2.5\times$ and $3.5\times$ for the other models; Appendix B: Tables B4, B5). The decline in rates at the high rates of mussel recruitment in the unimodal models in Fig. 9B–E were driven by the very high mussel recruitment rates that occurred at the two SINZ intermittent upwelling sites, WB and TMB (Fig. 9B–E). We address possible explanations for these patterns in the *Discussion*.

Barnacle colonization rate was also a monotonic predictor of species interaction strength, explaining 63.8% of the variance in competition (Fig. 10A), 64.2% in predation rate (Fig. 10B), and 84.1% in predation effect on colonization (Fig. 10C). The relationship with the effect of predation on final abundance increased at low barnacle colonization rates, then leveled off across intermediate to high colonization rates (Fig. 10D), explaining 32.1% of the variance. Model weights w_i were all >0.83 , but the confidence sets all included the next best model (Appendix B: Table B5). Likelihood ratios $w_{i\max}/w_{i\text{model}}$, however, were $\geq 4.9\times$

(Appendix B: Table B4) suggesting these were relatively strong models. The barnacle colonization vs. predation effect on final abundance curve suggests that by the end of the experiments, prey abundance in controls had reached similarly low levels across intermittent to upwelling sites. That is, despite differences in key rates, abundance of prey could be reduced to similar levels even at persistent upwelling sites.

Predation rate (Fig. 11A; 46% of the variance) and the effect of predation on colonization (Fig. 11B; 72.2%) were highest when competition was most intense. Model weights w_i were 0.958 and 0.945, respectively, and in both cases the monotonic model was the only one in the confidence set (Appendix B: Table B5). Likelihood ratios $w_{i\max}/w_{i\text{model}}$ were high, all $\geq 17.3\times$ (Appendix B: Table B4).

Both effects of predation increased with increasing predation rate, but the shapes of the relationships differed (Fig. 12A, B). The effect of predation on prey colonization accelerated with increasing predation rate, explaining 76.9% of the variance, while the effect of predation on final prey abundance approached an asymptote with increasing predation, explaining 46.9%

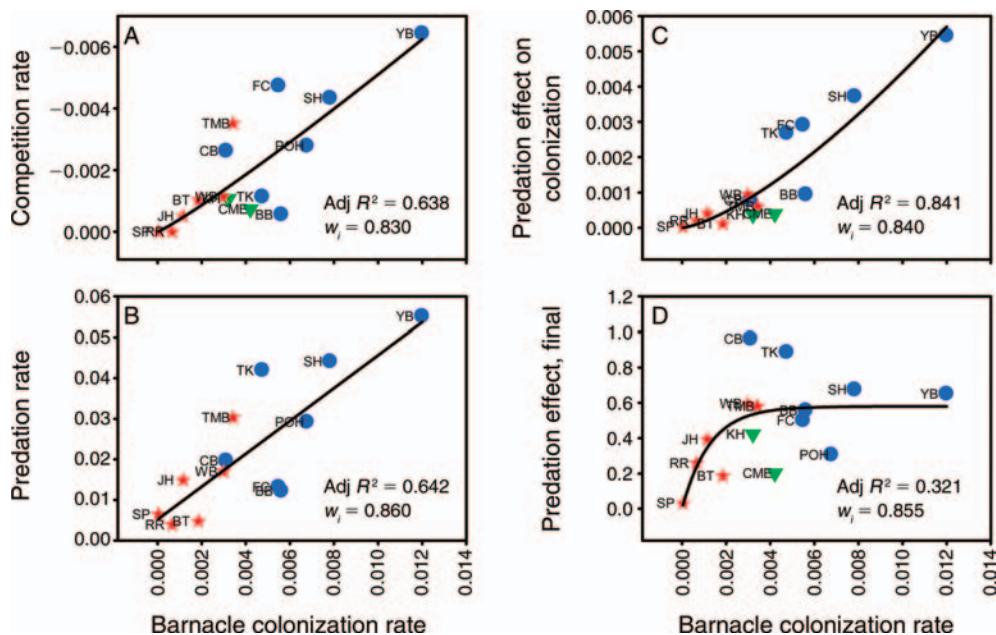


FIG. 10. Relationships between barnacle colonization rate (ln transformed) and four variables: (A) competition rate, (B) predation rate, (C) predation effect on prey colonization, and (D) effect of predation on final abundance. See Fig. 4 caption and Figs. 4–6 for labeling explanation and units of change for each response variable, respectively.

of the variance. Similarly, the effect of predation on final prey abundance also approached an asymptote, with the effect of predation on colonization (Fig. 12C), explaining 67.3% of the variance. Model weights w_i were 0.999, 0.903, and 0.998, respectively, and each was the only model in the confidence set (Appendix B: Table B5). Likelihood ratios $w_{i,max}/w_{i,model}$ were all $\geq 14.6\times$ (Appendix B: Table B4). The accelerating pattern (Fig. 12A) likely reflects a nonlinear influence of predator density on the predation rate, while the asymptotic patterns (Fig. 12B, C) may have a similar explanation to that given for Fig. 10D. That is, final prey abundance can be independent of rates.

DISCUSSION

Overall, the data we present are consistent with IUH predictions of unimodal relationships between upwelling intensity and all response variables (Figs. 3A, 4–6; phytoplankton, recruitment of sessile invertebrates, colonization of prey, growth rates of prey, and resulting rates of species interactions). In contrast, the prediction of monotonic increases of response variables with increased intermittency (Fig. 3B) was met in only 3 of 9 cases (mussel recruitment, mussel growth, and effect of predation on final prey abundance; Figs. 4–6). Why were most intermittency-related cases unimodal?

Inspection of Figs. 4–6 indicates that unimodality in intermittency vs. chl *a*, barnacle recruitment, barnacle colonization, predation rate, effect of predation on prey colonization, and competition, is driven primarily by low rates at highest intermittency by sites on the west coast of SINZ. One hypothesis that could help explain these

tendencies is that these sites have more frequent reversals in winds/currents; i.e., upwelling there might be “over-intermittent.” That is, switching between upwelling and relaxation/downwelling conditions might occur so frequently that rates of delivery of subsidies to the shore might be reduced, thereby slowing rates of prey responses and species interactions. Analysis of mean durations of upwelling and downwelling events is consistent with this possibility (Appendix B: Table B7). Upwelling event durations at CCLME intermittent upwelling (Oregon) sites were 5.46 ± 0.12 days vs. 3.66 ± 0.09 days at SINZ intermittent upwelling sites. Since phytoplankton blooms take about three days to spin up after upwelling favorable winds start, and average upwelling events on the SINZ west coast are only slightly longer than three days, wind/current reversal events often may occur too frequently for dense blooms to form. Alternatively, other conditions in New Zealand independent of upwelling pattern, for example, a deficiency of micronutrients such as iron (Hutchins and Bruland 1998, Kudela et al. 2008), may also play a role.

Among the species interactions, intermittency results from the SINZ west coast were relatively low in all cases except the effect of predation on final abundance of prey (Fig. 6G), and, with the CB site from the CCLME, clearly drive the unimodal models for the effects of predation on colonization and competition (Fig. 6E, F, H). The inter-hemispheric difference in predation rates (Fig. 6E) has been noted previously (Menge et al. 2002), and was attributed in part to differences in tidal regime between NZSLME and the CCLME. Like most temperate regions, the NZSLME has a semidiurnal tidal

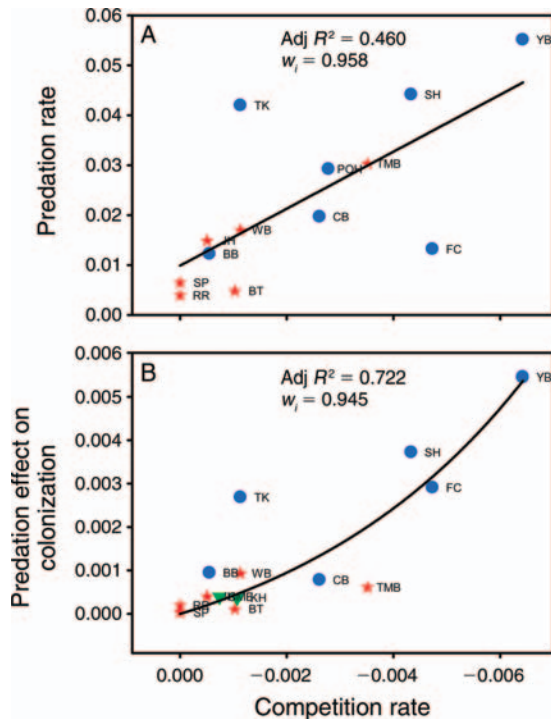


FIG. 11. Relationship between competition rates (based on arcsine-transformed abundances) and (A) predation rate and (B) effect of predation on prey colonization rate. See Fig. 4 caption and Figs. 4–6 for labeling explanation and units of change for each response variable, respectively.

regime, or two high and two low tides of approximately similar elevation per day (tidal information; *available online*).⁸ Thus, periods when sea stars, the primary predator type in these systems, are underwater, are interrupted approximately every six hours. Along the CCLME, the tidal regime is mixed semidiurnal, with high–high, high–low, low–high and low–low tides each day, meaning that sea stars can be underwater foraging for as long as ~18 hours per day. The results of the present analysis using longer and more extensive data sets suggest that the preliminary results presented in Menge et al. (2002) were robust.

The positive relationship between competition and predation (Fig. 11) seems contrary to expectation, as the idea that competition and predation are inversely related has a long history in ecology (e.g., Connell 1961a, b, Paine 1966, Menge and Sutherland 1976, 1987, Bruno et al. 2003). Recall, however, that this measure of competition was obtained in cages in the absence of predation, so these relationships actually indicate that competition potential, and not realized competition, was greatest where predation was strongest.

Surprisingly, the response of facilitation was independent of both upwelling intensity and intermittency (i.e., no regressions with either factor were significant). Since

facilitation of mussels by barnacles is a function of barnacle recruitment and colonization, which did vary with the upwelling regime, we expected to see unimodal relationships. Facilitation rate did increase as a function of barnacle recruitment, however, although this relationship was relatively weak compared to other analyses (Fig. 8D, $\text{adj. } R^2 = 0.293$).

Upwelling or temperature?

Since upwelling patterns can drive seawater temperature variation (see *Introduction*), and metabolic and activity patterns of heterothermic marine organisms are driven in part by temperature (Sanford 1999, Hochachka and Somero 2002, Blanchette et al. 2007, Menge et al. 2008, Pincebourde et al. 2008, 2009), it is reasonable to wonder about the role of temperature itself in driving the patterns we observed. To examine this possible alternative, we reanalyzed our response variables against locally measured seawater temperatures (data not shown). In general, the resulting statistical models were similar to the analyses shown here (unimodal or positive monotonic), but were typically weaker or in a few cases, nonexistent. An example of the latter was mussel growth vs. temperature, in which the intercept model was the “best” model (i.e., no relationship). A likely reason in this case is that mussel growth also depends on food availability (e.g., Menge et al. 2008, Bracken et al. 2012), which can confound the effect of temperature per se. That is, cold temperatures can signify good nutrient conditions for phytoplankton growth, but also can signify strong offshore transport of, and low abundance of, phytoplankton. Warmer temperatures can signal downwelling, and thus low nutrients and slow phytoplankton growth, but also can signify retention conditions. If this occurs right after upwelling, nutrients might be temporarily high, and with warming, support faster growth of phytoplankton. Hence, the better performance of upwelling metrics compared to temperature alone is likely due to the fact that upwelling integrates across several important factors (temperature, currents, nutrients, light, phytoplankton).

Where does the model apply?

The unimodal relationships between ecological subsidies, prey responses, and species interactions vs. upwelling strength suggests that the IUH may apply generally at broad geographic scales, at least to intertidal systems around the world that experience oceanographic regimes comparable to those analyzed here. Besides rocky shores, sandy beaches, estuaries, and subtidal habitats (e.g., kelp beds, rocky reefs, muddy bottoms, shelf pelagic) also occur within LMEs with differing upwelling regimes, and such meta-ecosystems also seem likely to be influenced by upwelling regime. Unfortunately, few studies have yet been conducted at scales appropriate to offer concrete examples. We are aware of just one, estuaries in the Pacific Northwest, where researchers have sought, and detected, influences

⁸ http://tidesandcurrents.noaa.gov/tide_predictions

of upwelling-driven inputs on community structure and dynamics (Hessing-Lewis and Hacker 2013).

We suggest that the model applies primarily to relatively simple, linear coastlines, where major currents flow parallel to the coast. Besides the CCLME and the NZSLME, the model is likely to apply in the other major upwelling-dominated systems (e.g., Peru–Chile, Benguela, and Canary Currents), and in downwelling-dominated systems beyond the SINZ, perhaps including such systems as the Kuroshio, East Australia, Agulhas, Brazil, Alaska, and Gulf Stream Currents. However, coastal systems can have complex dynamics, and as noted earlier, there are likely to be many sources of variation other than those incorporated in the simple model proposed here. For example, in addition to the periodic pulses of upwelling in downwelling-dominated systems, coastal downwelling also can drive shelf-break upwelling (e.g., Matano and Palma 2008), and such nutrient inputs seem likely to reach the coast under some conditions.

The IUH model, or a similar model characterized by “intermittency” of key environmental drivers of community structure and dynamics, may also apply to certain freshwater habitats, such as streams. Streams in northern California or southwestern deserts, for example, can vary both intraseasonally and annually in flooding frequency and intensity, and benthic stream communities can vary dramatically with such environmental variation (Power 1995, Bogan and Lytle 2011, McMullen and Lytle 2012). As in the present study, testing of an IUH-like model in these systems would require conducting identically designed and executed studies in a wide range of stream types at a large geographic scale (e.g., continental). We know of no appropriate terrestrial examples, but expect that at the appropriate (large) spatial scales, factors such as light, precipitation, temperature, and wind will exhibit a range of regimes from more persistent to more intermittent, and that such variation would be likely to influence community dynamics.

Sources of variability

How might other sources of variability modify the predictions of our model? Upwelling intensity explained between 27% and 71% ($53.4\% \pm 4.8\%$; mean \pm SE) and intermittency explained between 13% and 59% ($36.6\% \pm 4.5\%$) of the variation in ecological subsidies, responses of prey, and species interactions (Figs. 4–6; Appendix B: Table B6). In the context of the many other sources of variation that are known to influence processes such as phytoplankton blooms, recruitment, and species interactions, the ability of ocean currents and current-related variables to explain half of the variation in the dynamics of coastal ecosystems at an inter-hemispheric scale seems remarkable. Note also that in all cases, response and predictor variables are independent (Appendix B: Table B6). That is, calculation of upwelling and intermittency

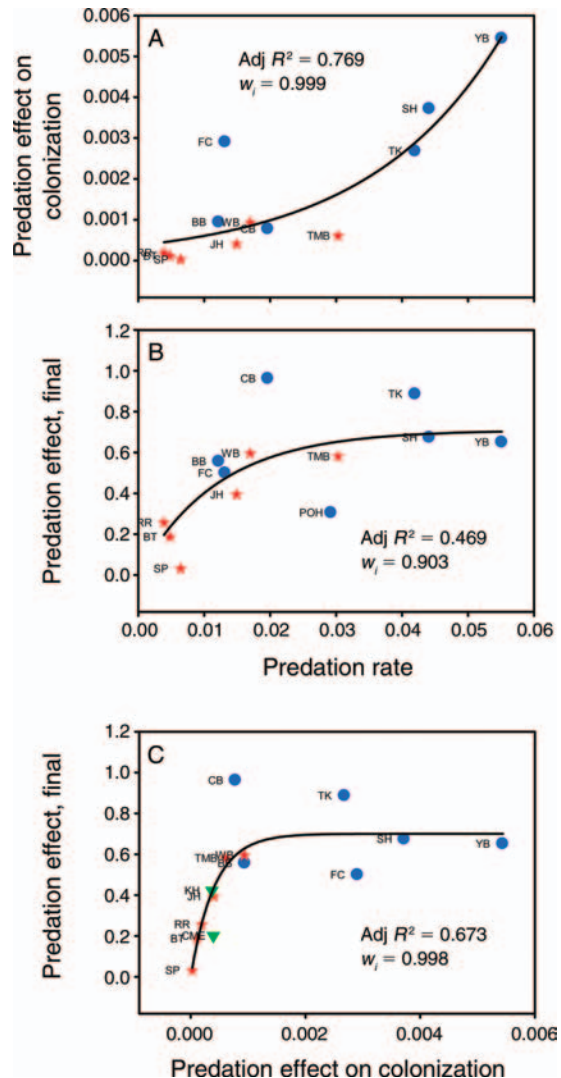


FIG. 12. Relationship between predation rates (ln-transformed) and (A) effect of predation on rate of prey colonization and (B) effect of predation over entire experiment (note that x-axis label applies to both panels A and B), and (C) predation effect on colonization and effect of predation over entire experiment. See Fig. 4 caption and Figs. 4–6 for labeling explanation and units of change for each response variable, respectively.

indices are in no way linked to measurements of ecological activities on the shore.

What factors are responsible for the remaining half of the variation in these measures and interactions? Many factors could have an influence, including evolutionary history (see Appendix A: Discussion), oceanographic, climatological, and geographic factors at larger or longer scales, and the many local to regional factors that are known to influence processes and interactions (e.g., Kudela et al. 2008). The latter include variation due to coastal heterogeneity (e.g., headlands vs. coves, proportion and distribution of rocky vs. sandy shores, sharp changes in the general trend of the coastline,

nature of adjacent subtidal communities), variation in width of continental shelf, eddies and currents, upwelling shadows, and organismal characteristics such as behavior, relative motility, habitat selection, and life history differences.

Geomorphology.—Coastal geomorphological differences at local to geographic scales can play an important role (Kudela et al. 2008). For example, headlands or sharp changes in coastline trend can create lee areas of slowed flows and gyres or “upwelling shadows” that can accumulate particles (e.g., Ebert and Russell 1988, Graham et al. 1992, Graham and Largier 1997). Similarly, in addition to influencing alongshore and cross-shelf transit times, variation in the width of the continental shelf can shift the main jet of coastal currents, causing eddies, gyres, and slower currents, thereby generating retention areas (e.g., Menge et al. 1997a, b, Castelao and Barth 2005, Kirincich et al. 2005). The most productive region in our analysis was the Cape Perpetua region along the central Oregon coast (e.g., Menge et al. 1997a, 2004, 2008, Leslie et al. 2005, Barth et al. 2007). This productivity (in phytoplankton and recruitment rate) was paralleled by high rates of mussel growth, predation and effects of predation, competition, and facilitation, and seems attributable to the gradual widening of the continental shelf across a distance of about 70 km of coast (Menge et al. 1997a, Castelao and Barth 2005, Kirincich et al. 2005, Kudela et al. 2008). This widening guides the California Current away from the shore, and generates a shoreward region of weak currents that leads to retention of phytoplankton and larvae (e.g., Woodson et al. 2012). This retention leads to high rates of ecological subsidies from nearshore waters that fuel the intertidal food web.

Another factor that varies with coastal geomorphology is oceanographic fronts. These form where water masses of different properties of temperature, salinity, and density collide (Colling et al. 2004). In coastal upwelling ecosystems, fronts commonly form between the coastal upwelling zone and warmer water to seaward (Wolanski and Hamner 1988, Roughgarden et al. 1991, Graham and Largier 1997, Woodson et al. 2012). Such fronts tend to accumulate phytoplankton and propagules, and are also, because of these accumulations, attractive to more mobile organisms at higher trophic levels. Fronts are not continuous along coasts, however, because of alongshore variation in width of the upwelling zone (related to bottom topography, coastal geomorphology, and wind velocity), and the tendency for “squirts,” “jets,” and eddies to form and separate from the outer edge of the upwelling zone (Strub et al. 1991). These complexities can transport or dissipate fronts. However, recent evidence suggests that moderately persistent fronts tend to form at spatially predictable locations along the coast, and that inshore of such fronts, phytoplankton blooms and recruitment of invertebrates and fish is high relative to adjacent areas (Woodson et al. 2012). Depending on their degree of

association with variation in upwelling regime, fronts could either enhance the upwelling mechanisms discussed here, or be an additional source of variation underlying the ecological patterns and processes.

A third geomorphological factor is the nature of the adjacent subtidal habitats. When adjacent habitats are rocky bottoms, typically with abundant kelps or habitats that support abundant populations of fish and mobile invertebrates, these high-trophic-level consumers can potentially forage up into intertidal regions during high tide (e.g., Menge and Lubchenco 1981, Menge et al. 1986, Taylor and Schiel 2010). For example, in a recent study, researchers in New Zealand (Rilov and Schiel 2006a, b, 2011) demonstrated that predation by subtidal-dwelling fishes and crabs on intertidally transplanted juvenile mussels varied with whether the adjacent bottom was rocky or sandy. Rocky bottoms tend to be steeper and offer shelter to these consumers, while sandy bottoms tend to slope gradually and offer little shelter for reproduction and avoidance of larger predators. Rates of mussel mortality were high at sites near rocky bottoms and low near sandy-bottom sites, presumably due to high and low abundances of consumers, respectively. This study was done in part in the central east coast of SINZ, where the intertidal studies reported in the present paper found a generally weak effect of predation over longer periods of time. Combining these studies suggests that the slow increase of mussels in our experiments at this site was likely jointly influenced by low rates of recruitment of prey and predation on mussel colonists. Many colonists escaped predator control, however, as mussels eventually became abundant in the presence as well as the absence of predators.

Downwelling region conundrum.—Although rates of inputs and interactions at downwelling-dominated regions like the SINZ east coast are low, these regions are far from barren, sometimes with high abundances of sessile invertebrates and/or macrophytes (e.g., Menge 1976, Lubchenco and Menge 1978, Menge et al. 1999, 2003, Schiel 2011). Although our model is focused on rates, not abundance or diversity, process and interaction rates in SINZ downwelling-dominated regions are not zero, raising the question, “What are the sources of nutrients for these regions?” First, downwelling dominance does not mean that no upwelling occurs (e.g., Fig. 2), so even in such regions pulses of upwelled nutrients may become available to the intertidal benthos (e.g., Shanks et al. 2000, Shanks and Brink 2005). Second, complexities such as shelf-margin upwelling occur in downwelling regions (Matano and Palma 2008), and topographically driven local upwelling is also likely to occur in these regions. Third, river or other freshwater inputs can also be important sources of nutrients (e.g., Kudela et al. 2008, Seitzinger et al. 2010). For example, major rivers occur on the east coast of SINZ, the east coast of North America, and elsewhere, and along with the infrequent and brief upwelling events that occur in



PLATE 1. Close-up of recruits of *Balanus glandula* that had settled a few days previously at the Tokatee Klootchman study site. Such events are relatively common at sites with intermittent upwelling and are rare to nonexistent at sites experiencing persistent upwelling or persistent downwelling. The recruits settled among older *B. glandula* and another barnacle *Chthamalus dalli*, juveniles of which are also visible in the lower and right center of the photograph. The ruler units are mm. Photo credit: B. A. Menge.

these regions, may be important sources of nutrients. Rivers may also be significant sources of nutrients in upwelled ecosystems (e.g., Kudela et al. 2008).

Disturbance.—Disturbance can vary across large to local spatial scales and long to short temporal scales. Classic studies have emphasized the key role that disturbance can play in structuring communities (Dayton 1971, Connell 1978, Sousa 1979*a, b*, Paine and Levin 1981), and such effects can occur on virtually any coast (e.g., Jonsson et al. 2006, Scrosati and Heaven 2008). Environmental stress (thermal, salinity, hypoxia) can also influence community dynamics across many scales, but likely has its largest effect on intermediate to local spatial scales (e.g., Menge and Sutherland 1987, Menge and Olson 1990, Bruno et al. 2003). Remaining variation is likely due to smaller-scale variation in physical and biotic environments, differences in temporal scales (e.g., time lags between rates of inputs and resulting competitive and predation effects) and annual variation in inputs.

Recruitment.—Other factors operate mostly at smaller spatial or shorter temporal scales. For example, a long-standing question has been the extent to which the abundance of adult populations is dependent on the inputs of recruits (e.g., Underwood and Denley 1984, Connell 1985, Gaines and Roughgarden 1985, Menge and Sutherland 1987, Roughgarden et al. 1988, Tilman 1997, Menge 2000*b*, Gouhier et al. 2010). Following Connell's (1985) suggestion, a later synthesis (Menge and Sutherland 1987) suggested that the relationship varied with recruitment density. At low rates of

recruitment, adult abundance was strongly dependent on recruitment, while at high rates of recruitment, the relationship was weak to nonexistent (see Menge 2000*b* and Navarrete et al. 2005 for examples). In marine systems, recruitment variation in space is commonly high at large spatial scales (e.g., Caffey 1985, Jenkins et al. 2000, Navarrete et al. 2005, Porri et al. 2006, Broitman et al. 2008). Yet in some cases, even at large scales the relationship between recruitment and adult abundance is weak (e.g., mussels; Menge et al. 2004), and additional variation is explained by post-recruitment processes such as competition, facilitation, and predation (e.g., Connell 1961*a, b*, Hacker and Gaines 1997, Menge et al. 2003, 2004, 2011*b*, Wieters 2005, Freidenburg et al. 2007).

Propagule biology.—Larval behavior may be an important cause of variation that is more or less independent of the "mixed-layer conveyor" (MLC) model of cross-shelf transit (Botsford et al. 2006, Yokomizo et al. 2010). Several recent studies (Morgan et al. 2009*a, b*, Shanks 2009*a, b*, Shanks and Shearman 2009) emphasize this possibility, noting that the position of larvae of several invertebrate species tends to remain at midwater and relatively close to shore regardless of whether upwelling or relaxation/downwelling occurred. Although Shanks and Shearman (2009) argued that the current reversal hypothesis was a "paradigm lost," in a 10-week study at a single site, Shanks (2009*b*) also found that upwelling was second in significance to tidal change as a factor determining patterns of barnacle settlement

at that site. Similarly, off North Carolina, Shanks et al. (2000) attribute larval transport to shoreward movement of upwelling fronts. Retention of larvae nearshore by vertical swimming does not necessarily invalidate the MLC model (e.g., Menge et al. 2011a). Instead, the wide range of factors involved in larval transport highlights the likelihood that delivery of larvae to the adult habitat is a complex, multifactorial process that varies on both spatial and temporal scales. For example, a current reversal or upwelling-related mechanism has been implicated in numerous studies (e.g., Farrell et al. 1991, Roughgarden et al. 1991, Wing et al. 1995a, b, Shkedy and Roughgarden 1997, Almeida and Queiroga 2003, Navarrete et al. 2005, Blanchette et al. 2006, Broitman et al. 2008, Dudas et al. 2009, Menge et al. 2011a). In most of these studies, however, upwelling-related processes do not explain all of the variance observed, and factors typically operating at shorter time scales and smaller spatial scales are cited as also being important. These factors include internal waves, tidal bores/tidal periodicity, sea breezes, wave action, river inflows, bio-foam, surf, and larval behavior (Pineda 1991, 2000, Shanks and Brink 2005, Castilla et al. 2007, Woodson et al. 2007, 2012, Rilov et al. 2008, Morgan et al. 2009a, b, Shanks 2009a, b). A major issue to be resolved by future research is determination of the relative influence of these local-scale factors compared to the larger-scale processes discussed previously.

Underlying mechanisms

With two exceptions, most regressions among the different variables showed increasing relationships with increases in the predictor variables (Figs. 7–12; Appendix B: Tables B3–6, Appendix C: Fig. C1). As expected from bottom-up/top-down theory (e.g., Oksanen et al. 1981), these relationships between and among the various ecological subsidies and species interactions suggest strong influences of subsidies on processes and interactions higher in the food web. For example, phytoplankton (chl *a*) was positively related to barnacle colonization rate, competition, and predation (rate and both measures of effect; Fig. 7). Similar positive effects were seen between barnacle recruitment and six of seven processes (Fig. 8), mussel recruitment and mussel growth rate (Fig. 9), barnacle colonization and four of four processes (Fig. 10), and among higher trophic level interactions (Figs. 11 and 12).

The exceptions were the barnacle recruitment-predation effect on final prey abundance and four of five mussel recruitment based relationships (Figs. 8G, 9B–E). The effect of predation on final prey abundance increased to a peak with increasing barnacle recruitment, then declined at the highest rates of barnacle recruitment (Fig. 8G). This pattern may reflect swamping of predators by very high rates of prey input. Such swamping has been seen at several of the sites that are in the cluster that makes the relationship decline at the highest rates of barnacle recruitment, including YB, SH, and TK in Oregon and

WB and TMB in New Zealand. In these cases, predators eventually “catch up” to the excess of prey, but the longer time span required reduces rates of predator impact (B. A. Menge, *unpublished data*).

The unimodal relationships between mussel recruitment and barnacle colonization, competition, and the two effects of predation (Fig. 9B–E) were driven by results at the SINZ west coast sites, and are likely interrelated. First, mussel recruitment was higher than barnacle recruitment rate at these sites (Fig. 8A). Mussel colonization is facilitated by prior presence of barnacles (Menge 1976, Menge et al. 2011b), however, and may not have kept pace because of lower barnacle recruitment and thus lower barnacle colonization (Figs. 8C, 9B). That is, a lower barnacle recruitment rate likely means that less facilitation surface will be available for mussels. Consequently, despite high mussel recruitment rates, competition between barnacles and mussels likely was less at WB and TMB because barnacle cover was relatively low (Fig. 9C). Slower barnacle colonization would also affect the effect of predation on prey colonization rate (Fig. 9D), and such an effect evidently carried through to the end of the experiments at these sites (Fig. 9E).

Most of the remaining relationships among processes and/or interactions seem sensible. One exception deserves comment. In view of the lack of a correlation between chl *a* and mussel growth ($P > 0.05$), the increase in mussel growth rate with increased barnacle recruitment was surprising (Fig. 8B). Mussels are capable of filtering zooplankton as well as phytoplankton and detritus, however, and it is possible that at high abundance, barnacle larvae could become an important supplement to these other food sources (e.g., Alfaro 2006).

Several of these relationships (Figs. 7–12) are suggestive of threshold effects (see suggested interpretations in *Results*), some of which can be understood as density-dependent responses by response variables to increases in predictor variables. An example would be a sudden shift from weak to strong competition with increasing barnacle recruitment (Fig. 8E). Another would be an accelerating effect of predation on prey colonization with increased predation rates (Fig. 12A), which is ultimately likely a reflection of variation in predator density. That is, effects of predators on colonizing barnacles may show a time lag when predators are sparser (and predation rates are lower), but increase rapidly once predators are sufficiently abundant to have an impact on small and presumably energetically unattractive prey.

The strength of links from lower levels to upper levels of these ecosystems increases as the number of levels from the top level decreases. For example, average variance explained by ecological subsidies (chl *a*, recruitment) linked to prey responses and interactions was $46.1\% \pm 3.6\%$ ($n = 17$), by prey responses linked to interactions was $61.05\% \pm 10.8\%$ ($n = 4$), and among interactions was $61.9\% \pm 6.5\%$ ($n = 5$). Similarly, model

weights w_i for the same linkages were 0.773 ± 0.033 , 0.846 ± 0.007 , and 0.961 ± 0.018 . These patterns seem consistent with the idea that as one considers responses ranging from larger scales (ecological subsidies) to more local scales, the amount of variability explained by inputs increases.

Incorporation of herbivores and macrophytes?

Because the exclusion experiments did not manipulate herbivores, and we have yet to devise a reliable method of quantifying macrophyte recruitment, this analysis focused on the phytoplankton–sessile invertebrate–sea star and whelk subweb of intertidal communities. However, this subweb is linked via spatial interactions to macrophytes and via predation, omnivory, and biotic disturbance to herbivores (e.g., Paine and Vadas 1969, Dayton 1975, Lubchenco and Menge 1978, Lubchenco 1986, Freidenburg et al. 2007), so an important goal will be to evaluate how the macrophyte–herbivore subweb responds to upwelling forcing.

First principle arguments suggest that on a global scale, the macrophyte–herbivore subweb may function differently, although with important cross-linkages (i.e., competition, facilitation) with the phytoplankton–invertebrate subweb. For instance, the supply of nutrients should increase monotonically rather than unimodally along the gradient of persistent downwelling to persistent upwelling. However, this increasing trend may not lead to a strongly correlated increase in macrophyte abundance. Kelps and other large macrophytes can be long-lived, and have the capability of sequestering nutrients, for example, thereby providing a form of insurance against periods of low nutrient availability (Fujita 1985). Thus, even downwelling-dominated, low-nutrient regions like the east coast of SINZ can have abundant populations of large macrophytes (e.g., Menge et al. 1999, 2003, Schiel 2004, 2011, Schiel and Lilley 2007). Further, with high nutrients, bottom-up effects (high macrophyte abundance or productivity) may support higher densities of herbivores, leading to a reduction in macrophyte abundance in persistent upwelling regimes. Comparative experiments manipulating both grazers and predators, and on interactions between macrophytes and sessile invertebrates, would go far in helping modify the IUH conceptual framework for the entire invertebrate–macrophyte system.

Conceptual generality

Ecologists have long sought to determine the relationships between environmental gradients and the structure and dynamics of the communities and ecosystems along them (e.g., Dayton 1971, Menge and Sutherland 1976, 1987, Oksanen et al. 1981, Abrams 1995, Hacker and Gaines 1997, Tilman 1997, Menge 2000a, Bruno et al. 2003, Loreau et al. 2003). In the context of the present analysis, models relating community structure to underlying gradients of productivity are

relevant (e.g., Oksanen et al. 1981, Menge 2000a), but the added importance of another type of ecological subsidy, propagule inputs, requires the expanded purview of the meta-ecosystem concept (e.g., Loreau et al. 2003). The IUH is thus a conceptual model for how coastal meta-ecosystems function. Further model development is needed, however, both to consider the plant–herbivore subweb in a meta-ecosystem context, and to consider what form an expanded model might take to explain the ~50% of the among-ecosystem variability not explained by the IUH. Given the hierarchy of scales over which explaining this variation must occur, it is easy to imagine (but likely difficult to formulate) a nested design model, with predictable effects of smaller or shorter scale variables incorporated into a more complex IUH-type model. Analytical modeling approaches are also likely to be an important complementary direction to take (e.g., Leroux and Loreau 2008, Gouhier et al. 2010, Gravel et al. 2010a, b).

Conclusions

Ecologists have long debated the relative importance of top-down vs. bottom-up influences, and more recently, the importance of inputs of propagules in determining the structure and dynamics of communities and ecosystems. The position we take here, consistent with the recent synthesis of Estes et al. (2011), is that all these factors are integrally important, and that understanding at a global scale requires a synthesis of how each influence varies in relation to each other and to environmental gradients. We suggest that the IUH is a step in this direction, and can help to understand a substantial fraction of the variation in ecosystem structure and dynamics across large, geographic and oceanographic scales. Beyond this, we foresee several directions for future efforts. First, future studies should address the extent to which such an approach applies to other similar systems (i.e., to what extent do coastal ecosystem dynamics in [e.g.] Chile, or Brazil, or Japan, conform to the predictions of the IUH?), or to different systems, whether they are other marine systems, terrestrial, or freshwater. Second, identifying sources of “unexplained” variability will help to generalize, and to constrain the model. Third, extending the model to include macrophyte-based parts of these systems will be an important step. Fourth, we urge a focus on downwelling-dominated systems, ideally from an integrated ecological–oceanographic perspective. The issue of spatial coupling in such systems remains poorly understood.

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SUPPLEMENTAL MATERIAL

Appendix A

Comparison of New Zealand and Oregon/California intertidal communities by taxon and functional groups (*Ecological Archives* M083-010-A1).

Appendix B

Seven tables and three figures showing locations of study sites, details of the calculation of the intermittency index, types of ecological data taken at each site, details of statistics and data used in model selection for the relationships among upwelling, inputs, prey responses, and interactions, and an analysis of length of upwelling events in each region (*Ecological Archives* M083-010-A2).

Appendix C

Diagrams of methods of analysis of species interaction rates and an example of experiments showing changes in mussel and barnacle cover in exclusion cages (*Ecological Archives* M083-010-A3).

Data Availability

Data associated with this paper have been deposited in the PISCO archive: https://data.piscoweb.org/catalog/d1/mn/v1/object/doi:10.6085/AA/publication_data.1.1