SPECIES INTERACTION STRENGTH: TESTING MODEL PREDICTIONS ALONG AN UPWELLING GRADIENT

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Abstract. A recent model predicts that species interactions in benthic marine communities vary predictably with upwelling regimes. To test this model, we studied the *Pisaster–Mytilus* interaction at 14 rocky intertidal sites distributed among three oceanographic regions along a 1300-km stretch of the U.S. West Coast. Regions included an intermittent-upwelling region (northern), a persistent-upwelling region (central), and a region of weak and infrequent upwelling (southern). We quantified predation rates by the sea star *Pisaster ochraceus* on its main prey *Mytilus californianus* by transplanting mussels into the sea star's low-zone foraging range and comparing the rate of mussel loss in +*Pisaster* plots to those in −*Pisaster* plots. To evaluate the relation between predation rates and key ecological processes and conditions, we quantified phytoplankton concentration and rates of mussel recruitment, mussel growth, mussel abundance, and sea star abundance.

Predictions of the model are expressed as responses of predator and prey abundance, and species interaction strength (per capita and per population or total impact at the population level). As predicted by theory, *per capita* predation rates were independent of upwelling regime, with no variation with region. Contrary to expectation however, per-population predation rates were similar between intermittent- and persistent-upwelling regions but were greater under strong upwelling than under weak upwelling conditions. The greatest variation in *per-population* predation rates was at the level of site within region. Also contrary to theory, average abundances of prey (mussel cover) and predators (sea stars) were similar among oceanographic regions and varied mostly at the site level.

As expected from theory, predation rate was high where sea star density was high, a condition that often coincided with a high food supply (phytoplankton) for filter feeders, including larvae, and high recruitment. With the exception of two sites having dense sea star populations and thus high predation, low values of either or both were associated with low predation, suggesting that the supply of prey often depended on conditions that favored subsidies of both phytoplankton and new larvae to prey populations. The occurrence of high predator density and high predation at sites of low inputs of particulate food and propagules suggests that understanding sea star life history is a key to a fuller understanding of variation in predation on a coastal scale. Evidence suggests that often sporadic recruitment of sea stars along the coast is balanced by great longevity, which tends to even out predation impact on coastal intertidal communities.

Key words: California Current; keystone predation; larval transport; mussels; Mytilus californianus; *phytoplankton;* Pisaster ochraceus; *recruitment; rocky intertidal; species interaction strength; upwelling.*

INTRODUCTION

Inspired in part by Levin (Levin 1992), Carpenter and colleagues (Carpenter et al. 1985, 1987, 1998, 2001) and others, ecologists have increasingly incorporated larger-scale perspectives in efforts to understand community dynamics. Although such efforts impose challenges for the rigorous design, execution, and analysis of field studies (Carpenter et al. 1989, Lodge et al. 1998), incorporation of larger-scale perspectives was prompted by possible limitations to inferences

from small-scale experiments (Dayton and Tegner 1984). For example, the experimental ''whole lake'' approach was implemented to address concerns about the community relevance of microcosm or mesocosm experiments (Carpenter 1996, Carpenter et al. 1996, 2001). Although larger-scale studies are accompanied by an alternative set of shortcomings (increased logistical difficulties, low replication, impossibility of manipulating some factors), the combination of large-scale and small-scale studies has added power to and increased confidence in inferences about lake community and ecosystem dynamics (Carpenter et al. 1987, 1996, 2001, Drenner and Mazumder 1999). Another example comes from the studies of the community con-

sequences of allochthonous inputs from marine environments ("ecological subsidies") on terrestrial community dynamics in the Gulf of California (Polis and Hurd 1995, 1996, Polis et al. 1997, 1998). Here the expansion of scale from arthropod–plant communities on desert islands to a larger terrestrial–marine scale, looking at the influence of marine inputs to terrestrial communities in an archipelago, suggested important effects of allochthonous inputs on food-web structure and dynamics. Among other effects, marine inputs elevated abundance of spiders on small islands, and variation in the magnitude of marine biomass inputs to island communities triggered large fluctuations in spiders that were driven by previously unsuspected interactions (Polis and Hurd 1995, Polis et al. 1998). Realization of the occurrence and dynamic importance of such linkages between adjacent ecosystems is increasing (Wallace et al. 1997, Power et al. 1998, Nakano and Murakami 2001).

In the coastal ocean, spatial scales, as calibrated by major oceanographic current systems, can be immense, spanning hundreds to thousands of kilometers. The parallel but independent traditions of oceanographers and marine biologists adds to the complexity of "scaling up" in the ocean (Menge 1992). The past 10–15 years have seen an upsurge in research focused on understanding the linkages between coastal benthic communities, particularly rocky shores, and the waters bathing them (Duggins et al. 1989, Gaines and Bertness 1992, Minchinton and Scheibling 1993, Bustamante et al. 1995*a*, *b*, Bustamante and Branch 1996*a*, *b*, Menge et al. 1997*a*, 1999, Menge 2000, Robles and Desharnais 2002). Such efforts reflect a multi-scale, integrated approach to coastal marine ecosystems that incorporates important oceanographic, physical, and biological influences on community structure (Menge 2000). This perspective adds larger-scale, oceanic environmental gradients in supplies of propagules, nutrients, and particulate food (including detritus and phytoplankton) to the traditional, more local-scale gradients in wave action, physical and physiological stress, and species interactions as determinants of community dynamics.

Studies that have incorporated processes varying on oceanic scales (10's to 1000's of kilometers) suggest that, in addition to well-documented effects of competition, disturbance, and top-down processes, bottom-up forces (nutrients, phytoplankton, detritus) can be important determinants of rocky intertidal community structure. For example, in South Africa, decreases in nutrient concentration occurring across scales of 1000's of kilometers from western through southern to eastern South Africa are correlated with decreases in macrophyte biomass and production (Bustamante et al. 1995*b*). These changes underlie decreases in abundance of both sessile and mobile consumers, suggesting strong bottom-up effects on higher trophic levels (Bustamante et al. 1995*a*, *b*). In New Zealand, between-coast differences in top-down (predation and grazing)

and bottom-up (prey recruitment, nutrients, filter-feeder growth, macrophyte biomass accumulation) factors were associated with large-scale differences in oceanographic conditions (intermittent upwelling vs. downwelling) (Menge et al. 1999, 2002, 2003).

Background: the California Current ecosystem

The coastal oceanography of the U.S. West Coast is dominated in summer by the California Current system (Hickey 1979, 1998) (Fig. 1), one of the world's major upwelling ecosystems (Gross 1990, Bakun 1996). From north to south along the study region, three distinct oceanographic regimes can be identified (Strub and James 1995, 2000, Harms and Winant 1998, Barth et al. 2000). (1) Along the coasts of Washington and Oregon to about Cape Blanco (43° N), summer upwelling alternates between periods of upwelling (characterized by equatorward coastal winds) and relaxation of upwelling (cessation and even reversal of winds) on approximately a 3 to 10 day cycle. The California Current is relatively close to shore (20–50 km) and is approximately parallel to the coast (Strub and James 1995). We refer to this as the "intermittent upwelling region" (IUR). (2) From Cape Blanco to Point Conception (34°C), summer upwelling is nearly continuous (e.g., Barth et al. 2000) and the main current ranges from 50 to 300 km offshore, developing a complex undulating structure with meanders, filaments, and eddies (Strub and James 1995). We refer to this coastal region as the "persistent upwelling region" (PUR). (3) In the Santa Barbara channel region, the coastal region is dominated by west-northwestward alongshore currents driven by an alongshore pressure gradient (Harms and Winant 1998, Hickey 1998). Upwelling events are infrequent, brief, and largely restricted to spring (Harms and Winant 1998, Hickey 1998). We refer to this coastal region as the "weak upwelling region" (WUR).

These differing oceanographic regimes have potentially important implications for coastal ecosystems with respect to impacts on coastal ecosystems. With intermittent upwelling, both larval transport back to the adult habitat (Roughgarden et al. 1988) and shoreward transport of particulates (phytoplankton, detritus) should be high (Menge 1992). This is because offshore transport is frequently reversed, and the oceanographic front (border between the California Current and the shoreward upwelled water) is close to shore. This means that larvae, nutrients, and particulates are likely retained closer to shore, and oscillate between movement away from, and towards, the coast. With persistent upwelling, both larval transport back to the adult habitat and shoreward transport of particulates should be low. This is because offshore transport is more continuous and the front is far from shore; hence larvae, nutrients, and particulates are likely to be swept seaward with few opportunities to return to the coast. In the weak upwelling region, shoreward larval transport,
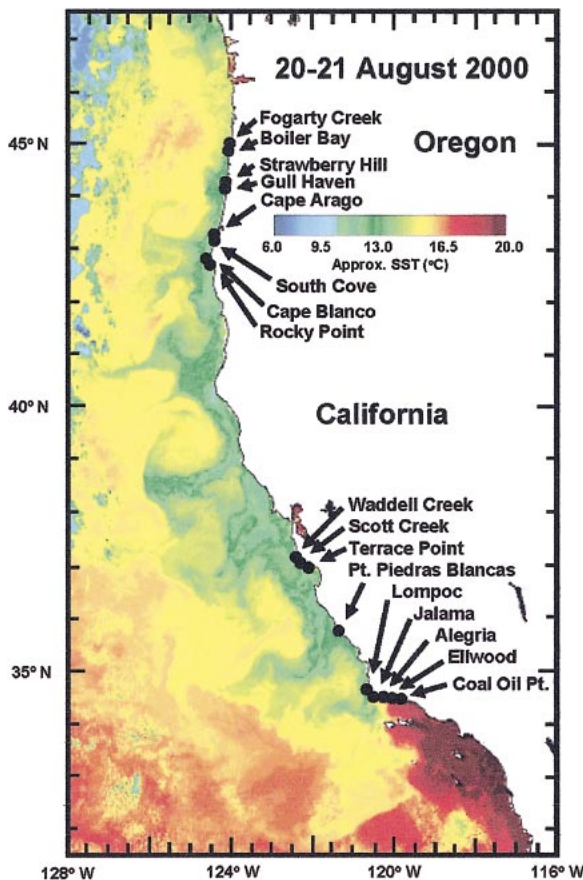
FIG. 1. Composite AVHRR sea surface satellite image from 20–21 August 2000 showing the variable thermal structure of the California Current ecosystem from southern Washington to southern California (USA). Site names are listed in order from north to south (see Appendix A for latitude and longitude). Sites at Fogarty Creek and Boiler Bay are 0.5 km apart; sites at Strawberry Hill and Gull Haven are 3 km apart. SST = sea surface temperature.

injection of nutrients, and particulates should all be low even though the west-northwestward prevailing current direction implies that with Ekman transport, surface waters should move coastward (Hickey 1998). This is because larval sources are likely to be distant and indirect, and nutrient pulses are rare and therefore phytoplankton blooms are also infrequent.

Coupled benthic–pelagic dynamics

Early ecological research suggested that community dynamics in this and similar ecosystems were dominated by tension between competition for space on the one hand and top-down forces and environmental stress on the other (Paine 1966, 1974, 1984, 1994, Dayton 1971, Connell 1975, Menge and Sutherland 1976, 1987). Later research suggested that, as argued by Underwood and Denley (1984), propagule supply could have important effects on population abundance and zonation of barnacles (Grosberg 1982, Gaines and

Roughgarden 1985). Connell's retrospective analysis (Connell 1985) suggested such effects could be geographically widespread. These observations implied that the delivery of larvae to the adult habitat was variable in space and time, and, in combination with the variable spatial and temporal structure in physical oceanography suggested by satellite imagery of sea-surface temperatures, led Roughgarden and colleagues (Roughgarden et al. 1988) to propose a model that suggested rocky intertidal community dynamics varied predictably along the U.S. West Coast. Noting that the California Current tended to be closer to shore off Oregon and Washington than off California and that periods of upwelling cessation were longer and more frequent to the north, Roughgarden et al. postulated that northern sites should receive a higher larval return than do southern sites. This is because the larvae-bearing front between the seaward California Current and the coastal upwelling zone was likely to brush the coast more frequently to the north during upwelling relaxations. They thus postulated that northern rocky intertidal communities should have recruitment densities sufficiently high to saturate the shore, and thus that post-settlement interactions among adults should be the primary determinants of community structure. In contrast, southern rocky intertidal communities should have low recruitment densities, and thus community structure primarily should reflect settlement patterns (Roughgarden et al. 1988).

This hypothesis suggests that along the north–south latitudinal gradient we should observe declining abundance and rates of recruitment of sessile invertebrates. Further, species interactions should be stronger to the north and have a greater impact on patterns of community structure. More recently, Connolly and Roughgarden (1999b) offered a formal model of the Roughgarden et al. (1988) hypothesis, explicitly incorporating the impacts of upwelling intensity (quantified as offshore advection rate, with high advection reflecting stronger upwelling) on species interactions. The model differs from traditional Lotka-Volterra species-interaction models by assuming that predator and prey have "open" populations (i.e., that emigration and immigration are >0). Connolly and Roughgarden (1999b) first present a competition model predicting the outcome of interactions between a dominant and a subordinate competitor under conditions of increasing losses of larvae due to offshore transport. A predator–prey model then examines the effects of a predator on a sessile prey, also under conditions of increasing larval loss. The competition model predicts that, with increasing upwelling (increasing advection rate or rate of larval loss): (1) abundance of the competitive dominant decreases while abundance of the competitive subordinate increases (because decreasing recruitment reduces the rate of competitive displacement of the subordinate) and (2) both *per capita* and *per-population* interaction strength of the dominant on the subordinate

decrease. The predator–prey model predicts that, with increasing upwelling: (3) prey intrinsic growth rate, prey carrying capacity, and predator larval production decrease; (4) predator abundance decreases (thereby reducing the impact of predation) and consequently prey abundance increases; (5) *per capita* interaction strength of prey on predators (impact of consumption of prey) decreases but *per capita* interaction strength of predators on prey is constant (because predators do not influence recruitment); and (6) *per-population* interaction strength of prey on predators is constant (because the decreasing *per capita* effect is canceled by increasing prey abundance) but *per-population* interaction strength of predators on prey decreases (because predator abundance decreases).

Recent evidence is consistent with the competition model's predicted gradients in abundance and recruitment of both the mussel *Mytilus californianus* and the barnacle *Balanus glandula* (dominant decreases but subordinate increases with increased upwelling) (Connolly and Roughgarden 1998, Connolly et al. 2001). To our knowledge, no attempt has yet been made to test the predictions of the predator–prey model.

An alternative, or possibly complementary, effect to larval transport is bottom-up effects (see above). Upwelling provides nutrient pulses to coastal waters, supporting phytoplankton blooms. If coastal waters move seaward slowly, or are returned during relaxation (as in the IUR), dense blooms can be retained close to shore, feeding both planktonic larvae and benthic filter-feeding adults (e.g., mussels, barnacles). Persistent off-shore flow (as in the PUR) would remove such food resources from the coastal zone, and weak and infrequent upwelling (as in the WUR) would prevent such dynamics from even getting started. Therefore, to evaluate the associations between bottom-up effects, propagule supply, prey and predator abundance, and top-down effects, and to test the models summarized above, we quantified prey food concentration, prey recruitment rates, prey growth rates, predator and prey abundance, and rates of predation (both per capita and per population) at multiple sites within each of the three oceanographic regions.

Here we present the results of an effort to test aspects of Connolly and Roughgarden's (1999*b*) model. Specifically, we test three predictions. Along the U.S. West Coast, (1) Does prey abundance increase but predator abundance decrease with increased upwelling (prediction 4 above)? (2) Is *per capita* interaction strength of predators on prey constant (prediction 5)? (3) Does *per-population* interaction strength decrease with increasing upwelling (decreasing latitude; prediction 6)? Predictions regarding the dynamics of the competition model were addressed by Connolly and Roughgarden (1998), and those regarding prey r, K, and reproductive output (prediction 3) were beyond the scope of this study. We also examine the relationship between bottom-up effects and species interactions.

METHODS

Study regions and sites

In addition to the large, regime-scale oceanographic variability described above, oceanographic conditions also can vary on intermediate scales to local scales, and such variability can be associated with differences in processes in communities (Menge 1978, Ebert and Russell 1988, Wing et al. 1995*b*, Menge et al. 1997*a*, Morgan 2001, Bertness et al. 2002, Sponaugle et al. 2002). We thus selected study sites using a nested design, with study sites representative of the range of conditions within each region nested in each of the three oceanographic regimes. The 14 study sites (Appendix A) spanned a total range of ~1300 km. They were rocky shores selected within the constraints of feasibility and appropriate access (Fig. 1, Appendix A). To minimize the well known effect of variation in wave exposure on community dynamics (Lewis 1964, Menge and Branch 2001), sites were located on or near headlands in relatively wave-exposed locations. However, because significant wave height declines from north to south (e.g., Denny 1995; G. C. Schoch, G. Allison, S. Etchemendy, M. Kavanaugh, S. Wood, J. Lubchenco, and B. A. Menge, *unpublished data*), wave exposures were lower in the south. The length of coastline spanned by our study sites was 240 km in Oregon, 360 km in central California, and 80 km in southern California. Excluding the northern California–southern Oregon sector of coastline, which was not studied, our study sites spanned about 52% of the total distance from the most northerly to the most southerly. In order from north to south, the six main IUR (intermittent-upwelling region) sites were Fogarty Creek, Boiler Bay, Strawberry Hill, Gull Haven (see Plate 1), Cape Arago, and Cape Blanco; the five main PUR (persistent-upwelling region) sites were Waddell Creek, Scott Creek, Terrace Point, Piedras Blancas Point, and Lompoc; and the three main WUR (weak-upwelling region) sites were Jalama, Alegria, and Coal Oil Point. Additional data were included in analyses, where appropriate, from Stonefield Beach (IUR), Sand Hill (PUR), and Ellwood Beach (WUR). With respect to macro-topography, sites were selected to be relatively uniform in having gently to moderately sloping rocky benches present, with sufficient rock surface to allow replicated sea-star removal or exclusion experiments (Appendix A). Although macro-topographies were similar among sites, local topography (degree of heterogeneity from pools, surge channels, outcrops) varied among sites, and substratum composition varied among regions. Substrata in Oregon were mostly basaltic with some areas having mudstone (Appendix A). Rock at central California sites was part of the Monterey shale formation and was softer, primarily consisting of siltstone and/or mudstone. Southern California sites also consisted of Monterey shale. Although differences in substrate could conceivably have some influence on our

PLATE 1. Rocky intertidal habitat, showing an experimental setting and techniques for quantifying recruitment and growth of mussels at the Gull Haven site in June 2000: 1, the fenced plot; 2, the partial fence showing mussels within; 3, a mesh cover over mussels being transplanted for quantification of growth rates, a pad for mussel recruitment, and a barnacle recruitment plate. Mussels (*Mytilus californianus*) are above the fence, and barnacles are scattered over the otherwise bare rock in the lower two-thirds of the photo. Photo credit: B. Menge.
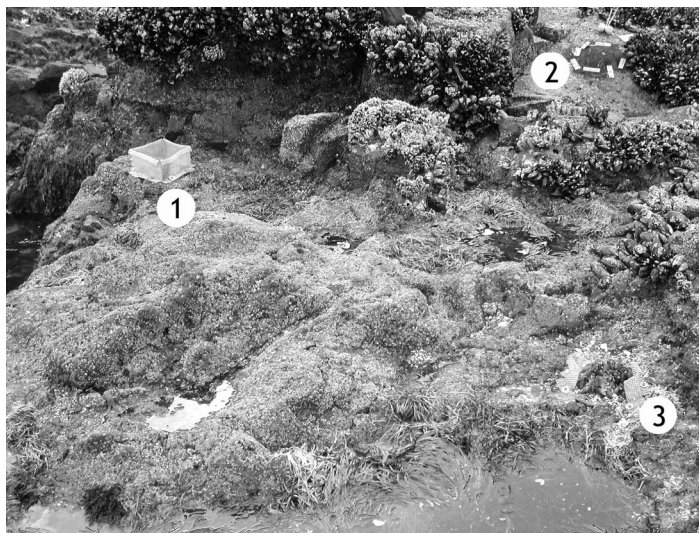
results, the differences between community dynamics in central and southern California with similar substrata, and the differences in community dynamics among sites in Oregon despite similar substrata (see *Results*, below) suggests that substrate differences are unlikely to explain our results.

Our main focus was to determine the extent to which oceanographic regime was associated with variation in individual and population parameters. As noted, the spatial breadth of our study encompasses three major oceanographic regions. Sites within region vary with respect to upwelling and other oceanographic features, but are considered to be representative of the region. A major analytical issue is one of inference. Because each region represents geographic location as well as oceanographic regime, there is no way to partition variance into a spatial component separate from a component attributable solely to oceanographic regime (i.e., there are no replicates of regime independent of space). This is a problem with most investigations of large-scale forcing. Although we believe that our results are interpretable in the context of oceanographic regime (see *Discussion*, below), we wish to be clear that there is a potential problem of inference.

Study system

Because of its central importance to the structure of rocky intertidal communities on the U.S. northwest coast, we focused on the well-known *Pisaster–Mytilus* interaction (Paine 1966, 1974, 1980, Menge et al. 1994, Navarrete and Menge 1996, Sanford 1999, Navarrete et al. 2000). Both species have planktonic larvae, and *Mytilus californianus* is the dominant competitor in a hierarchy that has the gooseneck barnacle *Pollicipes polymerus*, the mussel *M. trossulus*, and the barnacles *Balanus glandula* and *Chthamalus dalli*/*C. fissus* as successively subordinate species. At all sites, middle zones were dominated by the mussel *Mytilus califor-*

nianus with barnacles as subdominant space occupiers. Low zones had populations of the primary predator of mussels, the sea star *Pisaster ochraceus*, as well as other flora and fauna characteristic of wave-exposed rocky shores. A smaller mussel *M. trossulus* (north) or *M. galloprovincialis* (south) often occurs in successional gaps in *M. californianus* beds, and at some Oregon sites can be abundant in the low zone. Whelks (*Nucella* spp.), another potential mussel predator (Sanford et al. 2003), also occurred at all sites.

Study design

We investigated the rate of predation on mussels by sea stars and the variation in community patterns and processes in different oceanographic regions and sites within a region. Our studies were done in the intermittent (IUR), persistent (PUR), and weak (WUR) upwelling regions. Although Connolly and Roughgarden (1999*b*) used upwelling-induced variation in advection rate as the driving oceanographic factor, their intent was clearly focused on the supply rate of larvae to shore. Since the WUR should also have a low larval-supply rate, although due to a different oceanographic mechanism, we wanted to see if model predictions held under weak upwelling conditions as well as strong upwelling conditions. Thus, we inferred that predator and prey dynamics in the PUR and the WUR, both with low larval-supply rates, should be comparable, and different from dynamics in the IUR with high larval-supply rates.

The study was done in the low intertidal zone (~0 to 0.6 m) from April 1999 to June 2001. We quantified concentration of phytoplankton (using chlorophyll *a*, termed ''chl *a*,'' as our estimate [see Menge et al. 1997*b*]), recruitment of prey, growth of mussels, abundance of mussels in middle and low zones, abundance of sea stars, size structure of sea stars, *per capita* predation rates, and *per-population* predation rates. To as-

sess the relation between these factors and recruitment of predators within the intermittent upwelling region, we also quantified sea star recruitment at four Oregon sites.

Our analyses focus on data collected in 1999–2000, but our data sets for chl *a*, recruitment, and mussel growth and abundance at many of the sites are more extensive, ranging from as early as 1989 to the present (2004) for the most thoroughly studied sites. Although presenting these larger data sets are beyond the scope of the present paper, we summarize relevant information from them to inform the discussion.

Methods of quantification

Chlorophyll a.—Filter feeders such as mussels consume "particulates," a category that includes phytoplankton, particulate organic matter derived from dead phytoplankton and macrophytes, and smaller particles (bacteria, protozoans) (Hawkins and Bayne 1992). We used phytoplankton concentration (estimated as chlorophyll *a*) as our measure of the primary food source for mussels. Particulate organic matter (POM), another component of the food used by filter feeders, was not quantified in this study. Earlier studies (Menge et al. 1997*a*) had shown that concentrations of POM and chl *a* were positively related at Oregon sites, and results suggested that most POM was derived from phytoplankton. Further, more recent studies along the Oregon coast have shown that fastest mussel growth occurs at sites with a higher fraction of phytoplankton relative to POM in the particulate component (Bracken 2003), and that diatoms are the primary component of phytoplankton (Wetz and Wheeler 2003).

Concentration of chl *a* was quantified from bottle samples taken from shore at each site (Menge et al. 1997*b*). Replicated (*n* = 5) acid-washed opaque 250-mL HDPE plastic bottles were filled at ~30-cm water depth at low tide. Depending on site, region, and prior sampling done to determine the most appropriate volume, 50 to 200 mL of water were filtered through 22-mm combusted Whatman glass-fiber filters with a pore size of 0.7 μm. Chlorophyll *a* concentration was determined using a Turner Designs 10 fluorometer (Turner Designs, Sunnyvale, California, USA) after extraction in 90% HPLC acetone for 12 h in the dark at −20°C. Prior calibration of the fluorometer was done using a pure chl *a* standard purchased from Sigma Chemical Company (Saint Louis, Missouri, USA).

Mussel recruitment.—Potential mussel recruitment rates were quantified using standardized plastic mesh collectors or Tuffys (SOS Tuffy pads; The Clorox Company, Oakland, California, USA) (Menge 1992, Menge et al. 1994, 1999, Leonard et al. 1998). The mesh of these collectors mimics the preferred filamentous substrata of mussel larvae such as finely branched algae and mussel byssus (Paine 1971, 1974). Replicate collectors (*n* = 5 collectors per site from Cape Blanco south, *n* = 8 collectors per site north of Cape Blanco)

were fastened to middle-zone surfaces with lag screws inserted into wall anchors in holes drilled into the rock. Collectors were replaced monthly. In the laboratory, using the method of B. Hayden (*personal communication*), mussel recruits were detached from the mesh by dissolving their byssal threads in bleach for 5 min, shaking the jar, and collecting the mussel juveniles on a 53-μm sieve. Recruits were counted and identified to genus under a dissecting microscope.

These collectors attract larvae of all mussel species, and besides *Mytilus californianus*, one or two other species were present at our sites (*M. trossulus* in Oregon and central California, *M. galloprovincialis* in central and southern California, and a *M. trossulus–M. galloprovincialis* hybrid in central California) (McDonald and Koehn 1988). Although some have succeeded in distinguishing *M. californianus* from *M. trossulus* and *M. galloprovincialis* using morphological characters (Martel et al. 1999), we were unsuccessful in so doing, and thus we present total mussel recruit numbers.

Mussel growth.—We quantified mussel growth as the change in length of marked translocated mussels. Mussels were collected individually from single sites (one each in Oregon and California) and marked by filing notches on their posterior shell edge. To reduce mortality from sea stars, mussels were translocated back to mid-zone plots (*n* = 8 plots in Oregon, *n* = 5 plots in California). In May or June of each year, groups of 50 mussels were placed ventral side down in their natural position and covered with plastic mesh cages to allow them to reattach to the rock with their byssal threads. We had observed in earlier experiments that few threads are produced if the cages remain snug, so to encourage the more rapid production of byssal threads, we loosened the cages (increased the space between the mussels and the mesh) after two weeks. After six to eight weeks under the mesh, we removed the cages. In Oregon, initial mussel length was 4–5 cm, while in California, initial mussel length was 3–4 cm (1999) or 4–5 cm (2000). Mussel growth was estimated 12 months later as the shell added since translocation, quantified as the increment between the notch and the new shell edge.

Mussel abundance.—To quantify mussel abundance in the middle and low zones at each site, we used the transect-quadrat method (Menge 1976, Lubchenco and Menge 1978). Ten quadrats 0.25 m² in area were placed randomly along transect tapes laid parallel to the water's edge along a 30–50 m distance from the shore. Transects were placed in the middle of the middle mussel zone and between mean low low water (MLLW) and 0.5 m above MLLW. At most sites this level was approximately just below the lower edge of the mussel zone but from Point Conception south this level was within the mussel bed. Each quadrat was divided with cord into a grid of 5 × 5 = 25 subquadrats, each 10

× 10 cm in size. Thus each subquadrat represented 100/25 = 4% of the total area. Percent cover of sessile organisms was quantified by visually (Meese and Tomich 1992, Dethier et al. 1993) estimating cover of each species or bare rock in each subquadrat and totaling across the entire quadrat to obtain a per quadrat estimate of cover. We present average cover of mussels, mostly *M. californianus*, in the middle and low zone at each site.

Predator densities.—We estimated predator density by counting the numbers of sea stars and whelks in four quadrats in a grid centered over each replicate. In 1999 Oregon experiments, whelks were counted in a grid divided into four 1 × 2 m plots that were centered over each replicate mussel plot. Because they were of larger body size and sparse at some sites, sea stars were counted in a similar grid of four 2 × 5 m plots. In 1999 central California experiments, whelks were counted in 50 × 50 cm plots and sea stars were counted in 2 × 5 m plots. In 1999 southern California experiments, whelks and sea stars were both counted in 1 × 2 m plots. In all 2000 experiments, whelks were not counted and sea stars were counted in plots (2 × 5 m in Oregon, 2 × 4 m in California) centered over each replicate.

Sea star size structure.—Size structure of sea star populations was sampled in summer 2001. At all sites but WC, SC and TP in the Monterey Bay area, sea stars were weighed (wet body mass) and measured (arm length; madreporite to tip of opposite arm) in the field. At the Monterey Bay sites, arm length only was measured in 2000 at the start of the experiment; wet mass was estimated from these measures using a wet mass–arm length regression calculated from pooled Oregon samples: ln(wet mass) [in grams] = −1.722096 + 2.807602 ln(arm length) [in centimeters]; $P < 0.0001$, df = 1, 549, $R^2 = 0.946$. Sea stars sampled were those counted in survey plots supplemented by additional animals sampled beyond the survey plots to increase sample size when appropriate. An effort was made in all cases to search carefully for small as well as the more obvious larger individuals.

Predation experiments.—Experiments quantifying predation rates were replicated in time, with separate experiments done in 1999 and 2000. Using methods identical to the mussel-growth studies, we translocated mussels from the middle intertidal mussel bed to the low intertidal foraging range of the sea stars and whelks (Menge et al. 1994). Following removal of cages after the mussels had all reattached, survival in the different treatments was determined by periodic counts in each plot. In all cases, predation experiments were located along stretches of shore that ranged from ~50 to 100 m in length, and from ~5 to 20 m from the low-tide mark shoreward. Some aspects of the design of the experiments differed between years. In 1999, to separate the effect of sea stars from the effect of whelks, we tested the effect of both types of predator in a factorial design (+sea stars +whelks, +sea stars −whelks,

−sea stars +whelks, −sea stars −whelks). Two general methods are available to achieve such designs, manipulations that use barriers or manual alteration of abundances. In Oregon, following prior practice, we used manual removals to achieve these treatments (Menge et al. 1994, Navarrete and Menge 1996). Replicate sets of outcrops ($n = 3$) that were semi-isolated by surge channels, tidepools, and boulder patches served as experimental units. Because sea star foraging is concentrated near aggregations of prey and prior experience demonstrated that sea star reinvasion rates in manual removals varied with proximity to such aggregations (Menge et al. 1994, Robles et al. 1995, Navarrete and Menge 1996), sea star treatments were assigned nonrandomly. We located +sea star treatments near outcrops having prey concentrations (mid-zone mussel beds) and −sea star treatments away from such outcrops. Within-replicate distances between + and −sea star treatments were ~5–10 m, and care was taken to ensure that the community context (macrophyte and animal abundance and composition) was similar among all replicates within each site. Whelk treatments were assigned using a coin flip. In deletion treatments, sea stars and whelks were removed from each outcrop at least twice monthly, and usually more often.

All California experiments and the 2000 Oregon experiment used stainless-steel exclusions to manipulate abundances of predators. As has been addressed by prior users of this technique (e.g., Connell 1961, Dayton 1971, Menge 1976), employment of such devices can be accompanied by potential artifacts, including alteration of flow, inducement of sedimentation, and shading. The usual solution is to establish a device control treatment, with mesh present but not excluding or including consumers. In most prior studies, mesh artifacts usually had little influence on results, especially at low intertidal levels (above references and Connell 1970, Menge et al. 1986, Navarrete 1996, Berlow 1997, Menge 2003). In this study, the design in 2000 included a complete and a partial fence so that mesh was present in both treatments. While partial fences would not influence flow or sediment accumulation as much as complete fences, we saw no evidence of sediment accumulation in any of our experiments. Each replicate block in 2000 consisted of a complete and a partial fence.

One possible consequence of the stronger flow that would be expected in partial fences vs. complete fences is the possible dislodgement of mussels by waves rather than consumption of mussels by predators. Thus, if wave dislodgement occurred, we could erroneously conclude that mussel mortality was due to predation when in fact mortality was due to waves. Devising a control for such an artifact would be difficult. Instead we took steps to check for losses due to waves. First, as noted, we did not remove the mesh holding mussels to the rock until byssal attachment was firm, as determined by manual tugging on transplanted mussels. Sec-

ond, experiments were done in the summer when wave forces are at their seasonal low (Menge 1976, Paine and Levin 1981), reducing the likelihood that waves would cause mussel loss. Third, we checked experiments frequently, especially immediately after removal of the mesh. Loss from waves would be more likely to remove the entire clump, while loss from predation would remove individual mussels at a more steady rate. We never saw loss of entire clumps over short intervals that could not be attributed to severe predation (i.e., the sea stars causing the rapid mortality were observed in situ eating the mussels). Fourth, in similarly designed experiments at Strawberry Hill, Sanford (1999) found that in the absence of sea stars, mussel survival immediately after cage removal was high (97% after 14 days). For these reasons, we believe that most mortality in +sea star plots was due to predation by sea stars. Further, ''background'' mortality as revealed by losses in −sea star fences or cages was always relatively low.

In both California regions the 1999 design employed cages and fences to manipulate predator presence and absence. Replicates (southern California, $n = 8$; central California, $n = 4$) consisted of a marked plot (+sea stars +whelks), a fenced plot (+sea stars −whelks), a whelk-enclosure cage (−sea stars +whelks), and an exclosure cage (−sea stars −whelks). This alternative design in California was a consequence of the difficulty of finding replicate outcrops within each of the somewhat smaller rocky benches in these regions compared to Oregon.

In the 2000 experiments, we simplified the design, eliminating the whelk treatments and using fences (−sea stars) and partial fences (+sea stars) to manipulate sea star abundance at all sites ($n = 6$ replicates; Appendix B). This modification was made because in 1999 no whelk effect was detected, and because the 1999 experiments demonstrated that fences were likely to effectively exclude sea stars in Oregon as well as in California. In all regions, experiments were run until mussels were nearly or completely eliminated at least at one site. See Appendix C for experiment start dates and durations.

These experiments were used to calculate per-population predation rates (rate of mussel loss in +*Pisaster* plots) and per capita predation rates (rate of mussel loss per predator). We followed the approach used in Navarrete and Menge (1996); linear regressions were fitted to the proportion of mussels lost in each replicate vs. days since initiation. We used the slope of each regression as our estimate of loss rate, and took the average of these slopes to represent the per-population predation rate per experiment × site. To avoid skewing the slope estimates, in those replicates where mussels were completely eliminated, we excluded all dates beyond the first date at which no mussels were left (since a string of zeroes over time would bias the slope toward smaller values than the actual rate). Estimates of rep-

licate per capita rates were obtained by dividing the per-population rate of each replicate by the average sea star density in each replicate plot. When two density estimates were made at a site, we used the average of the two for a mean summer sea star density.

Sea star recruitment.—We estimated recruitment of sea stars using ''turfies,'' 20 × 20 cm squares of plastic turf (Astroturf), attached to the substratum in the low zone at each of four sites along the central Oregon coast. Comparison studies (R. Emlet, *personal communication*; B. Menge, *unpublished data*) using these and other artificial surfaces had indicated that turfies were most effective at sampling sea star recruits. Turfies ($n = 5$ squares/site) were deployed from May to September, 1996–1998; these collectors were returned to the laboratory in plastic bags. Recruits were removed by swirling the inverted collectors in a plastic tub filled with water, and pouring the removed material through a sieve. Sea star recruits were counted under a dissecting microscope. Only recent recruits (~1 mm in diameter, unpigmented) were counted to avoid counting juveniles that had crawled into the collector from nearby algal turf.

Data analysis.—Analyses were performed using SYSTAT (SAS Institute 2000) and JMP (SAS Institute 2001). All data were transformed prior to analysis. Proportional or percent-cover data were arcsine-square-root transformed, and all other data were log transformed [$\ln(x + 1)$]. In all tests we examined probability plots of residuals for the assumption of normality, and plots of residuals vs. estimated values for independence of error terms. In nested analyses with random effects, the numerator mean square was tested over the mean square of the next lower source of variation containing that source. For example, we tested the oceanographic-region mean square over the site(region) mean square, year and site(region) mean squares over the year × site(region) mean square, and the year × site(region) mean square over the error mean square. Linear contrasts were used to test for differences among categories.

We analyzed differences in chl *a*, mussel recruitment, and mussel growth with a two-way nested ANOVA with oceanographic region and year (1999 and 2000 only) classed as fixed factors and site(region) and year × site(region) classed as random factors. Differences among region and sites, and between years, were evaluated using linear contrasts. Among-site differences in mussel recruitment were done separately for 1999 and 2000 because of large between-year differences in recruitment.

To test differences in mussel abundance, we used a nested two-way ANOVA with oceanographic regions (IUR, PUR, WUR) and zone (middle and low) classed as fixed factors and site(region) classed as a random factor. Data were the mean mussel cover per replicate transect (10 to 11 quadrats/transect) for each site in each zone.

Variation in sea star densities was tested by region, year, and sample nested within year. To test for variation in predation rates, we first performed a three-way ANOVA on rates categorized by oceanographic region, year (1999 and 2000), and treatment (+*Pisaster*, −*Pisaster*), all classed as fixed factors. Because the number of sites varied between regions and years, we analyzed among-site variation for each oceanographic region separately (two-way ANOVA).

In addition to testing for how community variables (mussel recruitment, mussel abundance, mussel growth, sea star abundance, predation rate), responded to differences in region, site, and year, we also wanted to evaluate relationships between predation rates and community variables and/or phytoplankton abundance, particularly mussel recruitment and chlorophyll *a*. The measures of these variables were heterogeneous, and the wide range of values encompassed by many of these measures often led to heteroscedastic variances, so we chose a simpler approach in analysis. Using data shown in Figs. 2–6 and abundance of *M. trossulus*/*M. galloprovincialis* (S. Gaines, B. Menge, and P. Raimondi, *unpublished data*), we categorized each variable × site × year combination as "low" or "high" (see caption for Fig. 10 for site categorizations for each variable). We then evaluated variation in predation rate against low or high levels of mussel recruitment, chlorophyll *a*, mussel growth, mussel abundance, sea star density, sea star recruitment, and abundance of "bay" mussels in the low zone (*Mytilus trossulus* in the IUR, *M. galloprovincialis* in the PUR and WUR). Below we provide relevant statistical results in the text; detailed results of analyses are presented in Appendix D.

RESULTS

Chlorophyll a

Monthly average phytoplankton concentration, as reflected by chlorophyll *a* concentration, was highly context dependent, varying by year, region, and site (Fig. 2; nested two-way ANOVA; year × site(region) interaction; $F = 2.93$, df = 11, 191, $P = 0.0013$). In 2000, chl *a* was 13.7 times (95% confidence interval: 7.6–24.5 times) greater in the IUR (intermittent upwelling region) than the PUR (persistent upwelling region) (Table D1: linear contrasts) and 12.7 times (6.3–24.9 times) greater in the IUR than the WUR (weak upwelling region) (Table D1: linear contrasts). No among-region differences occurred in 1999. Within the IUR among-site variation was high (two-way ANOVA, year × site interaction; $F = 4.64$, df = 5, 81, $P < 0.0009$), but no among-site differences occurred in the PUR (two-way ANOVA; $F = 1.11$, df = 4, 68, $P = 0.37$) or WUR ($F = 0.70$, df = 2, 42, $P = 0.63$). Both earlier and more recent samples indicate that concentrations of chl *a* are typically much greater in the IUR than was observed during 1999. The relatively low IUR values during the study period are likely due to the 1999 La
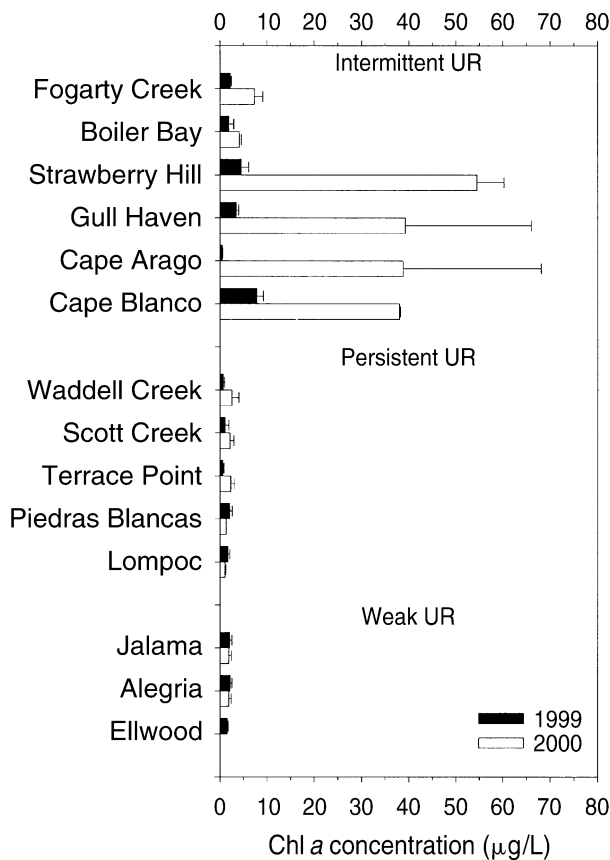

FIG. 2. Chlorophyll *a* concentration (in micrograms per liter; mean and 1 SE) at each site along the U.S. West Coast. Data are from monthly samples (*n* = 5 samples per month per site). More extensive sampling in Oregon (1993–2004), central California (2001–2004), and southern California (1996–2004) (data not shown) indicate that these averages reflect among-region and among-site variability in chl *a* concentration. In this figure and Figs. 3–8 and 12, the sites are listed from north to south, starting at the top, and grouped by oceanographic upwelling regions: intermittent, persistent, and weak (IUR, PUR, WUR). Regional means (untransformed micrograms per liter) were 23.05 ± 3.27 (IUR, *n* = 93), 1.64 ± 0.24 (PUR, *n* = 77), and 1.87 ± 0.16 (WUR, *n* = 52).

Niña event, during which upwelling was strong and offshore transport was high off the Oregon coast (Peterson et al. 2002).

Mussel recruitment

As a prior but spatially less extensive data set has shown (Connolly et al. 2001), mussel recruitment is far greater north than south of Cape Arago (Fig. 3). Mussel recruitment was variable at all scales (nested two-way ANOVA; year × site(region) interaction, $F = 8.50$, df = 9, 123, $P < 0.0001$). In 2000 (but not 1999), recruitment was 23.3 times (95% CI: 4.5–100.3 times) greater in the IUR than the PUR (Table D2: linear contrasts) and 47.7 times (6.3–324 times) greater than in the WUR (Table D2: linear contrasts). Mussels recruited more heavily in the IUR in 2000 than in 1999
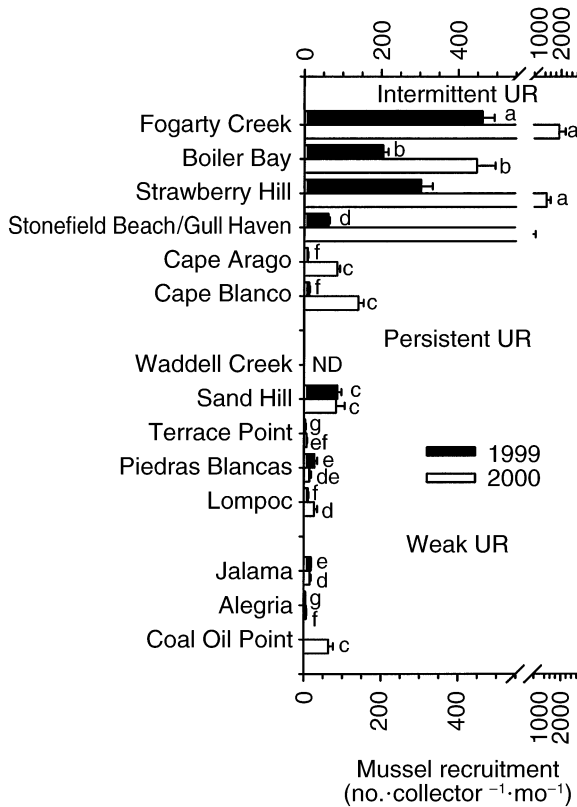
er in 2000 in the IUR than in the PUR, and grew 2.9 times and 7.0 times faster in 1999 in the WUR than in 1999 and 2000 in the PUR, respectively.

Mussel growth variability among sites was striking (Fig. 4; two-way nested ANOVA; site(region), $F = 30.05$, df $= 9, 9$ $P < 0.0001$). Growth rates were highest at Strawberry Hill (IUR) and at Jalama and Alegria (WUR) (Fig. 4). Lowest rates occurred uniformly across all sites in the PUR and at Cape Arago and Cape Blanco (IUR).

Mussel abundance

In Oregon and California, abundance of *Mytilus californianus* in the middle zone at our experimental sites was generally high, ranging from about 50% to 90% cover except at Piedras Blancas and Lompoc (Fig. 5). As has been noted elsewhere for sites in Washington and Oregon (Paine 1974, Menge et al. 1994), *M. californianus* was essentially absent from the low zone at all northern sites, but from Lompoc southward low-zone cover was relatively high, ranging from about 40% to 60% (Fig. 5). Mussel abundances differed between zones within oceanographic regions (Table D4, two-way nested ANOVA: zone $\times$ site(region) inter-

FIG. 3. Mussel recruitment (*Mytilus* spp.) at the 14 study sites in the upwelling region (UR) along the U.S. West Coast. Recruits are difficult to sort to species (Martel et al. 1999), but genetic work (G. Pogson, *personal communication*) on central-California samples with *M. californianus* and *M. galloprovincialis* and the predominance of *M. trossulus* in juvenile mussel beds on the shores at our Oregon sites suggest that the latter species is the dominant recruit at most of our sites. No data (ND) were available for Scott Creek, so we show data for Sand Hill, a nearby site to the north of Scott Creek. Regional means (untransformed number of recruits per anchored Tuffy per month) were 477.95 + 68.18 mussels (mean + 1 SE) (IUR, $n = 89$ monthly site samples), 30.98 + 5.86 mussels (PUR, $n = 38$), and 11.1 + 1.58 (WUR, $n = 20$). Bars with the same lowercase letters are not significantly different across regions at $P < 0.05$.

but between-year differences were minimal in the PUR and WUR (Fig. 3; linear contrasts). Among-site variation was also great, especially in the IUR (Fig. 3).

Mussel growth

Mussel growth was high on average but variable among IUR sites, consistently low at PUR sites and consistently high at the WUR sites (Fig. 4). Mussel growth varied among regions and differed by year (two-way nested ANOVA; year $\times$ region interaction, $F = 12.4$, df $= 2, 9$, $P = 0.0026$). The year $\times$ region interaction was due to several among-region $\times$ year differences (Table D3: linear contrasts). In 2000, growth in the IUR and PUR was 1.2 times and 2.4 times greater, respectively; than in 1999. Mussels grew 3.9 times fast-
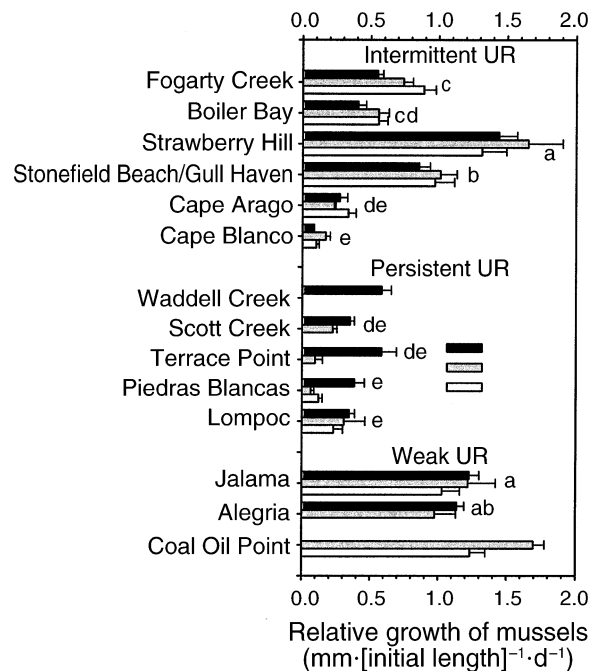

FIG. 4. Growth rates of *Mytilus californianus* at the 14 upwelling-region study sites (mean + 1 SE). In Oregon, mussel growth data at two sites, Stonefield Beach (in 1999) and Gull Haven (in 2000), were included in the analysis as a single site because of their proximity (~1 km apart) and ecological similarity (B. Menge, *personal observations*). Regional means (untransformed relative growth) were 0.72 ± 0.06 (IUR, $n = 87$ samples [i.e., total number of replicate transplant plots (each with 50 mussels) $\times$ (number of sites per region) $\times$ 2 yr]), $0.34 + 0.03$ (PUR, $n = 67$), and $1.16 + 0.05$ (WUR, $n = 40$).
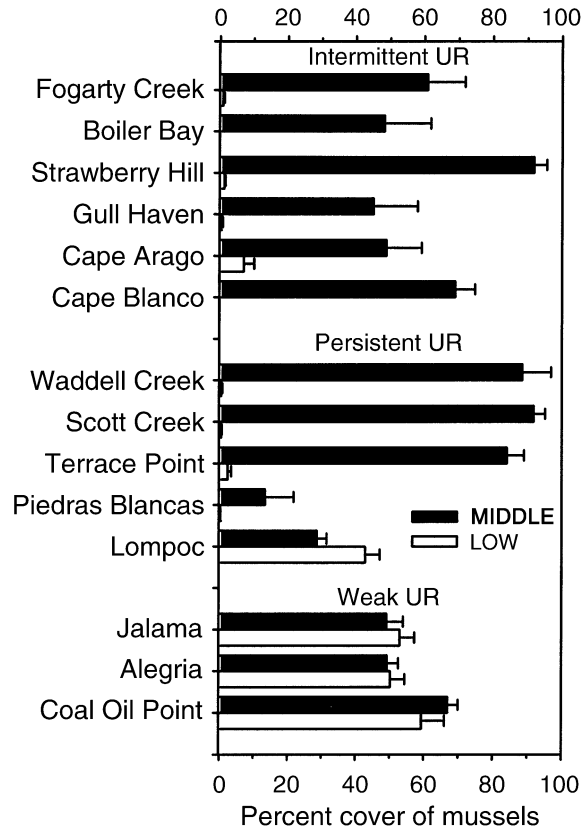
FIG. 5. Abundance of *Mytilus californianus* (percent cover, mean + 1 SE) in the middle zone at each site. See *Methods: Methods of quantification: Mussel abundance* for details of sampling protocol. Regional means (untransformed percent cover) were 3.7% ± 1.9% (IUR low, $n = 15$; n is number of transects per site × number of sites per region), 59.4% ± 3.8% (IUR mid, $n = 18$), 18.9% ± 9.0% (PUR low, $n = 7$), 52.0% ± 13.0% (PUR middle, $n = 7$), 39.0% ± 7.7% (WUR low, $n = 11$), and 55.9% ± 2.6% (WUR middle, $n = 12$).

gesting that the sea star *Pisaster ochraceus* was the primary invertebrate predator in these experiments. Densities of sea stars varied in a complex way among oceanographic regions, and between years and samples (early vs. late summer) (Fig. 6, Table D7A: region × sample(year) interaction; $F = 3.09$, df = 4, 245, $P = 0.017$). These predators are highly mobile, however, and rapidly aggregate in response to food concentrations (Robles et al. 1995) and to temperature changes in sea water (Sanford 1999). Thus, because temperature changes resulting from shifts between upwelling and non-upwelling conditions are a regular and unpredictable occurrence at these sites, and because food density can vary between years, differences between samples and even years is not surprising. The large mean square for the region effect (Table D7A) suggests that the largest amount of variability in this analysis is explained by this factor. Densities in the IUR and PUR did not

action; $F = 4.51$, df = 10, 44, $P = 0.0002$). These differences were due primarily to the higher abundance of mussels in the low zone in the WUR vs. the IUR and the PUR (Fig. 5). Analyzing zones separately indicates that in the middle zone (Tables D5 and D6), no differences in mussel cover occurred among regions ($P = 0.96$) but that cover varied among sites ($P = 0.0016$). In the low zone, mussel cover was 5 times (95% CI: 2–14.3 times) greater in the WUR than in the PUR and 36.4 times (11.6–58 times) greater in the WUR than in the IUR. Within regions, among-site variation in mussel cover occurred in the PUR region (two-way ANOVA, site × zone interaction; $F = 25.1$, df = 4, 4, $P = 0.004$), but no among-site differences occurred in the IUR or WUR regions (two-way ANOVAs, $P > 0.05$).

Predator density

As indicated earlier, whelk predation was insignificant in the 1999 experiments (data not shown), sug-
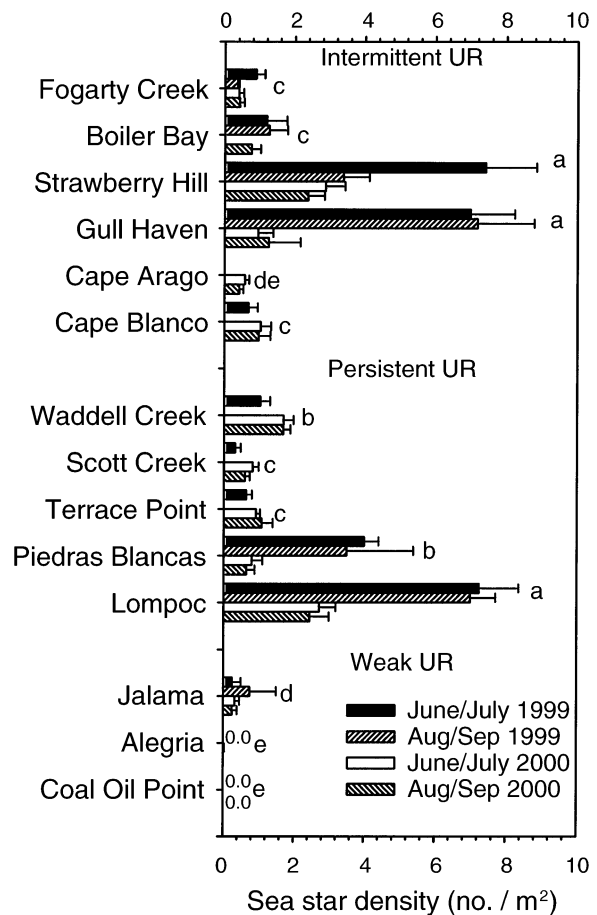

FIG. 6. Density (mean and 1 SE) of sea stars, *Pisaster ochraceus*, in the low zone in 1999 and 2000 at each U.S. West Coast upwelling-region (UR) site. Regional means (untransformed number/m²) were 2.31 ± 0.25 sea stars/m² (mean ± 1 SE) (IUR, $n = 117$ replicate quadrats sampled), 2.10 ± 0.24 sea stars/m² (PUR, $n = 88$), and 0.16 ± 0.07 sea stars/m² (WUR, $n = 52$). Bars with the same lowercase letters are not significantly different across regions at $P < 0.05$.

differ, but densities in the IUR were 10.4 times (95% CI: 6.7–14.6 times) greater than in the WUR and densities in the PUR were 12.0 times (8.1–17.3 times) greater than in the WUR (Table D7A: linear contrasts).

Although density differed among regions, among-site differences within regions were also large (Fig. 6; Table D7B, nested ANOVA: site(region) accounts for 60% of the variance). Densities at two Oregon sites (Strawberry Hill, Gull Haven) and one central California site (Lompoc) were highest. Southern California sites included the lowest density sites, but sites of comparably low density occurred in both of the more northerly regions (Cape Arago in the IUR, Scott Creek in the PUR). Large among-site variation with a trend towards higher sea star densities northward was also observed in a broad survey of North American west-coast sites ranging from Cabo San Lucas, Mexico, to Shelikof Island, Alaska (Sagarin and Gaines 2002).

Per-population predation rates

Excluding predators from mussel transplants greatly increased survival of mussels, but this effect differed by the combination of oceanographic region, year and treatment, and among sites within regions (Fig. 7, Table D8A, region × treatment interaction; Table D8B, site(region) effect). Per-population predation rates did not differ between years ($P = 0.59$). Interestingly, rates did not differ between the IUR and the PUR (linear contrasts, $P = 0.80$), but those in the PUR were 2.96 times (95% CI: 1.65–4.27 times) greater than in the WUR (linear contrasts, $P = 0.003$), and those in the IUR were 3.08 times (1.82–4.36 times) greater than in the WUR (linear contrasts, $P = 0.001$). Predation impact was very strong in the IUR (mussel survival in $-Pisaster$ plots was 15.5 times that in $+Pisaster$ plots) and in the PUR (a 24.4-fold difference) but, as indicated by the lack of a treatment effect, was weak in the WUR.

Differences among sites within the IUR and the PUR were large but rates did not differ between years (Fig. 7). In the WUR, rates differed between years but not sites. In the IUR and the PUR, the range of predation rates among sites was similar, with each region having sites of high, intermediate, and low predation (Fig. 7). In the WUR, predation was low (Jalama, Alegria) to nonexistent (Coal Oil Point; Fig. 7).

Per capita predation rates

Sea stars were too sparse at the WUR sites for reliable per capita estimates, so only the PUR and IUR were compared. In contrast to per-population predation rates, per capita predation rates did not differ between oceanographic regions (Fig. 8, Table D9, two-way nested ANOVA). Per capita rates evidently differed between years at certain sites but this effect was weak (Table D9: year × site(region) interaction; $F = 2.28$, df = 8, 84, $P = 0.03$) and due primarily to an extremely
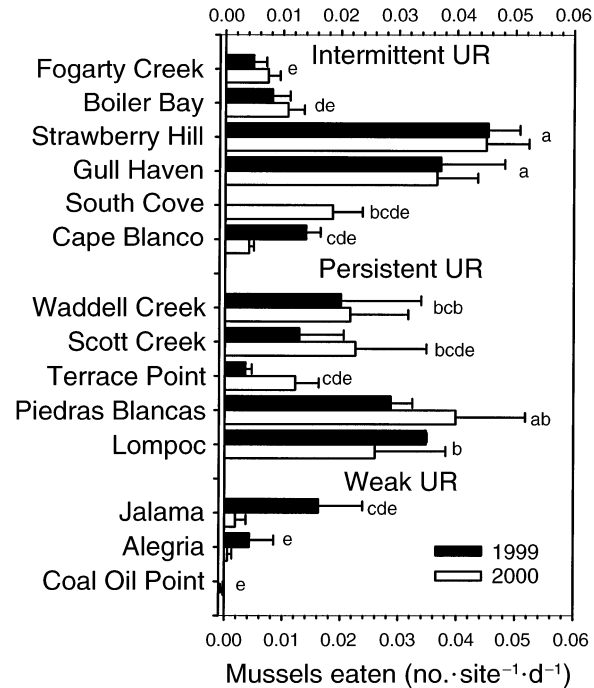

FIG. 7. Per-population predation rates (mean and 1 SE) in the low zone in 1999 and 2000 at each U.S. West Coast upwelling-region (UR) site. Data are mussel loss rates, corrected for background mortality, estimated as the difference between paired replicate $+Pisaster$ and $-Pisaster$ treatment plots. Linear contrasts indicate that bar pairs with the same lowercase letter are not significantly different at $P = 0.05$. Regional means (untransformed rates) were 0.0241 ± 0.0025 mussels eaten·(site)$^{-1}$·d^{-1} (IUR, $n = 96$ replicates), 0.0238 ± 0.0032 mussels eaten·(site)$^{-1}$·d^{-1} (PUR, $n = 50$), and 0.005 ± 0.002 mussels eaten·(site)$^{-1}$·d^{-1} (WUR, $n = 26$).

low mean per capita rate at Scott Creek in 1999 (Fig. 8).

Relationship to subsidies

We examined relationships between predation rates and subsidies (mussel recruitment, chl a) or factors potentially related to subsidies (mussel growth, mussel cover, sea star density) in two ways. In regression analyses using the continuous numerical data (site means for each factor), per-population predation rates were unrelated to rates of mussel growth, mussel recruitment, and concentration of chl a in coastal waters ($P > 0.22$ or more; df = 1, 19 or 1, 20 or 1, 21, respectively). Predation rates were also unrelated to abundance of mussels in the middle, low, or middle and low zone combined ($P > 0.33$ or more, df = 1, 21). Similarly, per capita predation rates were not related to any of these factors ($P = 0.06$ for mid-zone mussel cover, $P > 0.18$ or more for the others; df range = 1, 16 to 1, 19). Both predation rates were correlated with sea star density, however (Fig. 9). As expected (Menge et al. 1994), increasing per-population rates were associated with increasing abundance of sea stars, while
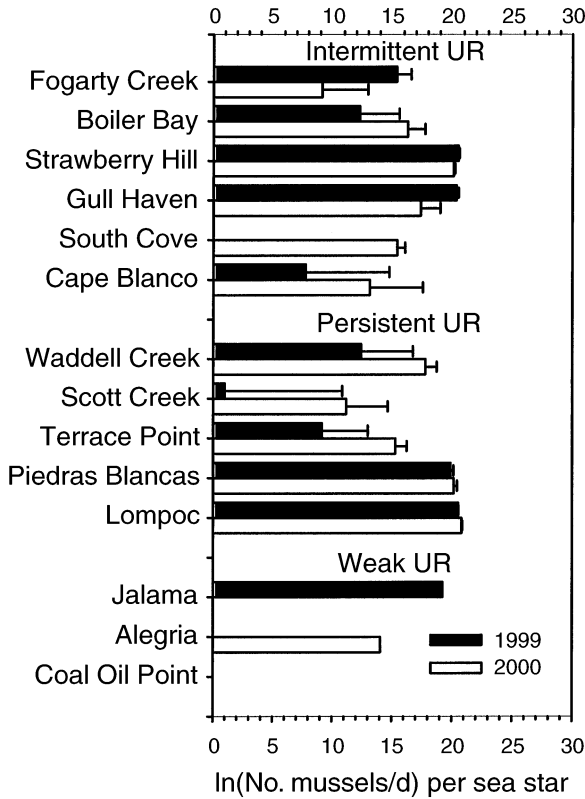
FIG. 8. Per capita predation rates (mean and 1 SE) in the low zone in 1999 and 2000 at each U.S. West Coast upwelling-region (UR) site. To make values positive, values of ln(Mussels per day per sea star) were coded by adding 21 to each value. No per capita rates could be calculated at Alegria in 1999 and at Coal Oil Point because sea stars were absent from the experimental areas.
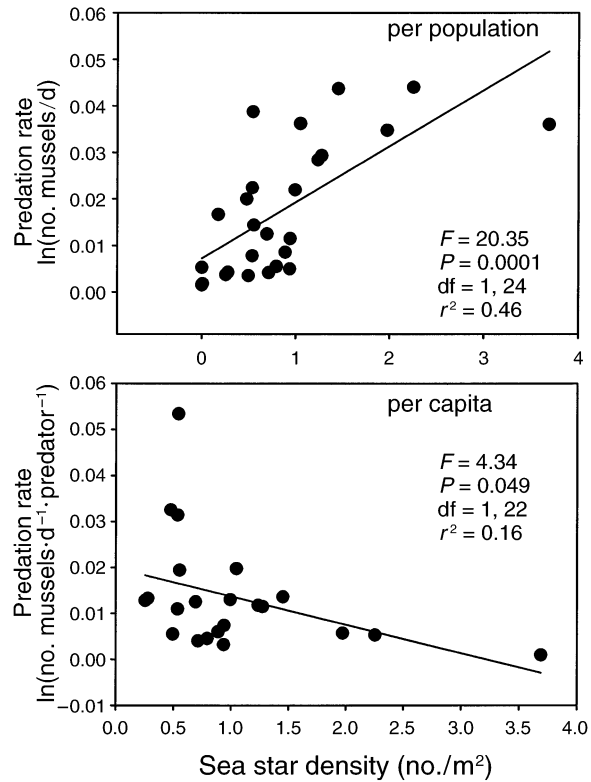

FIG. 9. Regressions of per-population and per capita predation rates vs. sea star density across 14 sites along the U.S. West Coast. Removal of the highest density point improves the fit for both regressions (per population, $F = 25.9$, $P < 0.0001$, $r^2 = 0.53$; per capita, $F = 6.14$, $P = 0.02$, $r^2 = 0.22$).
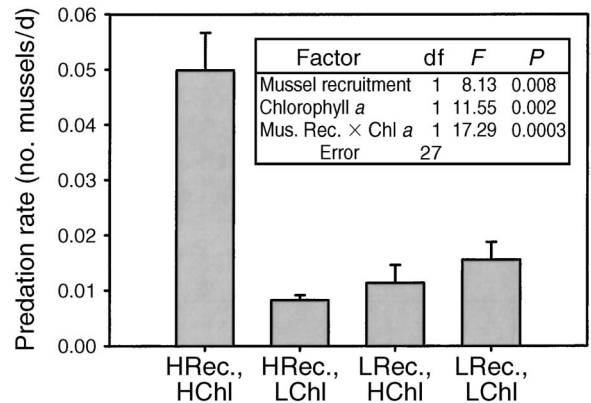
per capita rates varied weakly inversely with increasing sea star density (Fig. 9). This latter trend suggests the possibility of a negative effect of increased intraspecific competition on individual feeding rates at high sea star density.

Although the regression analysis did not support the hypothesis that phytoplankton (chl a) concentration and mussel recruitment were positively associated with predation rate, the categorical analysis suggested that the interaction between these factors was crucial in determining the magnitude of predation (Fig. 10). When mussel recruitment and phytoplankton concentration are both high, high rates of predation are observed. The implication is that without high food availability for mussel larvae and/or mussel recruits, survival of recruits is low. Thus, evidently high recruitment of mussels leads to a high supply of mussels as sea star prey primarily when phytoplankton concentration is also high. Consistent with this, the categorical analysis also indicates that high predation is associated with high abundance of small mussels (*M. trossulus* or *M. galloprovincialis*) in the low zone (Fig. 11). Further, as indicated by the regression analysis, predation rate

FIG. 10. Predation rate in relation to mussel recruitment (Rec.) and chlorophyll a (Chl), each categorized as high (H) or low (L). Categorizations for all variables: Mussel recruitment, high = FC, BB, SH, GH [all others low]; Chlorophyll a, high = SH, GH, CB [all others low]; sea star recruitment, high = SH, GH, WC, SC, AL [all others low]; mussel growth, high = SH, GH, JA, AL, COP [all others low]; cover of bay mussels, high = SH, GH [all others low]; low-zone mussel cover, high = LO, JA, AL, COP [all others low]; sea star density, high = SH, GH, PB, L [all others low]. For site codes see Fig. 12 legend.
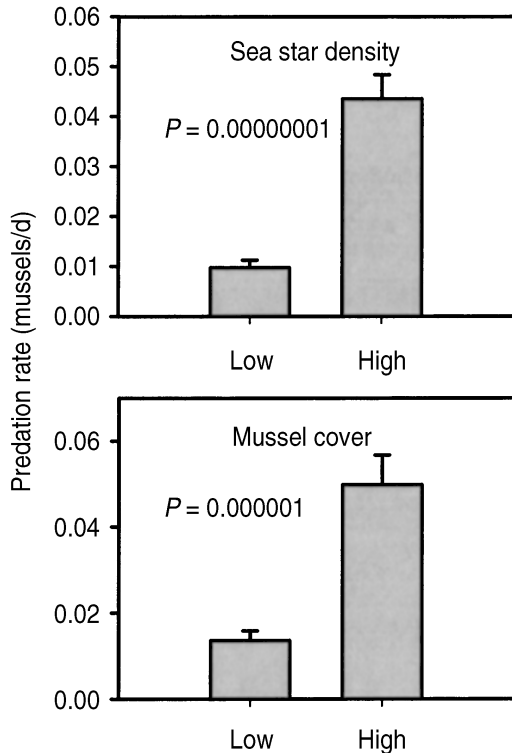
FIG. 11. Predation rate mean and 1 SE in relation to sea star density (high vs. low) and abundance of bay mussels (*Mytilus trossulus* or *M. galloprovincialis*) in the low zone of U.S. West Coast upwelling-region sites.

also increased with increased sea star density (Fig. 11). Thus, high availability of small mussels may lead to high densities of sea stars, through aggregation and perhaps high survival of juvenile sea stars, and this in turn should lead to elevated predation by sea stars on prey in general, including adults of the California mussel. These associations are not universal however; high predation also occurred at two California sites of low recruitment and low chl *a* (Lompoc and Piedras Blancas; Fig. 7). Possible factors (e.g., life-history characteristics) related to such exceptions are examined in the *Discussion*, below.

These analyses suggest that predation rate can be strongly related to subsidies (of larval food and propagules of the primary prey of sea stars) and to sea star population dynamics, including patterns of recruitment, growth, and survival of *Pisaster*. To begin evaluating the latter effects, we compared the size structure of *Pisaster* populations at each site (Fig. 12). Although size structure is likely to vary both with rates of input of new recruits and local rates of sea star growth, examining the distribution of sizes can suggest whether or not recent (i.e., most likely the last 1–5 years) recruitment events have occurred. As suggested by Fig. 12, populations with the largest proportions of small sea stars (<50 g wet mass) tend to occur primarily in more northerly sites. All eight populations from Scott

Creek north had a substantial fraction of small individuals (ranging from 15 to 55% of each population) while only two of six populations from Terrace Point south had a high proportion of juveniles, and only one of these, Alegria, had a proportion (0.49) similar to northern sites.

These varying fractions of small individuals (most of which are likely to be juveniles; Menge 1975) may reflect settlement rates, growth rates, and post-settlement mortality rates. High settlement and low post-settlement mortality of sea stars in response to high settlement and high recruitment of mussel prey would increase the proportion of young, while high growth rates would tend to reduce the proportion of young as individuals grew quickly to adulthood. Unfortunately, satisfactory measures of sea star growth remain elusive, so we cannot address this issue. We do have estimates of sea star recruitment from several Oregon sites, however, and these are instructive (Fig. 13). Recruitment of sea stars at two sites in areas of lower phytoplankton productivity, Boiler Bay and Fogarty Creek, was lower than at two sites in areas of higher phytoplankton productivity, Strawberry Hill and Seal Rock (Fig. 13 and B. Menge, *unpublished data*). The differences were spatially and temporally consistent; although recruitment varied between years, within any given year the northern areas always had lower recruitment than the southern ones.

DISCUSSION

Based on the fact that upwelling increases in magnitude and duration with decreasing latitude along the U.S. West Coast, at least to Point Conception, and that Ekman transport (the movement of upper layers of water away from the coast) increases with increased upwelling, Connolly and Roughgarden (1999b) predicted that offshore larval transport would increase from north to south. This inference was based on the increasing body of evidence that the meroplanktonic larvae of benthic invertebrates living in coastal environments are carried by currents, and that patterns of settlement and recruitment often reflect the extent to which coastal waters are advected offshore (Farrell et al. 1991, Roughgarden et al. 1991, Gaines and Bertness 1992, Wing et al. 1995a, b, 1998, Morgan 2001). Using this information, Connolly and Roughgarden (1999b) developed a model that predicted how predator and prey populations with meroplanktonic larvae would vary with the intensity of offshore larval transport, and the consequences for their interaction on the shore. Their model suggested that as larval loss (indexed by upwelling intensity) increased, predator abundance should decrease due to low predator recruitment. Prey abundance should actually increase with upwelling because in their model prey populations respond primarily to the dynamics of predator, not prey populations. Their model also predicted that *per-population* effects of predators on prey should decrease with increased
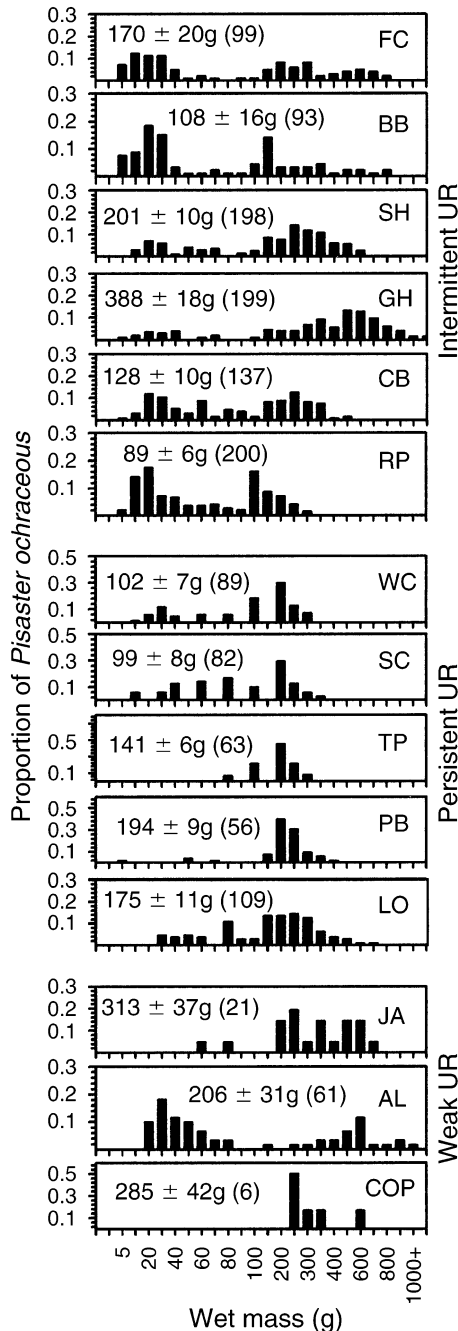
FIG. 12. Size structure of *Pisaster ochraceus* at each site in summer 2000 (WC, SC, TP) or 2001 (Oregon sites and PB, LO, JA, AL, COP). For each site, the wet mass (mean ± 1 SE) and the number of sea stars sampled (in parentheses) are presented on the figure. The 2000 data were taken as radius length (in centimeters) and were converted to wet mass (in grams) using an equation derived from Oregon sea stars: for all sites combined, ln(wet mass) = −1.7221 + 2.8076 × ln(arm length). The 2001 data were from direct measurement of wet mass in the field. The *y*-axis increments are in units of 5 g up to 10 (0–4.9, 5–9.9), 10 g from 10 to 100 (10–19.9, 20–29.9, etc.), and 100 g from 100 to 1000+ (100–199.9, 200–299.9, etc.) Site codes: for IUR (intermittent-upwelling region), FC = Fogarty Creek, BB = Boiler Bay, SH = Strawberry Hill, GH = Gull Haven, CB = Cape

upwelling, while *per capita* effects of predators on prey should be independent of upwelling.

Our results were consistent with some but not all of these predictions. As predicted by the predator–prey model (Prediction 5; see *Introduction*: *Coupled benthic–pelagic dynamics,* above), per capita effects of predators were independent of upwelling (Fig. 8). We found no decrease in average per capita predation rate between the intermittent (IUR) and persistent (PUR) oceanographic upwelling regions. Contrary to Prediction 6 (predator–prey model) (Roughgarden et al. 1988, Connolly and Roughgarden 1999*b*), however, our results suggested that per-population predation rate did not vary consistently with upwelling intensity (Fig. 7). Further, neither prey nor predator abundance varied as expected with upwelling. The competition model (Connolly and Roughgarden 1999*b*) predicted that the competitive dominant (in this case, *Mytilus californianus*) would decrease with increased rate of larval loss, while the predator–prey model predicted that prey abundance (also *M. californianus*) would increase with increased rate of larval loss (because prey abundance responds to predator abundance, not upwelling). In our study, the predictions of the competition model are more likely to apply to the abundance of mid-zone mussels because predation effects are weak in the middle zone, while the predictions of the predator–prey model are more likely to apply to abundance of low-zone mussels where predation effects are strong, at least at sites in Washington and Oregon (Paine 1966, 1974, Menge et al. 1994).

Contrary to the prediction of the competition model (Prediction 1), mussel cover in the middle zone did not vary latitudinally (Fig. 5). Contrary to the prediction (Prediction 4) of the predator–prey model that mussel abundance will increase and predator abundance will decrease with increased upwelling, mussel abundance in the low zone was consistently low in both the IUR and PUR (at least the sites in the Monterey Bay vicinity; Fig. 5), and predator abundance was unrelated to upwelling (i.e., did not differ between IUR and PUR), at least at the large, whole-coast scale. The predictions that prey will be abundant and predators scarce with low rates of larval input are met only at the WUR sites and the most southerly PUR site, all of which had low mussel recruitment (Fig. 3). This low mussel recruitment, however, is most likely a consequence of different oceanographic mechanisms than those in more strongly upwelled regions. As noted earlier (*Introduction: Background: the California Current system,*

←

Blanco, RP =Rocky Point; for PUR (persistent-upwelling region), WC = Waddell Creek, SC = Scott Creek, TP = Terrace Point, PB = Point Piedras Blancas, and L = Lompoc; and for WUR (weak-upwelling region), JA = Jalama, AL = Alegria, and COP = Coal Oil Point. There were no data for Cape Arago, South Cove, or Ellwood.
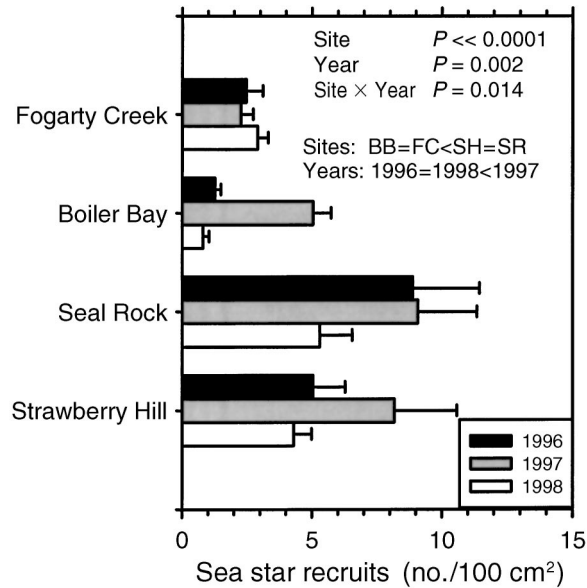
Fig. 13. Recruitment of sea stars into collectors (Tuffys) at four sites along the central Oregon (USA) coast. For site codes, see Fig. 12 legend.

above), the Santa Barbara channel region is dominated by a northwest flow along the coast, and oceanographic conditions here are unlikely to foster shoreward larval transport. Sea star abundance varied with oceanographic region, but the differences were between the weak-upwelling region (WUR) vs. the IUR and PUR rather than between IUR and PUR as the model predicts. As with mussel abundance, the largest regional differences were generally between the strongly upwelled regions north of Point Conception and the weakly upwelled region southeast of Point Conception.

The lack of a latitudinal trend in mid-zone mussel cover was somewhat surprising, as our subjective impression (and the results of Connolly and Roughgarden 1998) suggested that mussels are more abundant in the IUR. In fact, a more detailed study that includes mussel-bed depth (G. Allison, B. Menge, *unpublished data*), suggests that mussel *abundance* is in fact greater in the IUR even though mussel *cover* may not be. In contrast to most mussel beds in California in which mussels form a monolayer, mussel beds at many sites in Oregon are multilayered, and mussel-bed thickness can reach 1 meter (G. Allison, B. Menge, *unpublished data*). The thickest mussel beds tend to occur at sites with the highest concentrations of phytoplankton in adjacent coastal waters. Thus, use of mussel density would most likely make our mid-zone results consistent with Prediction 1 of the competition model (Connolly and Roughgarden 1999).

In many of these analyses, among-site differences were larger than were among-region differences (Figs. 6 and 7, Appendix D). Both per-population predation rates and sea star abundance varied dramatically among

sites, and equivalently among sites in the IUR and the PUR. Although mussel growth varied little among PUR or WUR sites, it varied widely among IUR sites. Why were among-site differences greater than among-region differences?

One issue is that the scales of the upwelling indices used to define the upwelling gradient, and upon which the Connolly and Roughgarden (1999b) model was based, do not always match the scales at which patterns of larval transport and other factors influence coastal communities (e.g., Ebert and Russell 1988, Strub and James 1995, Wing et al. 1998, Morgan 2001). It is evident from satellite imagery (e.g., Fig. 1), for example, that the structure of the California Current upwelling system (CCS) is nonlinear. That is, changes in current structure do not occur uniformly with latitude, but rather, large shifts in current structure occur relatively abruptly. At the large scale, the CCS changes rather sharply from a relatively simple southward flow along the Washington and central Oregon coast, to a highly complex flow with many gyres and eddies and a strongly undulating pattern from southern Oregon to Point Conception (Strub and James 1995c: Fig. 1). Examination of time series of coastal upwelling in advanced very high resolution radiometer (AVHRR) images shows that these structural elements are highly persistent, at least on the coastal side of the system (Strub and James 1995). Further examination suggests that these persistent features are often associated with coastal morphology and the topography of the continental shelf. On the Oregon coast, for example, a persistent eddy (visible in Fig. 1 as the green bulge offshore of Strawberry Hill/Gull Haven along the central Oregon coast) is associated with a widening of the continental shelf (Menge et al. 1997a). Similar discontinuities in coastal upwelling structure have been studied elsewhere along the coast (Graham and Largier 1997, Wing et al. 1998), and are readily observed in most satellite AVHRR images of upwelling coastal regions.

We therefore suggest that variation in the oceanographic processes that underlie variation in predation intensity are better scaled to more mesoscale features such as headlands, differences in the width of the continental margins, and similar morphometric features of the landscape and seascape. Two analyses are consistent with this hypothesis. First, most response variables varied strongly with site within region (estimated as a main effect of site(region) or via interactions with site(region); see *Results*, above, and Appendix D). Second, per-population predation rate varied with sea star abundance (Fig. 9). If sea star abundance is even crudely reflective of sea star recruitment, as the Oregon data suggest (Fig. 13, compare to Fig. 6), then this pattern is consistent with the Connolly and Roughgarden (1999b) prediction (Prediction 6): predation rate should increase with increased predator recruitment. The inference is thus that, if position along the spatial gra-

dient is ignored, at least some of our data are consistent with model predictions. This conclusion also suggests that model predictions may be more likely to be supported if scales of oceanographic (e.g., upwelling, larval advection, nutrients, phytoplankton) and ecological processes (e.g., recruitment, growth, abundance, predation) were more closely matched. That is, a finer scale of understanding of coastal oceanography, especially in the coastal-margin region, might provide a better link to site-specific community dynamics than does the larger-scale, more offshore oceanographic dynamics.

Role of phytoplankton blooms

Another factor that might improve the fit of models such as that of Connolly and Roughgarden (1999b) is the incorporation of bottom-up effects, again, especially in the waters just adjacent to the coast. Earlier more spatially limited studies on the Oregon coast suggested that both recruitment and particulate food for filter-feeding larvae and metamorphs were associated with the magnitude of predation (Menge et al. 1994, 1996, 1997a). At two sites on the Oregon coast (Boiler Bay [BB], Strawberry Hill [SH]), the magnitudes of mussel recruitment, mussel growth, phytoplankton concentration, sea star abundance, and abundance of the small mussel *M. trossulus* all covaried, and all were high at SH and low at BB. Similar differences with similar implications for dynamics have been documented in a completely different rocky intertidal community in New Zealand (Menge et al. 1999, 2002). Larger-scale studies in Oregon have largely been consistent with these results (Menge 2004). We were therefore surprised when a similar relationship between predation and either mussel recruitment or chlorophyll *a* did not emerge in our regression analysis across the entire upwelling gradient.

The categorical analysis suggests a possible reason for this lack of relationship. If predation rate is analyzed in relation to both mussel recruitment and chlorophyll *a* concentration simultaneously, the results suggest that high levels of both are often necessary to support a high rate of predation (Fig. 10). We interpret this to suggest that when particulate food (phytoplankton) is high, large numbers of mussel larvae reaching the shore are likely to result in high abundances of small mussels. Observations in Oregon over the past 15 years, for example, indicates that at SH, high abundances of the small mussel *M. trossulus* consistently appear in the low zone each winter following high mussel recruitment in the fall, while comparably high recruitment at Fogarty Creek, a site north of BB, almost never results in *M. trossulus* of any abundance in the low zone (e.g., Menge et al. 1994, 1997a). In other words, successful recruitment of mussels may depend on a high concentration of particulate food for the larvae.

Similarly, high abundances of mussel recruits may underlie high recruitment of sea stars. The higher recruitment at Strawberry Hill and Seal Rock could simply reflect higher delivery rates and/or high settlement, but the co-occurrence of high sea star and high mussel recruitment also suggests that the latter (high mussel recruitment) is necessary for the former (high sea star recruitment). Consistent with this, E. Sanford (*unpublished data*) has observed large increases in the abundance of juvenile sea stars in populations at Strawberry Hill and the south Newport (Oregon) jetty that have coincided with recent (since 1999) large increases in phytoplankton concentration along the Oregon coast (B. Menge, *unpublished data*). He interprets these changes as a consequence of increased survival of sea star larvae and recruits dependent on the increased abundance of phytoplankton and mussel recruits, respectively.

The among-site differences documented here suggests that these food differences are likely to occur on relatively local to mesoscales, on the order of kilometers to 10's of kilometers. Recent evidence showing a strong positive effect of high phytoplankton abundance on size and survival of mussel larvae (*M. galloprovincialis*) in both laboratory and field experiments in southern California are consistent with this hypothesis (Phillips 2002). As suggested by the high predation at two sites with low prey recruitment and low phytoplankton, however, other processes must also be important. As discussed in the next section, we believe that longevity of both predator and prey are another important piece of the explanation for our results.

Thus, we infer that the interaction dynamics of coastal communities are at least partly contingent on the interaction between two subsidies, larval abundance and transport, and the food supply for larvae and new recruits. Specifically, we suggest that the rate of predation by predators with planktonic larvae is likely to be greatest where larval transport (of both predator and prey) is high and where phytoplankton concentrations are also high. Except for the conditions discussed in the next section, low values of either are expected to be associated with low predation rates. This conclusion suggests that future modifications of the Connolly-Roughgarden model (Connolly and Roughgarden 1999b) might consider addressing the influence of food supply for larvae and new recruits as well as propagule supply.

Coastal community structure and dynamics

Our results offer further insight into the role of the keystone predator, *Pisaster ochraceus* in structuring rocky intertidal communities. Paine's original experiments (Paine 1966, 1974) showed the strong impact of *Pisaster* on intertidal community structure (mussel zonation, diversity of primary space-occupying macroinvertebrates and algae in the low zone) at sites in Washington state, revealing both the keystone predator

role (and concept) and the intermediate predation effect on diversity of this important species. Later experiments in Oregon (Menge et al. 1994, 1996, 1997*a*, Sanford 1999, 2002*a*, *b*, *c*) showed that keystone predation was strongly context dependent, and suggested a strong influence on predation intensity of subsidies such as prey inputs (mussel recruitment and growth) and environmental conditions such as wave action and temperature.

Several issues remained unclear, however. First, what is the relative importance of mussel recruitment (as a source of new individuals in prey populations) vs. phytoplankton concentration (as food for both larvae and adults of prey populations, and thus a source of secondary production of prey)? Our Oregon studies contrasted sites that had either low or high levels of both factors, and it was possible, for example, that just high recruitment was sufficient to support dense predator populations and thus generate strong top-down feedback on prey abundance. The present study suggests that, in fact, high levels of both recruitment and phytoplankton may underlie the enhancement of predation impact through "bottom-up" subsidies.

As predicted by Connolly and Roughgarden's model (1999*b*), however, our work also indicates that understanding the dynamics of *Pisaster* populations will be crucial to understanding how sea star predation varies in space. Sea star density was the factor most strongly related to predation rates on mussels, suggesting the need to study *Pisaster* larval transport, recruitment, growth, and survival. Another factor, suggested by Sanford's (1999) finding that *Pisaster* foraging activity is highly sensitive to temperature changes, especially the sharp thermal drops that occur during upwelling, is sea star physiology. Still other factors include wave action and seasonality. Sea star foraging activity is inhibited by waves, for example (Menge et al. 1996), and wave action decreases with decreased latitude along the U.S. West Coast (C. Schoch, *unpublished manuscript*). If sea star foraging activity increases with warmer conditions, with reduced wave action, and with longer warm seasons, for example, then the high predation rate at sites in California despite the low rate of prey input might be partly explained by milder climatic conditions in the south. Research on some of these questions is underway.

Our predation-rate experiments do not necessarily reveal the impact of predation at each site. And, in fact, in the final analysis all mussels were consumed in our transplant experiments at most sites, it just took longer at "slow" predation sites than at "fast" predation sites. The consistently low abundance of mussels in the low zone at sites north of Point Conception, and the high abundance of mussels south of Point Conception (Fig. 5) where sea star abundance (Fig. 6) and predation rates (Fig. 7) are lower, are consistent with the idea that *Pisaster* predation maintains the lower level of the *Mytilus californianus* zone along most of the wave-ex-

posed rocky coastline of the U.S. West Coast. Thus, the *effect* of *Pisaster* predation on the community may be less sensitive to shorter-term processes such as fluctuations in prey supply, sea star recruitment, or thermal environment than is the *rate* of predation. What then, might allow sea star predation to be a consistently strong determinant in space and time of mussel zonation patterns?

We suggest that another life-history characteristic, longevity, both of sea stars and mussels in this system, is the key to understanding the temporally and spatially persistent effect of *Pisaster* predation in maintaining intertidal community structure along the U.S. West Coast. Both *Pisaster* and *M. californianus* (in sea star-free refuges like the middle zone) have estimated life spans that range into decades (Menge 1975, Paine and Levin 1981, Paine 1984). Thus, once populations are established, they are likely to persist many years without the necessity of a high influx of new members in the population. Such a dynamic has been termed the "storage" effect (Warner and Chesson 1985). Evidence from a variety of sites along the U.S. West Coast suggests that *Pisaster* recruitment can vary dramatically in space. On the Washington coast and in the San Juan Islands, *Pisaster* recruitment, as suggested by the presence of small individuals in the population, tended to be a rare event at most sites except at locations in the San Juan Islands where the local-scale oceanography suggested larval retention was likely (Menge and Menge 1974). On the Oregon coast *Pisaster* recruitment is substantial at most sites (Figs. 12 and 13), and the size-structure data along the California coast suggests that some sites have greater recruitment than others. Recent observations in the Channel Islands indicates that a pulse of recruitment has occurred sometime during 1998–2002, leading to large increases in abundance of both *P. ochraceus* and *P. giganteus* at sites where numbers of both species had been low since the mid-1990s (C. A. Blanchette, *unpublished data*). Since these species were both abundant at the same sites in the early 1970s (B. Menge, J. Lubchenco, *personal observations*), it seems evident that large population fluctuations in these predators can occur, but evidently on decadal scales. The general implication of these patterns is that across large spatial scales, *Pisaster* recruitment can vary between steadily high, to almost none, for long time periods with occasional large influxes of new recruits.

Conclusions

These experiments suggest that understanding the dynamics of coastal ecosystems requires integrating a wide range of patterns and processes in intertidal communities with the oceanographic processes and conditions in the waters bathing them. The large-scale influence of upwelling envisioned in Connolly and Roughgarden's (1999*b*) model was only partly successful in predicting the predator–prey dynamics of the

Pisaster–Mytilus interaction on a coastal scale. But it seems clear that the conceptual linkage of these processes has opened a powerful approach to understanding the dynamics of these systems. When applied at more intermediate scales, we predict that understanding the influence of oceanographic processes will provide insight into community dynamics that smaller-scale studies have been unable to elicit.

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APPENDIX A

A table listing study sites by region, with latitude and longitude and physical characteristics, is available in ESA's Electronic Data Archive: *Ecological Archives*: M074-015-A1.

APPENDIX B

A photograph of a replicate of the predation rate experiment at Gull Haven, Oregon, USA, is available in ESA's Electronic Data Archive: *Ecological Archives*: M074-015-A2.

APPENDIX C

A table showing timing and duration of predation-rate experiments is available is ESA's Electronic Data Archive: *Ecological Archives*: M074-015-A3.

APPENDIX D

Nine tables showing results of statistical analyses on variation in (1) chlorophyll *a*, (2) mussel recruitment, (3) mussel growth, (4) mussel cover, (5) mussel cover in the middle zone, (6) mussel cover in the low zone, (7) sea star density, (8) predation rates (per population), and (9) predation rates (per capita) is available in ESA's Electronic Data Archive: *Ecological Archives*: M074-015-A4.