Environmental Stress, Bottom-up Effects, and Community Dynamics: Integrating Molecular-Physiological and Ecological Approaches[1]

Bruce A. Menge,[2,]* Annette M. Olson,* and Elizabeth P. Dahlhoff†

*Department of Zoology, Oregon State University, Corvallis, Oregon 97331-2914 and
†Department of Biology and Center for Environmental Studies, Santa Clara University, Santa Clara, California 95053

Synopsis. Environmental stress and nutrient/productivity models predict the responses of community structure along gradients of physical conditions and bottom-up effects. Although both models have succeeded in helping to understand variation in ecological communities, most tests have been qualitative. Until recently, two roadblocks to more quantitative tests in marine environments have been a lack of (1) inexpensive, field-deployable technology for quantifying (e.g.) temperature, light, salinity, chlorophyll, and productivity, and (2) methods of quantifying the sub-organismal mechanisms linking environmental conditions to their ecological expression. The advent of inexpensive remote-sensing technology, adoption of molecular techniques such as quantification of heat-shock proteins and RNA:DNA ratios, and the formation of interdisciplinary alliances between ecologists and physiologists has begun to overcome these roadblocks. An integrated eco-physiological approach focuses on the determinants of: distributional limits among microhabitat patches and along (local-scale) environmental gradients (e.g., zonation); among-site (mesoscale) differences in community pattern; and geographic (macroscale) differences in ecosystem structure. These approaches promise new insights into the physiological mechanisms underlying variation in processes such as species interactions, physical disturbance, survival and growth. Here, we review two classes of models for community dynamics, and present examples of ecological studies of these models in consumer-prey systems. We illustrate the power of new molecular tools to characterize the sub-organismal responses of some of the same consumers and prey to thermal stress and food concentration. Ecological and physiological evidence tends to be consistent with model predictions, supporting our argument that we are poised to make major advances in the mechanistic understanding of community dynamics along key environmental gradients.

Introduction

What are the determinants of community structure? This is a central question in ecology, and despite great progress, a synthetic model of the causes of patterns of distribution, abundance, diversity, size structure, and spatial pattern remains elusive. Two classes of conceptual models that provide a context-dependent framework for understanding, and hopefully predicting community dynamics have been termed "environmental stress models" and either "nutrient/productivity models" or the "food chain dynamics hypothesis" (Connell, 1975; Menge and Sutherland, 1976, 1987; Fretwell, 1977, 1987; Grime, 1977; Oksanen et al., 1981; Menge and Olson, 1990; Menge, 2000; Menge and Branch, 2001). Environmental stress models assume that community structure results from species interactions and disturbances, and how these are modified by underlying gradients of environmental stress (where stress is a consequence of environmental conditions such as temperature, moisture, salinity, etc.). Similarly, nutrient/productivity models also assume that community structure results from species interactions, but emphasize the role of bottom-up factors (nutrients, productivity) as determinants of variation in the effects of interactions. Both models postulate that communities can be ordered along environmental gradients, and that those in the most austere environments (i.e., those having the harshest physical conditions or the lowest productivity), will have simple communities whose structure is determined directly by severe stress or nutrient shortage. Increasing moderation in environmental conditions leads to increased abundances, more complex trophic structure, and increased influence of species interactions on structure (Menge, 2000; Menge and Branch, 2001).

These models are venerable, having been proposed in the late 1970s, and their roots go back even further, to the well known model of Hairston et al. (Hairston et al., 1960). Both types of model have succeeded in helping to understand variation in community structure, but most tests to date have been qualitative. Why haven't we progressed more rapidly in developing a more quantitatively based literature on context-dependent community dynamics? We suggest that until recently, progress was hindered by three major roadblocks. First, we have lacked reliable, inexpensive, and field-deployable equipment for quantifying environmental conditions. Second, methods of quantifying the sub-organismal physiological processes, or mechanisms, that underlie the ecological responses to stress or nutritional conditions under field conditions were generally unavailable. Third, there was little encouragement to form the alliances among individuals in the relevant biological subdisciplines that would permit the application of appropriate expertise to what was fundamentally an interdisciplinary problem.

During the past decade, important progress has been

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[2] E-mail: mengeb@bcc.orst.edu

made in removing these hindrances to progress in ecology. The advent of the microchip underpinned dramatic strides in affordable, conveniently-sized and sturdy remote-sensing technology, including devices that can record continuously, at appropriate temporal scales, temperature, light, salinity, chlorophyll-a, and productivity (or their proxies). Simultaneously, the rise of molecular biology has led to the development of potentially powerful techniques to quantify organismal response to stresses or to the food environment (Coleman *et al.*, 1995; Somero, 1995; Feder and Hofmann, 1999). In particular, these measures (*e.g.,* heat shock proteins, RNA:DNA ratios) offer insight into sublethal and/or subtle and/or short-term responses that can be impossible or at least difficult to quantify, especially on short time scales, using standard ecological measures (*e.g.,* growth, survival, reproduction). Finally, growing awareness of the potential power of a hybrid, interdisciplinary approach to mechanistic studies of community dynamics has led to increased cross-fertilization among relevant subdisciplines in collaborative studies of eco-physiology in an experimental field context.

Here we examine these issues, with the dual goals of evaluating the current state of the art, and suggesting possible future directions for research. We first review two classes of environmental stress models and, to test the predictions of these models, we present field experiments that illustrate the effects of stress on consumer-prey interactions. We then consider recent studies that have aimed at examining externally undetectable, sub-organismal responses to stress or nutritional conditions, and linking them to the ecological field context in which the responses occur.

MODELS OF COMMUNITY STRUCTURE

Environmental stress models

We first consider a simple two-level food chain, with consumers (*e.g.,* herbivores or primary carnivores) and prey (*e.g.,* plants or basal species) (Fig. 1). The term ''basal species'' (Pimm, 1982) accommodates sessile marine invertebrates into this scheme. Trophically, sessile marine invertebrates are herbivores/detritivores, but as space users, they are ecologically more comparable to benthic macroalgae, and like macroalgae, obtain resources from the water column. Thus, for example, in marine communities, both limpet-alga and whelk-barnacle interactions are two-level food chains.

We next consider how food chain length (equivalent to trophic complexity) varies along monotonic environmental gradients of ''environmental stress'' (or below, ''productivity''). In the Environmental Stress Model (ESM), under the most stressful conditions, no organisms can persist (Fig. 1). With moderation, organisms can colonize, but are still too scarce for interactions to have an impact (effective food chain length = EFCL <1, where an effective trophic level means one that interacts strongly). With ever-decreas-
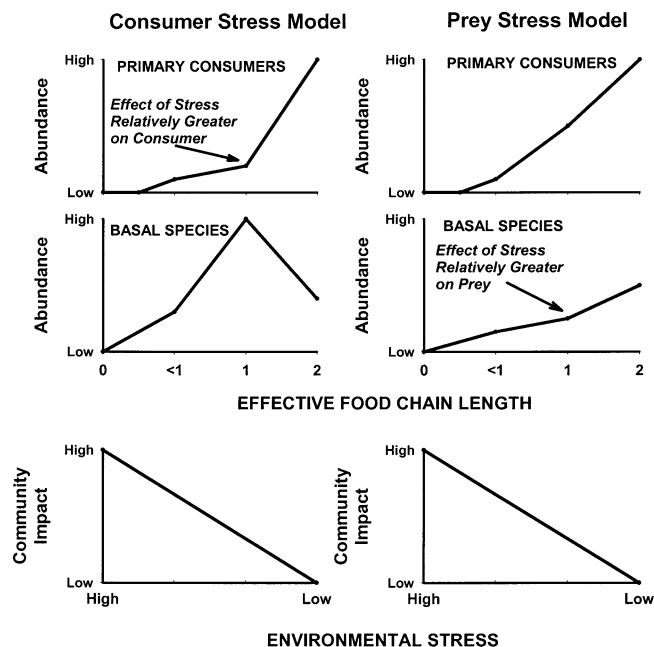

FIG. 1. Environmental stress models (simplified, after Menge and Olson, 1990). In consumer stress models (CSMs), consumers are assumed to be more affected by stress than are prey. In prey stress models (PSMs), consumers are assumed to be less affected by stress than are prey. As stress moderates, basal species control by consumers occurs either under the most benign conditions (CSM) or intermediate stress conditions (PSM). Effective food chain length (EFCL) refers to whether no species are present (EFCL = 0), species are present but scarce (EFCL = <1), one trophic level (basal species or consumer) is dominant (EFCL = 1), or both levels are abundant (EFCL = 2).

ing stress, EFCL increases, with first one, then two effective levels.

As proposed by Menge and Olson (1990), the predictions of the ESM depend on whether the consumer or the prey is most strongly affected. Consumer Stress Models (CSMs) describe changes in trophic structure and relative impacts of interactions under the assumption that consumers are more severely affected by stress than are their prey (Fig. 1, left panels). Such a difference can arise when consumers are larger than their prey, are unable to shelter when conditions become harsh, or too slow-moving to temporarily vacate the habitat for locations with more moderate conditions (Menge, 1978*a, b*; Denny *et al.*, 1985; Menge and Sutherland, 1987; Denny, 1988). With stress, consumers devote the majority of their resources to stress responses and are therefore ineffective in controlling prey, making EFCL = 1 (Fig. 1 left, top and middle panels).

Prey Stress Models (PSMs) describe changes expected under the assumption that prey are more severely affected by stress than are their consumers (Fig. 1, right panels). Such a difference can arise when consumers are smaller than their prey, can find shelter near prey (or on/under the prey itself), or are fast-moving and can move quickly between harsher prey habitat and more moderate conditions nearby (Louda, 1986,

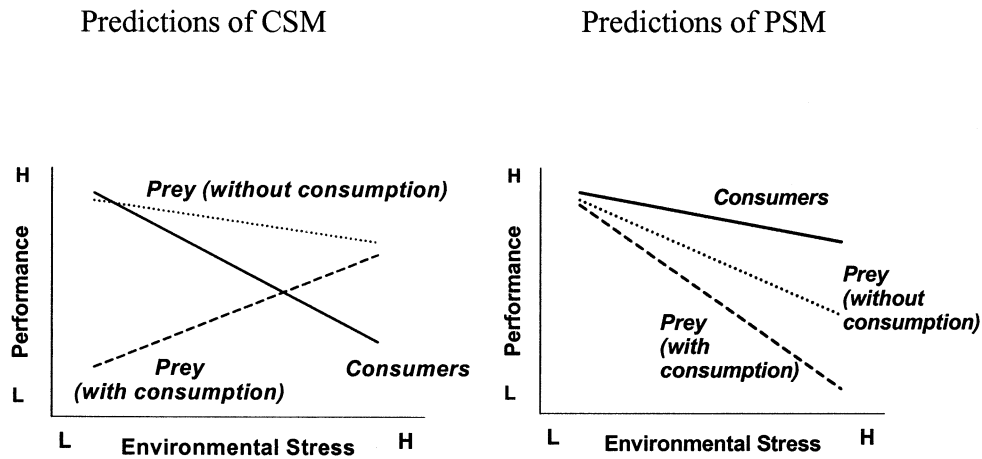Predictions of CSM   Predictions of PSM

Fig. 2. Predictions of CSMs and PSMs (after Menge and Olson, 1990). See text for further explanation.

1988; Menge and Olson, 1990; Louda and Collinge, 1992; Olson, 1992). With stress, prey devote the majority of their resources to stress responses and are therefore relatively more susceptible to consumer pressure, again making EFCL = 1. Under benign conditions, stress impacts are minimal, and both members of the interacting pair can devote the majority of their resources to biotic interactions.

These alternative versions of the ESM make contrasting predictions regarding performance of the prey in the presence and absence of consumers (Menge and Olson, 1990; Fig. 2). In the CSM, consumer performance decreases more sharply than does prey performance with increasing stress (Fig. 2, left). When consumer and prey coexist in harsh conditions, the effects of consumers on prey are weak because predators are under severe stress and devote most of their time and energy to survival (Fig. 2, left). In more benign portions of the environmental stress gradient, consumers occur under optimal physical and physiological conditions and can devote most of their time and energy to prey capture and consumption (Fig. 2, left).

In contrast, in the PSM, consumer performance decreases less sharply than does prey performance with increasing stress (Fig. 2, right). When consumer and prey coexist in harsh conditions, consumer effects on prey are stronger than in benign conditions because prey defenses are weakened. In more benign environments, prey defenses are stronger, making prey less vulnerable to consumption.

Nutrient/productivity models

Here too we assume a simple two-level food chain, with consumers and prey varying in biomass along a monotonically increasing gradient of productivity (Fig. 3). As envisioned by Oksanen et al. (1981), this model predicts, initially, that with increasing productivity, basal species increase from 0 biomass at very low productivity (EFCL 0), to sparse biomass (EFCL < 1), to the point where production is sufficient to support an abundant basal species level that competes for space,

but is insufficient to support more than sparse consumer abundance (EFCL 1). With further increases in productivity, consumer abundance increases, and through increased consumption intensity, offsets the increased basal species productivity, maintaining a constant biomass of basal species (from EFCL 1 to 2; Fig. 3).

This model thus predicts that with increased productivity, both prey and their consumers will be increasingly well off nutritionally. Ecological measures such as growth rate, feeding rate, and reproductive output and physiological measures reflecting these rates should therefore increase with increased productivity.

Performance and temporal scale

In these models, "performance" typically refers to readily measured characteristics such as feeding rate, growth, survival, or reproduction. All of these measures, however, are relatively long-term integrative measures that reflect an average physiological state. Feeding rate, for example, might be expected to decline if organisms experience stresses (e.g., thermal or desiccation) that impair cell, tissue and organ function, and should increase again once conditions improve and sub-organismal repair is complete. Feeding rate can also decline due to behavioral avoidance mechanisms, if possible, and if not, consumers may die under persistent severe conditions. Growth should also slow or stop with stress as the organism's cellular machinery devotes energy to protein repair or destruction, and resume again with improved conditions. Under field conditions, measures such as growth, feeding rate and reproduction can often be quantified, although field detection of changes in these measures can take months to years. Environments can change on many temporal scales, however, ranging down to seconds, minutes, hours and days, and molecular and cellular responses also tend to occur on these more rapid time scales. Thus, growth or feeding performance in the field as necessarily measured over longer temporal scales has no hope of pinpointing the short-term events that might be the critical events that generate the long-term

average patterns that ecologists can quantify. Only measures that can quantify organismal condition on temporal scales relevant to those upon which sub-organismal changes occur can provide this level of insight. Such measures can also provide a "common currency" with which to quantify organismal condition or performance across taxa.

Complexities

We recognize that these simple models do not capture many important elements involved in community dynamics. Species interactions within a trophic level, for example, can modify these simple food chain predictions, sometimes dramatically (Abrams, 1993; Rosemond *et al.*, 1993). Incorporation of density can also modify model predictions by introducing positive effects of species interactions (facilitation, associative defenses) (Burnaford, 1997, 2001; Bruno and Bertness, 2001). Despite the lack of detail in these models, exploring the links between ecological performance and sub-organismal processes is itself a complex issue. We believe that starting with a simple scenario and adding complexity and detail when appropriate seems the most productive way to approach the problem.

TESTING THE MODELS: ENVIRONMENTAL STRESS

As summarized by Menge and Olson (1990), evidence consistent with the assumptions and predictions of ESMs and N/PMs was available for marine and non-marine systems in the 1970s and 1980s. Since then, considerable effort has been focused on testing N/PMs, mostly in the context of top-down/bottom-up theory (Menge, 2000). Less effort has been directed towards specific tests of ESMs (Louda and Collinge, 1992; Leonard *et al.*, 1999), although considerable effort has been focused on the organism-to-community impacts of environmental stress (Louda and Collinge, 1992; Bertness and Leonard, 1997; Helmuth, 1998, 1999; Leonard *et al.*, 1998; Bertness *et al.*, 1999; Bruno and Bertness, 2001). Below, we present the results of a study aimed at testing ESMs.

Study system

To test the simple ESM models outlined above, two of us (BAM, AMO) carried out field experiments in 1990–91 at Colin's Cove on San Juan Island, Washington, USA. We evaluated two "model" consumer-prey interactions. We examined whelk-barnacle interactions to test the predictions of the CSM with interactors that fit the assumptions (consumer larger and more susceptible to stress than prey). Because an earlier study of limpet-algal interactions (Olson, 1992) produced results partially consistent with the PSM, we also assessed a limpet-red algal interaction. In this study, we tested whether those results would hold if assumptions (consumers smaller than sheltering prey) were relaxed.

In both whelk and limpet experiments, we manipulated stress levels in two ways: (1) by placing experimental units in microhabitats differing in inundation
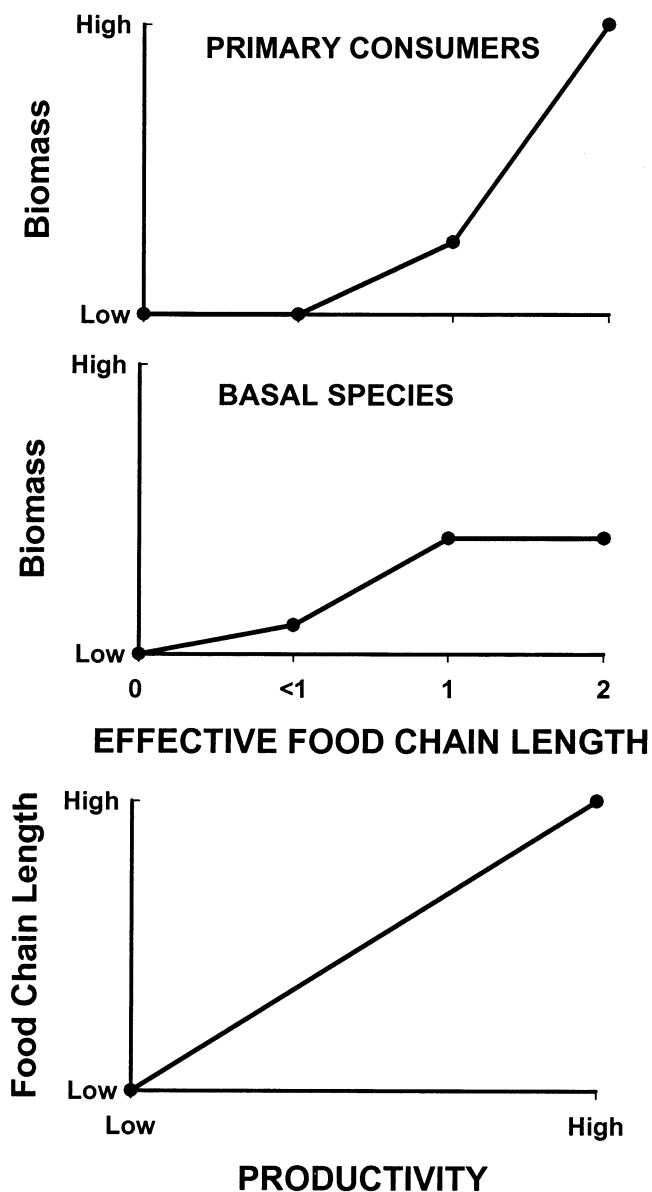
Nutrient/Productivity Model

FIG. 3. Nutrient/productivity model (simplified, after Menge and Olson, 1990; Oksanen *et al.*, 1981). As productivity increases, food chain length is predicted to increase (bottom panel). At EFCL < 1, productivity is sufficient to support a sparse basal species level but insufficient to support consumers. With increased productivity, first basal species (EFCL 0 to <1 to 1) then consumer species increase in abundance (EFCL <1 to 1 to 2), with first competition, then consumer pressure regulating basal species abundance.

and solar irradiance (high *vs.* lower mid-intertidal zone, sunny and shady sides of concrete blocks, respectively), (2) by providing artificial shade (small opaque plastic "huts") fastened into a subset of the experimental units (Fig. 4). Additionally, weather varied in the San Juan Islands during our experiments, creating another contrast in stress conditions. Warm,

FIG. 4.　Designs of whelk and limpet experiments. All cages or arenas were attached to the sides of cinder blocks placed on the gravel beach and anchored by rebar rods pounded into the substratum through the holes in the block (see upper right photo). Cages enclosed rocks with barnacles attached (see upper right photo). Limpet arenas were fenced and covered with lids (removed to allow inspection of arena layout) to contain limpets and exclude their predators. Clamps with neoprene gaskets were used to hold algal strips in place.

dry, and presumably more thermally stressful conditions occurred during the 1990 whelk-barnacle experiment, the second 1990 limpet experiment, and the second 1991 limpet experiment. Cool, cloudy and sometimes rainy weather, presumably low stress conditions, occurred during the first limpet experiments in 1990

and 1991, and the 1991 whelk-barnacle experiment (Table 1) (B. Menge, personal observations). In our analysis, we took advantage of these fortuitous differences by incorporating weather as a categorical factor.

　Three treatments were used to measure the intensity of interactions of both whelks and limpets with their

TABLE 1.　*Summary of whelk-barnacle and limpet-alga experiments at Colin's Cove, San Juan Island.*

Interacting species			
Consumers (Collection site)	Prey (Collection site)	Dates of trials	Weather conditions and notes
Whelks *Nucella ostrina* (Turn Rock)	Barnacles *Balanus glandula* (Argyle Lagoon outlet)	1990 15–20 August 1991 8–15 July	Partly sunny (last three days of trial) Cloudy, cool
Limpets *Lottia pelta* (Colin's Cove rocky benches)	Red algal gametophytes *M. splendens* (Friday Harbor Laboratory dock)	1990 16–18 August	Rain No stress effects detected
	Red algal gametophytes *M. splendens*	1990 18–21 August 1991 8–11 July 1991 23–25 July	Partly sunny Cloudy, cool Warm, sunny; algal strips bleached

prey: prey alone with no shelter (control, to characterize background mortality or tissue loss); prey with consumer, but no shelter (experimental, to detect consumer feeding); and prey with consumer and artificial shelter (experimental, to assess the effect of shelter on feeding). These treatments were applied randomly across experimental units within a given microhabitat (high *vs.* low, sun *vs.* shade). Two trials of the whelk experiment were done (warm in 1990 and cool in 1991), and four trials of the limpet experiment were done (one warm and one cool in each of 1990 and 1991). Response variables were number of prey eaten/ day in whelk experiments, and percent of the algal strip eaten/day in limpet experiments.

In whelk-barnacle experiments, we used *Nucella ostrina* (formerly *N. emarginata*; see Marko, 1998) as consumers and *Balanus glandula* as prey. In limpet-alga experiments, we used *Lottia pelta* as consumers and the red bladed alga *Mazzaella splendens* as prey. Prior studies (Olson, 1992) had indicated that the interaction of the limpets *L. digitalis* and *L. pelta* with another algal species, *M. cornucopiae*, was consistent with some predictions of the PSM. Grazing effects on *M. cornucopiae* were greatest at the upper, more stressful edge of the vertical range of this alga than lower on the shore. The mechanism of the limpet effect involved sheltering of the limpet by the foliose fronds of this turf-forming alga. To evaluate the hypothesis that the shade of the algal turf combined with thermal/ desiccation stress on the alga were key aspects of this interaction, we attempted to separate the sheltering and stress aspects in such limpet-alga interactions. We chose to use *L. pelta*, because it was shown to feed on mature blades of *M. cornucopiae*, while *L. digitalis* affected only the recruitment stages (spores and sporelings) (Olson, 1992). We chose *M. splendens* as the prey because of its abundance in the study area (*M. cornucopiae* occurs only on the wave-swept outer coast), and its close phylogenetic relationship to *M. cornucopiae*. In addition, the thalli of this alga are flat (rather than curly, as in *M. cornucopiae*), and could thus be offered to limpets in a manner that did not provide shade. Under such a scenario, we predicted that the limpet-alga interaction would be more consistent with CSM than with PSM predictions.

Design and installation of experimental units

Colin's Cove was selected as a study site because of its accessibility and minimal wave action. In addition, its wide beach offered a uniform habitat across a large intertidal range, and the gravel substratum allowed us to anchor the experimental units by pounding rebar stakes through the blocks (Fig. 4). To vary time of exposure to desiccation/thermal stress, we anchored one row of concrete blocks in the lower mid-zone (+0.3 m MLLW; low stress) and one row in the high zone (+1.68 m MLLW; high stress). To vary exposure to direct solar radiation, we placed experimental units on opposite sides of the concrete blocks, with the blocks oriented on the shore so that experiments faced either SE (sunny) or NW (shady).

Experimental units were either stainless steel mesh cages (whelk experiments) or arenas made of PVC plate (limpet experiments), which we bolted to the anchored concrete blocks (Fig. 4). To prevent uncontrolled losses of limpets to escape or predation, we provided all arenas with removable plastic mesh ''lids'' (removed for viewing in Fig. 4 photos). Although the mesh lids partially shaded all treatments, we reasoned that under appropriate conditions, the desired stress gradients would still exist.

For the whelk experiments, in each cage we placed a small rock with barnacles attached to it (Fig. 4, upper right photo). In each +whelk cage, we placed two *N. ostrina*. Whelks that died were noted and replaced. Each day of the experiment we counted the number of dead prey. Barnacle shells do not always show physical evidence of whelk drilling, so we depended on mortality rates of barnacles in −whelk (control) cages to quantify background mortality. When background mortality occurred (1991 experiment), we used average mortality in −whelk cages to adjust barnacle mortality rates in +whelk treatments.

In limpet experiments, we offered limpets rectangular strips (3 cm × 9.5 cm) of gametophytic blades of *M. splendens*. These were clamped against the plate surface so that they would lie flat, making them available as food, but limiting their utility as shelter (Fig. 4). Two limpets of similar length were placed in +limpet arenas. Grazing was quantified by drying the strips in an algal press and later quantifying the area lost to feeding using digitizing software on a PC.

Data analysis

The whelk experiments were analyzed using four-way ANOVA, with year (1990, 1991), zone (high, low), aspect on concrete block (sunny, shady), and artificial shelter (present, absent) as factors. Response variable was the number of prey eaten/day. Limpet experiments were analyzed using five-way ANOVA, with year, weather (cool, warm), zone, aspect on concrete block, and artificial shelter as factors. Percent of the algal strip eaten/day was the response variable in limpet experiments. Data were transformed prior to analysis ($ln [x + 1]$ for barnacles and mussels; arcsin for percent of the algal strip eaten) prior to analysis to meet the assumptions of normality, independent error terms and equal variances (Sokal and Rohlf, 1995). Unplanned comparisons were made and effect sizes estimated using linear contrasts (Ramsey and Schafer, 1997).

RESULTS

Nucella-Balanus *experiment*

In the whelk experiment, predation rate was affected by all factors and was strongly context-dependent (Table 2; significant statistical interactions). Feeding rates varied most dramatically with weather, with consistently higher rates occurring in 1990, the year of warm conditions during the experiment (Fig. 5). Whelks in 1991 ate nearly one less barnacle per day than did

TABLE 2. *Test of the effect of year (1990, warm conditions; 1991, cool conditions), intertidal zone (high, low), solar exposure (sun side vs. shade side of cement blocks), and artificial shelter (present vs. absent) on number of* Balanus glandula *eaten per day by* Nucella ostrina.[1]

Source of variation	df	Mean square	F	P
Year	1	29.1242	44.04	**≪0.00001**
Intertidal zone ("Zone")	1	0.0814	0.12	0.73
Solar exposure ("Sun")	1	4.9618	7.50	**0.007**
Shelter	1	0.1879	0.28	0.60
Year * Zone	1	0.1528	0.23	0.63
Year * Sun	1	0.3889	0.59	0.44
Year * Shelter	1	0.5628	0.85	0.36
Zone * Sun	1	3.8550	5.83	**0.017**
Zone * Shelter	1	2.7390	4.14	**0.044**
Sun * Shelter	1	0.0003	0.0004	0.98
Year * Zone * Sun	1	0.7880	1.19	0.28
Year * Zone * Shelter	1	4.7596	7.20	**0.008**
Year * Sun * Shelter	1	0.1633	0.25	0.62
Zone * Sun * Shelter	1	0.3735	0.56	0.45
Year * Zone * Sun * Shelter	1	0.6922	1.05	0.31
Error	111	0.6612		

[1] Significant values are indicated in boldface. Data were *ln*-transformed before analysis.
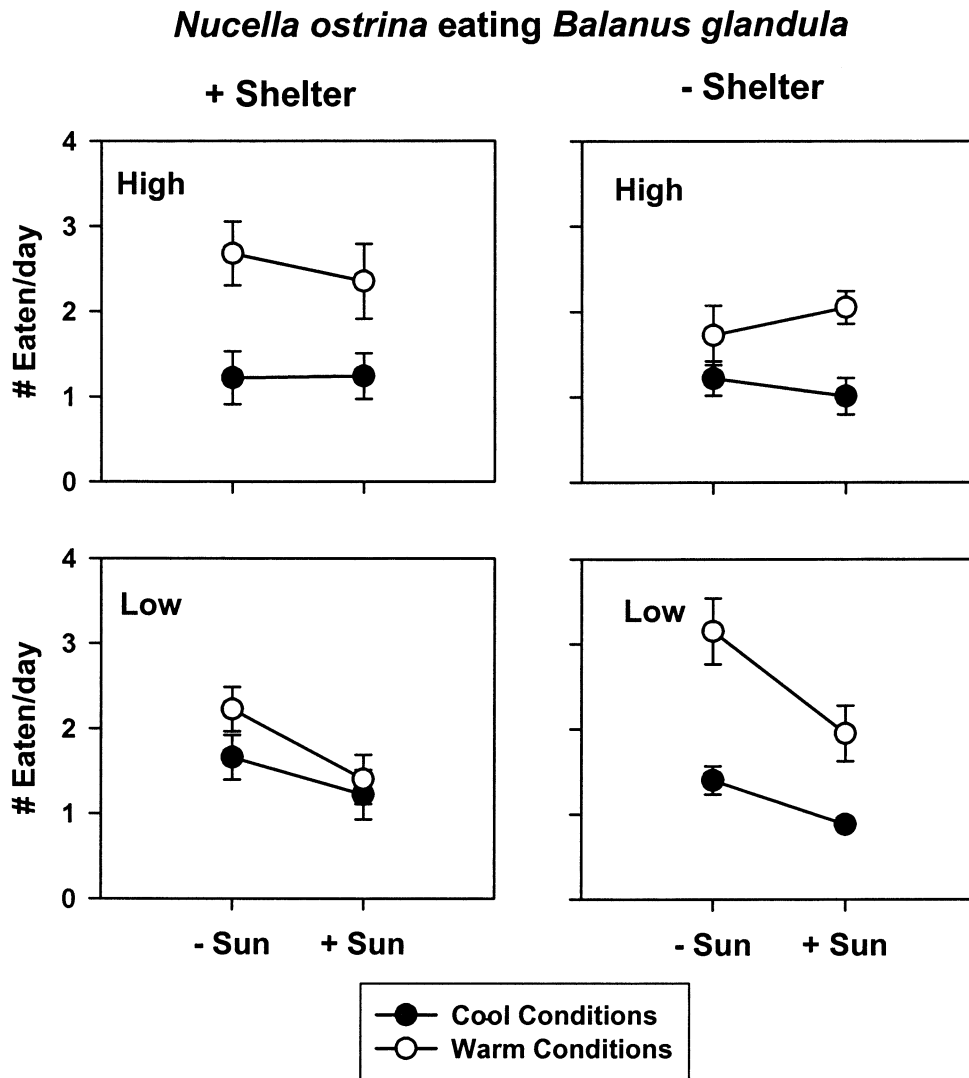

FIG. 5. Whelk experiment: feeding rates (number of barnacles eaten/day/cage) of *Nucella ostrina* on *Balanus glandula* in +shelter and −shelter arenas in high and low zones on +sun and −sun sides of concrete blocks in 1990 (warm conditions) and 1991 (cool conditions).
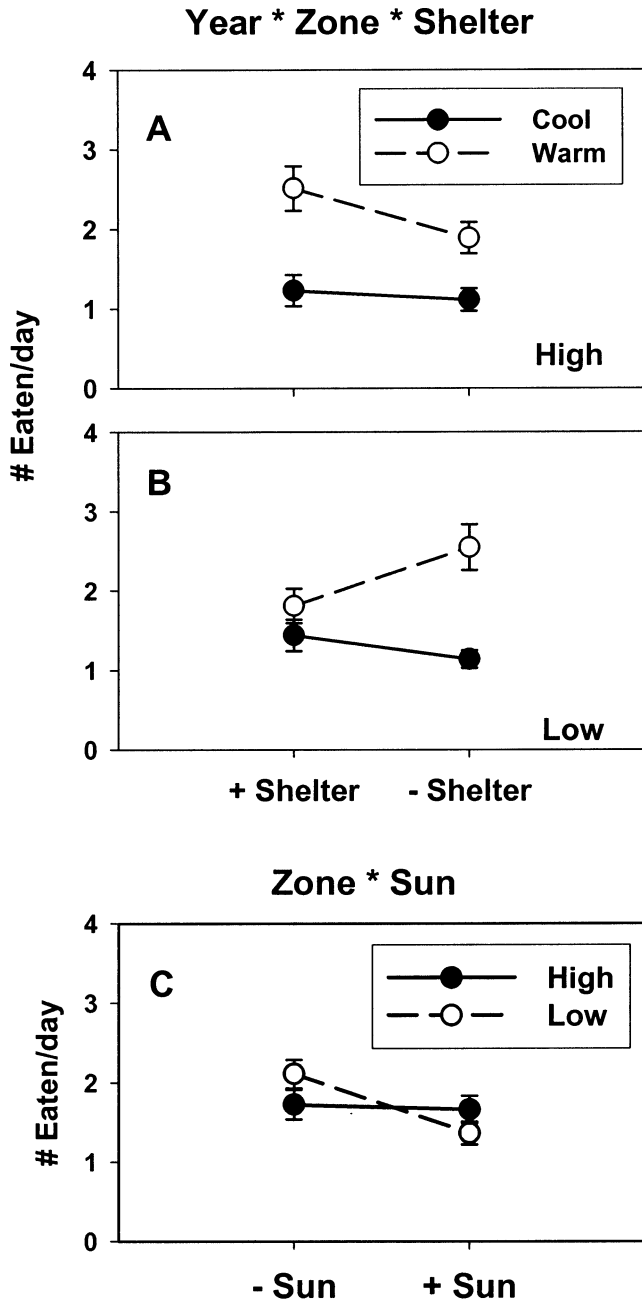
Year * Zone * Shelter

FIG. 6. Whelk experiment: year * zone * shelter and zone * sun interactions. See Table 2 and text for further details.

those in 1990 (year; linear contrasts: $P = \ll 0.00001$, effect size $= 0.96$ prey/day). The effects of shelter varied with year and zone (Table 2; year * zone * shelter interaction). As expected for the high zone, feeding was lower with no shelter, but only in the warm (1990) year (Fig. 6A; linear contrasts: 1990 $P = 0.03$ vs. 1991 $P = 0.69$). In the low zone, feeding varied with shelter, but was higher, not lower, without shelter in the warm (1990) year (Fig. 6B; linear contrasts: $P = 0.01$). Shelter had no effect in the cool (1991) trial (Fig. 6B; linear contrasts: $P = 0.29$). Feeding rate also responded to the more stressful conditions

on the sunny sides of the blocks in the low but not high zone (Fig. 6C; linear contrasts: $P = 0.0004$ and 0.82 in the low and high zones, respectively). We have no ready explanation for the unexpected results in the high zone. As expected under CSM predictions, predation was lower with high stress, but only at smaller spatial scales (low zone: sunny vs. shady sides of blocks, shelter vs. no shelter). Unexpectedly, at a more regional (weather conditions) scale, predation was higher in warm (1990) trial of the experiment.

Lottia-Mazzaella *experiment*

In the limpet experiment, all factors but artificial shelter influenced grazing rate (Table 3). As with whelks, *Lottia* grazing varied most strikingly with weather, and except for the 1991 high zone experiment and the 1990 low sunny experiment, was higher during warm weather (Fig. 7; linear contrast: $P \ll 0.00001$, % eaten was 10.9% higher in warm conditions). Limpet grazing was highly context-dependent, varying in mostly expected ways with the combinations of year, weather and zone, and weather, zone, and side of concrete block (Table 3, three-way interactions were significant). Grazing was reduced in the high zone, and slower in 1990, but the percentage reduction was greater in the high zone under cool vs. warm conditions and greater in the low zone under warm vs. cool conditions (Fig. 8, left panels). Grazing was reduced on the sunny side of the blocks, but the percentage decline was greater in the low zone under warm weather conditions (Fig. 8, right panels).

As expected under theoretical (CSM) predictions, grazing rates were reduced with higher stress, but only at smaller spatial scales (high vs. low, sunny vs. shady sides of blocks). Surprisingly, grazing rates were elevated under the presumed more stressful, regional-scale warm weather conditions. We consider the implications of both whelk and limpet results with respect to theory and to alternative explanations in the Discussion.

TESTING THE MODELS: NUTRIENT/PRODUCTIVITY EFFECTS

Nutrient/productivity models suggest that with increasing productivity, the ecological performance of both prey and consumers will increase. That is, increased nutritional resources should allow higher rates of growth, reproductive output, consumer abundance, and feeding rates. While such effects are well-known in freshwater communities (Carpenter et al., 1992), until recently, evidence for linked bottom-up/top-down effects from nearshore marine communities was sparse. This lack was due in part to an emphasis on studies at local scales, or scales too small to detect variation due to oceanographic variability (e.g., in nutrients or productivity). This led to the consequential inference that the scales of oceanographic variation that might generate bottom-up variation were too vast and too weakly linked to coastal communities to have much influence on community variation at intermedi-

TABLE 3. *Test of the effect of year (1990, 1991), weather conditions (cool, warm), intertidal zone (high, low), solar exposure (sun side vs. shade side of cinder blocks), and artificial shelter (present vs. absent) on the percent of the* Mazzaella splendens *blade area eaten in two days by* Lottia pelta *in arena experiments. Significant values are indicated in boldface.*[1]

Source of variation	df	Mean square	F	P
Year	1	1.2794	71.52	**≪0.0001**
Weather	1	0.7551	42.21	**≪0.0001**
Intertidal zone ("Zone")	1	0.8662	48.41	**≪0.0001**
Solar exposure ("Sun")	1	0.7365	41.16	**≪0.0001**
Shelter	1	0.0112	0.63	0.43
Year * Weather	1	0.0298	1.67	0.20
Year * Zone	1	0.3730	20.85	**≪0.0001**
Year * Sun	1	0.0395	2.21	0.14
Year * Shelter	1	0.0111	0.62	0.43
Weather * Zone	1	0.2542	14.21	**0.0002**
Weather * Sun	1	0.1602	8.96	**0.003**
Weather * Shelter	1	0.0001	0.008	0.93
Zone * Sun	1	0.1223	6.84	**0.009**
Zone * Shelter	1	0.0228	1.27	0.26
Sun * Shelter	1	0.0289	1.62	0.20
Year * Weather * Zone	1	0.1618	9.05	**0.003**
Weather * Zone * Sun	1	0.0870	4.86	**0.028**
Error	304	0.016825		

[1] Data were arcsin-transformed before analysis. Other 3-way interactions, all 4-way interactions, and the 5-way interaction were not significant and are not shown to save space.

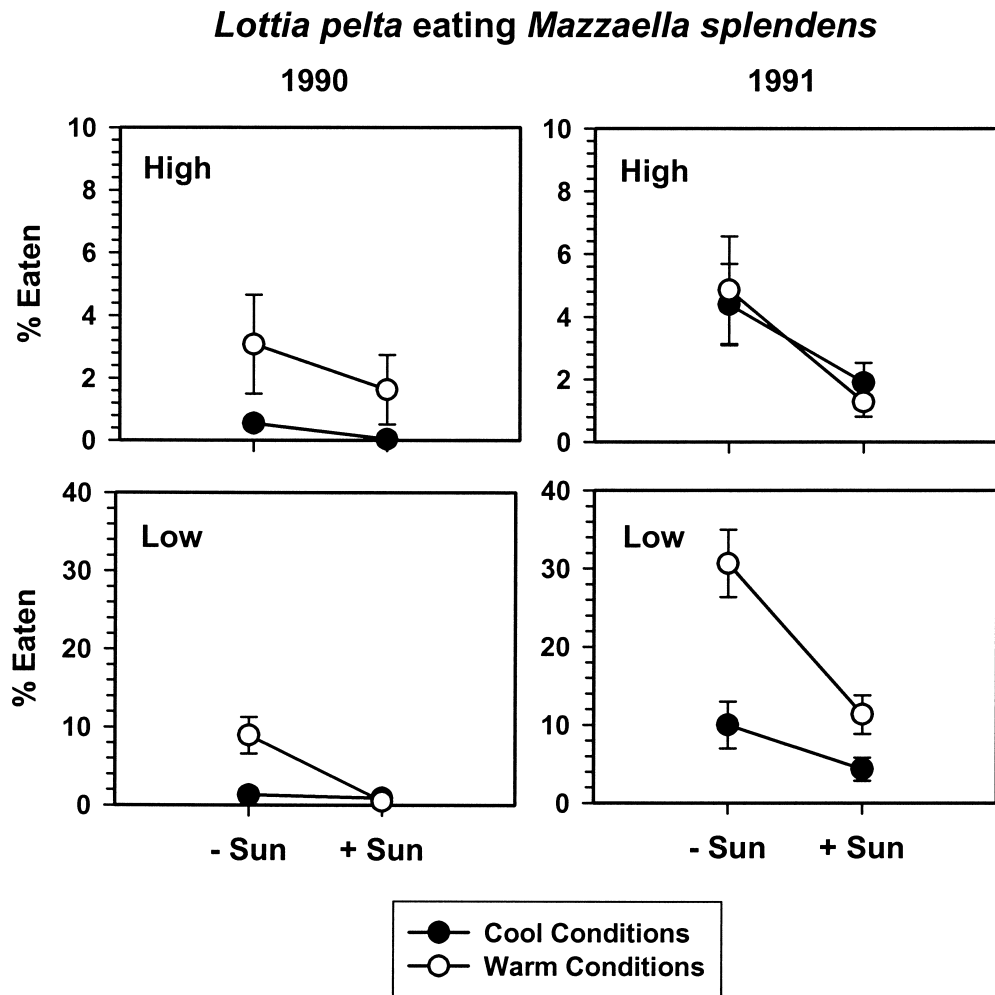## *Lottia pelta* eating *Mazzaella splendens*

FIG. 7. Limpet experiment: feeding rates (percent of blade eaten) of *Lottia pelta* on strips of gametophytic *Mazzaella splendens* in 1990 and 1991 in high and low zones on +sun and −sun sides of block under warm and cool weather conditions.
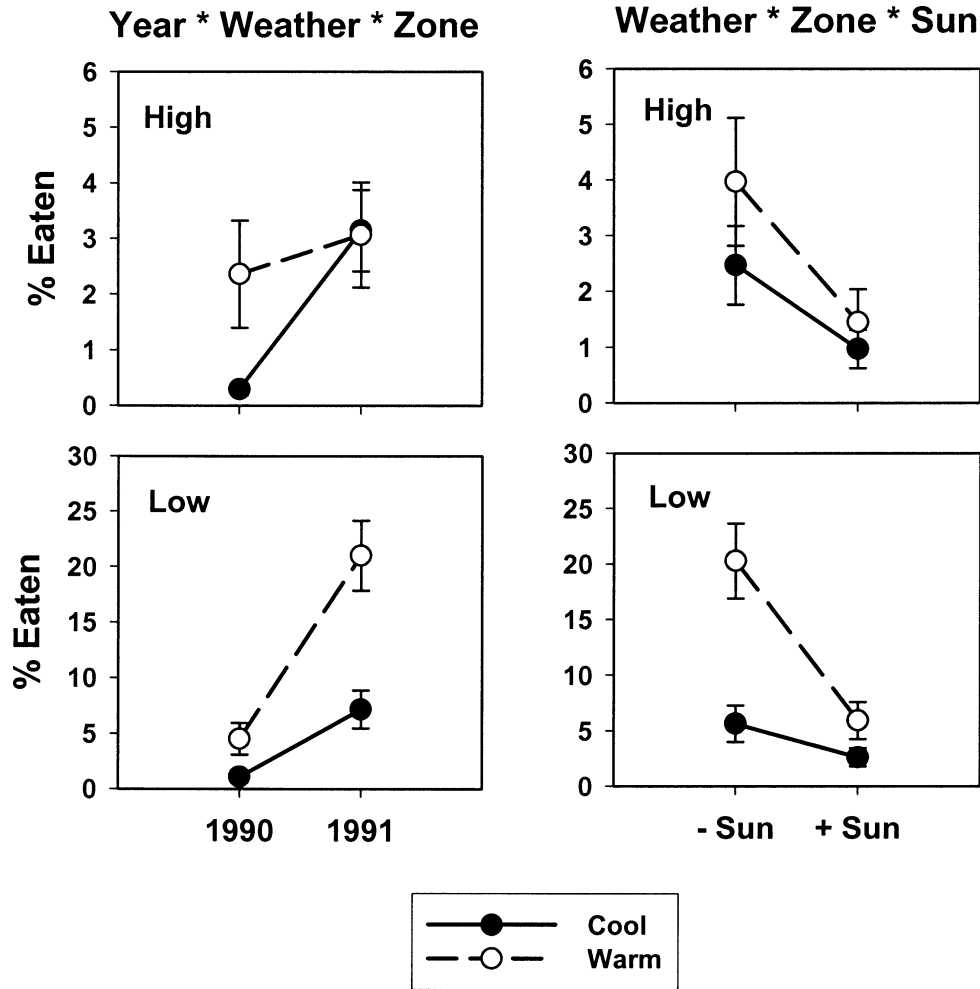
FIG. 8.   Limpet experiment: year * weather * zone and weather * zone * sun interactions. See Table 3 and text for further details.

ate spatial scales (*e.g.,* Menge, 1992). During the past decade, however, studies on coasts of the western U.S., South Africa, Chile, and New Zealand have revealed that mesoscale variation in ecological performance of prey and predator species is closely associated with oceanographic variation in nutrients and productivity of phytoplankton and benthic macrophytes (Menge, 1992, 2000; Menge *et al.,* 1994, 1996, 1997*a, b,* 1999, 2002; Bustamante *et al.,* 1995*a, b;* Bustamante and Branch, 1996*a, b*). Because this topic has been recently reviewed in detail elsewhere (Menge, 2000), we limit ourselves to a brief summary of such effects on ecological performance of basal species and their consumers.

Along the Oregon coast, sampling studies revealed that, as suggested by remote imagery (sea surface temperatures from AVHRR satellites), substantial and persistent variation exists in phytoplankton concentration and productivity. Due to persistent variation in nearshore oceanographic currents, certain sectors of coastline (*e.g.,* Cape Perpetua area, Three Capes area) have consistently higher summer phytoplankton concentrations than do others (*e.g.,* Cape Foulweather area, Cape Arago area) (Menge *et al.,* 1997*a*). Positively associated with these differences are differences in growth rate and abundance of filter-feeding invertebrates (mussels, barnacles) (Menge, 1992, 2002; Menge *et al.,* 1994; Sanford and Menge, 2001). Ecological performance of consumers of these common prey species such as sea stars and whelks is also positively associated with differences in bottom-up inputs. Predators are more abundant and have higher feeding rates at more productive sites (Menge, 1992; Menge *et al.,* 1994, 1996, 1997*a;* Navarrete and Menge, 1996; Navarrete *et al.,* 2000).

Similar variation has been observed on the south island of New Zealand (Menge *et al.,* 1999, 2002). Rocky intertidal communities on opposite sides of the south island experience contrasting oceanographic conditions (intermittent upwelling on the west coast, persistent downwelling on the east coast). These differences are associated with differences in rates of prey input, rates of prey growth, abundances of consumers, rates of predation on prey, and impact of predation, all of which are higher on the intermittent-upwelling coast.

We thus infer that with increased magnitude of bottom-up effects, ecological performance of both prey and consumers increases. Via trophic feedback, the higher abundances of consumers at high levels of bottom-up input have major negative impacts on prey abundance. These patterns are consistent with N/PM model predictions. Their similarity and occurrence in evolutionarily and historically distinct hemispheres suggests that comparable environmental conditions lead independently to comparable ecological structures, an observation of general significance.

LINKING ECOLOGICAL AND SUBORGANISMAL PERFORMANCE

As these examples hopefully serve to demonstrate, ecological performance can vary with environmental conditions in seemingly predictable ways. These conditions, stress or food concentration, can influence the physiological state of organisms, either by affecting the functioning and efficiency of molecular and cellular processes or by determining the rate of protein synthesis and cell multiplication. Since organismal performance (strength, activity levels, growth, feeding, survival, reproduction) ultimately depends on physiological state, we believe that full understanding of community structure and dynamics depends on understanding the linkage between ecological performance and physiological state. Further, the well-documented importance of species interactions as determinants of community structure dictates that we integrate ecological and molecular-cellular approaches in a framework of species interacting along environmental gradients.

In developing this approach, we need to address several questions. What is stress, and how is it linked to organismal response? How do we measure it in organismally relevant ways? In particular, how do we measure responses to stress before the effects are lethal? What conditions favor strong bottom-up responses by organisms? How do we quantify the nutritional state of organisms, particularly on short time scales? What are the time scales of response to variation in stress or food conditions?

Our ability to quantify environmental conditions has improved dramatically during the past decade. For example, our studies of whelk and limpet responses to stress in 1990–91 were hampered by a lack of affordable, field-deployable thermal sensors that could be used to *continuously* and *frequently* quantify environmental conditions or organismal temperature. Such devices are now readily available and miniaturization allows thermal monitoring at a frequency and detail one could only imagine a decade ago. Similarly, the advent of affordable and durable but sophisticated remote sensors for quantification of salinity, light, particulates, and fluorescence allows the continuous collection of data on food abundance and other factors at unprecedented frequency and precision. These advances, and the high rate of appearance of new and/or improved sensors set the stage for research programs that were previously impossible to conduct.

A comparably dramatic leap forward has been made in the availability of methods of quantification of physiological state, in the field, under meaningful ecological conditions. This symposium provides many relevant examples and explores the advantages and disadvantages of several measures, and examines areas where new, potentially powerful approaches are being developed.

Here we consider two of these methods, heat shock proteins (Hsp) and RNA:DNA ratios. We focus in particular on examples that have clear relevance to the issue of linking physiological condition to ecological performance, with the goals of demonstrating the potential power of such an approach, and of stimulating further, more integrated research on this issue. Our examples are taken from recent investigations of two key components of rocky intertidal communities, mussels and whelks.

Mussels in stress

The mussel *Mytilus californianus* is an ecological dominant, and a key interactor in wave-swept rocky intertidal communities along the west coast of North America (Paine, 1966, 1974, 1984; Menge *et al.*, 1994; Connolly and Roughgarden, 1998). Mussels are primary prey for sea stars (*Pisaster ochraceus*) and whelks (*Nucella* spp.) (Paine, 1974; Menge *et al.*, 1994; Navarrete and Menge, 1996; Berlow, 1999), and thus this interaction is an obvious potential target for studying the link between physiological state and ecological performance. One potentially useful tool in quantifying stress responses is the quantification of Hsp70, one of a class of proteins called molecular chaperones whose function is to refold stress-damaged proteins. Hsp70 occurs in two forms, a constitutive or normally-occurring form (abbreviated Hsc70) and an inducible form (Hsp70).

Mussels typically form a zone spanning the middle portion of the tidal gradient of relatively wave-exposed shores along the U.S. west coast. A common assumption regarding the determinants of the distributional limits of such zone-forming species is that upper limits are limited by physical environmental conditions and lower limits by biological factors (Connell, 1972). To determine if *M. californianus* occurring at the upper edge of its vertical distribution expressed elevated stress responses relative to mussels at the lower edge, Roberts *et al.* (1997) sampled mussels at upper wave-protected and lower wave-exposed edges of the mussel bed at Strawberry Hill, Oregon. Summer samples of relative levels of inducible Hsp70 isoforms were $> 3\times$ higher in the upper-protected mussels than in the lower-exposed mussels (Fig. 7 in Roberts *et al.* [1997]). In winter, these differences were absent. Relative levels were similar and low in upper-protected and lower-exposed mussels. Similar differences were observed in constitutive Hsc70 isoforms in summer and winter, except that winter levels tended to be intermediate between summertime upper-protected and lower-exposed levels.

These results thus suggest that, at least at the most severe end of an environmental stress gradient in the *M. californianus* bed, mussels respond physiologically by producing molecular chaperones to refold stress-damaged protein. Lower mussels, which are exposed to air for a shorter period and to more frequent wave splash, did not show elevated levels of Hsp70.

A follow-up study (Halpin *et al.*, 2002), showed that levels of Hsp70 in July 1999, during which air temperatures were high, were higher than in August 1999, during which cooler temperatures prevailed. In this study, a less extreme environmental gradient was sampled; mussels were collected from upper and lower levels of the mussel bed at sites of comparable, intermediate wave-exposure rather than upper-protected and lower-exposed sites. Perhaps as a consequence, patterns somewhat different from those observed by Roberts *et al.* were observed with shore level. Although low zone mussels usually had the lowest Hsp70 levels, high zone mussels did not always have the highest levels (*e.g.,* high and low mussels had similar Hsp70 levels at Boiler Bay [hereafter BB] in August, and at Strawberry Hill [hereafter SH] in July). Thus, in general these data suggest that the stress response varies through time as thermal conditions change, but that smaller scale, within-site variation can be idiosyncratic. Further study is needed to understand these complex changes.

Predators in stress

Whelks, *N. ostrina*, also responded to stress by differential synthesis of Hsp70, with whelks in more stressful conditions producing higher levels than those in less stressful conditions (Dahlhoff *et al.*, 2001). In this case, in summer months 1994, Hsp70 expression varied with site (BB *vs.* SH), exposure to waves (exposed *vs.* protected) and month (June, July, August), and was generally higher at the hotter site (SH) with the least wave splash (wave-protected) in the warmest months (July and August). Provision of shelter, in the form of empty mussel shells glued to the substratum in cages, alleviated stress (*i.e.,* snails with shelter had lower expression of Hsp70). These results were obtained from experiments in the lower mid zone at each site and exposure, in which shelter and food availability (mussels, *M. trossulus*) for the whelks were manipulated.

Mussels and food availability

Ecological evidence indicated that food concentration for filter feeders such as mussels and barnacles is consistently higher in summer at SH than at BB (Menge *et al.*, 1997*a, b*), with the apparent consequence that mussel and barnacle growth rates at SH are >2× those at BB (Menge *et al.*, 1994; Sanford and Menge, 2001). Determination of RNA:DNA ratios, an index of protein synthetic capacity or short-term growth potential, in naturally-occurring *M. californianus* at these sites, revealed that ratios were consistently higher at SH than at BB, and at wave-exposed than at wave-protected

sites (Dahlhoff and Menge, 1996). Moreover, these between-site differences could be induced to switch. In reciprocal translocation experiments, RNA:DNA ratios of BB mussels moved to SH increased to match those of native SH mussels within a month, and vice-versa. Maximum values of RNA:DNA ratios tend to coincide with maximal concentrations of phytoplankton (proxied by quantifying chlorophyll-a levels) during summer, and to reflect between-site differences (SH > BB; Dahlhoff and Menge, 1996; Menge *et al.*, 1997*a*).

Evidence suggesting that such responses are general was obtained in a similar study on the south island of New Zealand (Menge *et al.*, 1999). For the mussels *Perna canaliculus* (a native species) and *M. galloprovincialis* (an introduced species), RNA:DNA ratios were higher at a more productive, intermittent upwelling region on the west coast than at a less productive, downwelling region on the east coast. As in Oregon, ratios of reciprocally-translocated mussels diverged from those at their sites of origin and converged with those at the translocation sites.

Whelks and food availability

Whelk (*N. ostrina*) RNA:DNA ratios also responded positively to food availability (Dahlhoff *et al.*, 2001). Naturally-occurring *Nucella* sampled in July and November 1993 and February and July 1994 had higher ratios at SH than at BB in all but the November 1993 sample (when ratios were equal). In addition, metabolic activity as determined using estimates of malate dehydrogenase, an enzyme involved in both aerobic and anaerobic pathways of ATP generation, and respiration rates were also greater at SH. Thus, whelk RNA:DNA ratios and metabolism were elevated at the site with higher food availability. Note that these higher rates in apparent responses to food paralleled higher expression of Hsp70 in apparent response to higher stress levels.

DISCUSSION

We have advocated an intensified, integrative approach to the understanding of community dynamics based on ecological studies that incorporate quantification of physiological mechanisms using new technology and recent scientific advances. In particular, determination of how eco-physiological linkages vary along two major environmental gradients, stress and productivity, seems central to understanding a host of pressing ecological questions. Such efforts can also identify intriguing new issues and raise new questions. Below, we first discuss the implications of our tests of the predictions of environmental stress models, then examine the insights obtained by recent efforts to determine the sub-organismal mechanisms of ecological responses, and finally consider unresolved issues and future directions for research.

Experimental tests of stress models

Depending on the scale of the effect, experimental results seemed consistent with both CSM and PSM

predictions. On the smaller scales at which we varied stress (artificial shelters, opposite sides of blocks, different tide levels), as predicted by the CSM, whelks and especially limpets often reduced feeding rates with elevated stress (Figs. 5, 7). The smallest source of stress modification, the shelters (~25 cm^2 area covered), were associated with increased whelk predation in the high (but not low) zone, although the effect was relatively weak (Fig. 6). This effect, with the recent demonstration that the availability of small shelters (mussel shells glued to the rock) was associated with lower Hsp70 concentrations in *N. ostrina* on the Oregon coast (Dahlhoff *et al.*, 2001), suggests that such shelters may provide ecologically meaningful refuges from thermal stress and thereby alter the intensity of species interactions.

In contrast, shelters had no effect on limpet grazing (Figs. 6, 7). This may signify that shelter at this small scale is not of much use to limpets, and indeed, in the field, limpets are often found out in the open away from small shaded microsites. Alternatively, these shelters may have been poor mimics of the kinds of small-scale shelters that limpets would use normally, such as crevices or the spaces under algal fronds. The New Zealand limpet *Cellana ornata*, for instance, had higher levels of Hsp70 when out in the open on horizontal rock benches than when hidden in narrow crevices (Halpin *et al.*, 2002). In hindsight, we believe that the artificial shelters would probably have been more effective with both types of consumer if they had been just high enough (~5 mm for limpets, ~10 mm for whelks) for the consumers to fit under them instead of having ~30 mm of space between the consumer and the roof of the shelter.

With the exception of high whelk treatments, shady sides of blocks ($\sim1,000$ cm^2 area) were associated with relatively consistently enhanced feeding rates (Figs. 5, 7). Shade alleviation of physiological stress responses in the intertidal has been recently demonstrated for the mussel *M. californianus* in Monterey Bay, California (Helmuth and Hofmann, 2001). These and the whelk results suggest that vertical relief (boulders, channels, outcrops) in the intertidal creates a mosaic of meaningful thermal heterogeneity in stress conditions in this habitat. Thus, for example, in regions where high thermal stress is a common environmental condition during low tide, shores of high topographic complexity might be expected to have greater patchiness in the intensity of species interactions, and possibly higher overall grazing and predation rates than shores of low topographic complexity. Interestingly, consistent with this hypothesis, our Strawberry Hill, Oregon study site has substantially higher predation and grazing rates than does our Boiler Bay site, and Strawberry Hill also has substantially higher topographic complexity (Menge *et al.*, 1994; Navarrete and Menge, 1996; Menge, 2000). However, these sites also differ in oceanographic conditions in ways that are consistent with a bottom-up effect on predation and grazing rates (Menge *et al.*, 1997*a*, *b*; Menge, 2002), see **Testing the Models: Nu-**

trient/Productivity Effects). It would be revealing to carry out experiments designed to separate the relative impacts of bottom-up *vs.* thermal heterogeneity effects due to topographic complexity on the strength of species interactions.

For limpets, at least, high intertidal conditions were associated with sharp reductions in grazing rate, presumably because of longer periods of exposure to thermal stress while emersed. In Oregon, high intertidal limpets (*L. digitalis*) had elevated levels of Hsp70 relative to mid intertidal limpets (Halpin *et al.*, 2002), a pattern consistent with the reduced grazing rates of *L. pelta* seen on San Juan Island (Fig. 7). These results imply a stress-induced vertical gradient in grazing impact, although this gradient would also depend on limpet density, species composition, and effects of species interactions on limpets as well. Experiments that simultaneously examined limpet grazing effects and physiological responses along stress gradients would be welcome.

In contrast to the limpet results, overall whelk predation rate did not vary with tidal height (Table 2). That is, *N. ostrina* predation rate seems insensitive to the longer exposure to air at high tide levels, although in the experiment with warm weather conditions whelks on sun-exposed sides of blocks did respond with reduced feeding (Fig. 6). Whelks at more wave-sheltered sites on the Oregon coast had higher levels of Hsp70 than did whelks at more wave-exposed sites (Dahlhoff *et al.*, 2001), but to our knowledge no analyses of whelk heat-shock response have been done along a vertical tidal gradient. Further research will be necessary to understand this unexpected result.

In some respects the most surprising results of the whelk and limpet experiments was the strong and uniform response of feeding rate to weather conditions. From a metabolic rate standpoint, it makes sense that feeding rates should be elevated during warmer weather conditions. Recent laboratory experimental results with whelks and sea stars are consistent with our field experimental results: whelks (and sea stars) fed faster under continuously warm (12°C) water conditions compared to continuously cold (9°C) water conditions (Sanford, 2002), a difference that was maintained until the predators became satiated. To us, however, the surprise is that the effect on feeding of warmer weather conditions should be so large, especially since these consumers are most active during high tides when water temperatures were presumably low.

As noted earlier, we did not have temperature sensors available during our 1990–91 studies, but recent measurements taken in 2000–2001 by Drs. M. Dethier and S. Williams at Colin's Cove (see Dethier website: http://faculty.washington.edu/mdethier/) provide some insight into the air and water temperatures that can occur at this site. During July and August 2000, for example, water temperatures at Colin's Cove were relatively invariant, ranging between 10–11°C. Air temperatures, in contrast, were much more variable and higher, being commonly in the mid to high 20's and

ranging as high as 36°C. Thus feeding rates seemed more responsive to air temperatures than to water temperatures. This conclusion raises many additional questions that can only be resolved with additional study. It seems clear however, that thermal influences on rates of key processes in interacting organisms are complex, and can have non-intuitive effects.

Is the response to weather conditions consistent with PSM predictions? That is, are the elevated feeding rates in warm weather an indication that consumers are relatively less responsive than prey to thermal stress, or are the high rates simply a reflection of elevated metabolism at high temperature with no significance with respect to species interactions? Unfortunately, we cannot answer this question without additional study and measurement (on both prey and consumers simultaneously). What does remain clear from the ecological experiments and the relevant recent physiological measurements is that overlaid on this general climatic influence on feeding is a clear response of consumers to thermal stress that is consistent with the CSM: stressful conditions reduced feeding.

We conclude that, with the parallel ecological responses summarized above, the recent examples of sub-organismal responses to stress and to food availability in both prey and consumers in a rocky intertidal setting are consistent with our suggestion that such measures can help serve to link ecological dynamics to physiological mechanisms. Ecological responses of mussels and whelks (*e.g.,* lower growth and feeding rates) to stressful conditions (high temperature, low moisture) were associated with increases in the levels of molecular chaperones (inducible Hsp70). Ecological responses of mussels and whelks (*e.g.,* higher growth and feeding rates) to higher food concentrations were associated with increases in their protein synthetic capacity (*e.g.,* higher RNA:DNA ratios). These relationships seemingly set the stage for integrative, interdisciplinary studies of the community consequences of species interactions in the context of gradients in environmental stress and productivity.

Unresolved issues

Although we are excited and optimistic about the prospects for major progress in the testing these ideas, we also note the need for further exploration and development of these techniques. As others in this symposium have noted, for example, there remain certain inconsistencies in some data sets that make it clear that we still do not fully understand molecular-level responses to stress and food availability.

In the heat-shock response, for example, there remain questions of scale in both space and time. In view of the results of Roberts *et al.* (1997), Halpin and coworkers (Halpin *et al.*, 2002) were surprised to observe the inconsistent pattern of Hsp70 expression in mussels with tidal elevation at Boiler Bay and Strawberry Hill. These results suggest that there remains much to learn about the link between physiological state and ecological conditions. The variable results

could have occurred as a consequence of a lack of conditions during the period prior to sampling that were sufficiently stressful to induce Hsp70, or to our sampling across an environmental gradient that spanned only a narrow range of conditions. Similarly, in a study of the response of chitons (*Katharina tunicata*) to thermal stress, Burnaford (2001) observed that Hsp70 increased when tides shifted from nighttime to daytime in spring. In field experiments in which stress levels were manipulated using shaded *vs.* unshaded treatments, however, she found no change in inducible Hsp70 expression on either shorter- (weeks) or longer-term (months) time scales. Although some work suggests that the response to stress can be rapid, on the scale of hours (Hofmann and Somero, 1996), seasonal differences can persist for weeks to months (*e.g.,* Burnaford, 2001). We suggest that additional work is needed to understand both the spatial and temporal scales of the heat-shock response. A critically important aspect of this work must be the quantification of thermal stress conditions and organismal thermal response at high temporal and spatial resolution.

A second issue, hinted at earlier, concerns the relative roles of Hsp70 and Hsc70. One possible reason why standing-stock levels of heat shock proteins sometimes yield equivocal results is that molecular chaperones have two roles, both doing normal ''housekeeping'' protein synthesis and repairing damaged proteins following stress. Even more complex, both constitutive (Hsc70) and inducible (Hsp70) isoforms may serve both roles. For example, conditions favoring rapid growth may lead to high standing-stock levels of Hsc70 in support of protein synthesis. If the organism is heat-stressed, this high stock of Hsc70 may be able to handle the damaged protein and strong induction of Hsp70 is not needed. Conversely, with low rates of protein synthesis, an organism may have low stocks of Hsc70, and if stressed, may have to synthesize large amounts of Hsp70 to cope with damaged protein. Thus, high levels of Hsc70 may reflect rapid recent growth while high levels of Hsp70 may reflect high recent thermal stress, and if these isoforms are not distinguished, interpretations may be ambiguous. Fortunately, the two isoforms have slightly different molecular weights and can, and in future work should be, distinguished to help sharpen the resolution of this valuable tool.

Similar considerations apply to RNA:DNA ratio responses. For example, we still have a poor understanding of the temporal scale of the RNA:DNA response. The translocation experiments summarized above suggest that mussel ratios can change within one to two months, but the lack of data sampled at a higher temporal resolution prevents a more precise estimate of the response. Further, because they do not distinguish between ribosomal RNA, transfer RNA, and messenger RNA, RNA:DNA ratios are a relatively crude index of protein synthetic capacity. RNAs associated with the ribosomes (rRNA and tRNA) should turn over more slowly than mRNA, so fluctuations in total RNA

are not highly sensitive to the level of protein synthesis underway. Such problems may underlie some unexplained variation that usually occurs in RNA:DNA ratio studies of the relation between food, growth, and protein synthetic capacity (Dahlhoff and Menge, 1996; Menge *et al.*, 1997*a*, 1999). Thus, while analyses of RNA:DNA ratios in relation to feeding rates and food availability have provided valuable insights, we need to improve the ability of this tool to detect protein synthesis.

Future directions

We believe that we are poised to make significant advances in understanding the links among ecological conditions, performance responses of consumers and prey, and the sub-organismal mechanisms that underlie these responses. We envision two avenues of approach. The first is the continuation of research into the molecular and physiological aspects of organismal responses to stress and food abundance, exemplified by other papers in this symposium (*e.g.,* Hofmann, Dahlhoff, Tomanek, Somero). The second is the integration of the approaches and techniques of these mechanistic studies into a more explicitly ecological context, as suggested by several other papers in this symposium (*e.g.,* Sanford, Helmuth, Halpin).

Specifically, with respect to the former approach, we anticipate major advancement towards the addition of more powerful tools in the study of responses to stress and food. As noted above, methods exist that allow the more precise distinction between constitutive and inducible isoforms of heat shock proteins. Two-dimensional gel analysis, for instance, could be used to sort out the different isoforms, and to determine the relative amounts of each. More detailed study of the synthetic pathways leading to Hsps, and ultimately identifying and being able to manipulate the genes involved would greatly enhance the power of this approach (*e.g.,* Hofmann, 2002; Buckley *et al.*, 2001). Similarly, new methods for examining mRNA in the cell, and the ability to analyze environmental effects on gene expression and protein synthesis using DNA "chips" (*e.g.,* Somero, 2002) would dramatically advance our ability to study environmental effects of stress and food availability.

With respect to the latter, mechanistic/ecological, approach, we envision comparative-experimental, field-based and lab-complemented studies carried out in the context of gradients in environmental stress and productivity. For example, to determine the ecological and physiological factors underlying local-scale distributional boundaries, translocation experiments are needed that challenge the physiological state of species by placing them beyond the observed distributional limit. We note that simply quantifying the physiological state of mussels at the upper limit, and observing that they are close to tolerance limits determined in laboratory experiments is insufficient evidence in support of the hypothesis of direct limitation by stress. It is possible for instance that despite a stressed physio-

logical state, adult mussels can survive, grow and reproduce above their normal limit, but that recruits simply do not settle there. Or that adults but not juveniles can survive above the normal adult limit. The point is that field experimentation is necessary to evaluate such hypotheses.

Ecological experiments alone, however, are also limited in the insight they provide in such a scenario. If the translocated animals die, for example, we don't know why. If they survive, we do not know if they can persist, grow, or reproduce without performing long-term studies, with uncertainty about how long is "long enough." The availability of molecular tools to quantify physiological state *combined* with field experiments, however, provides a potentially powerful, and far more insightful approach to such questions.

The latter (combined) avenue for future research is perhaps the most exciting, as well as challenging; that is, the combination of ecological and physiological approaches that we advocate here in addressing community-level changes expected under a scenario of global warming (Lubchenco *et al.*, 1993). Although mitigation of such effects might be unfeasible, we will never be able to develop possible anticipatory strategies unless we understand what will and what will not happen, ecologically and physiologically. Of course, for accurate prediction we must have reliable atmospheric models that can forecast expected changes in environmental conditions at the regional, and ideally local scale. But even in the absence of such models, we can obtain understanding that may allow prediction of community change under alternative scenarios.

For example, if warming of air and seawater occurs along the US west coast, intertidal species will undoubtedly be affected, and shifts in vertical or latitudinal distribution might be expected. Mussels, for instance, could experience higher stress at upper levels of the shore and more severe predation at lower levels of the shore (because predators may feed faster in warmer waters; Sanford, 1999). If the upper limit of predation overlapped with the upper limit of physiological tolerance, mussel beds could disappear from rocky shores. Although myriad other changes and effects are possible, the point is that any hope we have of understanding the biotic consequences of climate change will depend on a marriage between ecological and physiological approaches. We are just beginning.

CONCLUSIONS

As is clear from these examples, and many of the papers in this symposium, the linkage between ecological responses and both the heat-shock response and the short-term capacity for protein synthesis (RNA: DNA ratio) needs further exploration and definition. Nonetheless, the evidence suggests that the molecular measures often can closely reflect measures of ecological performance that are quantifiable at the individual and population level. More importantly, perhaps, the measures can detect changes in the internal state of organisms very shortly after environmental conditions

change (hours to weeks). That is, such measures detect physiological changes on time scales that are generally too brief to observe responses such as growth, increased reproduction, diminished activity or increased sheltering to changing ecological conditions. We urge, and strongly support an increase in and intensification of research aimed at linking ecological, physiological, and molecular approaches to the study of community dynamics. Such efforts hold great promise for a more rigorous understanding of the interplay between organisms and environment, and how these generate patterns of distribution, abundance and diversity in both natural and human-modified communities.

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