

Publications

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Now in Print and Online

- ❖ Burford, M. O., G. Bernardi and M. H. Carr (2011). "Analysis of individual year-classes of a marine fish reveals little evidence of first generation hybrids between cryptic species in sympatric regions" Marine Biology 158: 1815-1827. <http://dx.doi.org/10.1007/s00227-011-1694-7>

As settled juveniles and adults, blue rockfish (*Sebastes mystinus*) are nonmigratory inhabitants of kelp and rocky reef habitats along the California coast, USA, and prior to settlement, they possess a pelagic larval and juvenile stage lasting 3-5 months. A previous study of adults revealed two cryptic species within *S. mystinus* and evidence of reproductive isolation in a region where both cryptic adults co-occur. Given this pattern of reproductive isolation, we investigated the degree of hybridization or introgression in individual year-classes shortly after juvenile settlement in two different years (2001 and 2002). Using microsatellite markers, we found little indication of hybridization in new juvenile year-classes despite an adult population that comprised both cryptic species. However, we found an average of two percent of hybrid or introgressed individuals in regions with a low frequency of one of the two species. Therefore, while the lack of hybrids or introgression supports the hypothesis of reproductive isolation between the cryptic species within *S. mystinus*, the age-structured analysis also revealed a spatial pattern of low-frequency differences in the number of introgressed individuals. These results suggest that reproductive barriers may breakdown when one of the two species predominates the regional adult gene pool.

- ❖ Caselle, J. E., S. L. Hamilton, D. M. Schroeder, M. S. Love, J. D. Standish, J. A. Rosales-Casián and O. Sosa-Nishizaki (2011). "Geographic variation in density, demography, and life history traits of a harvested, temperate, sex-changing reef fish." Canadian Journal of Fisheries and Aquatic Sciences 68(2): 288-303. <http://dx.doi.org/10.1139/F10-140>

Geographic variation in ecological and environmental factors may lead to intraspecific differences among populations. For the California sheephead (*Semicossyphus pulcher*), an important predator in kelp forests and a target of commercial and recreational fisheries, we evaluated the degree to which different populations exhibited variation in density, demography, and life history traits. We assessed biogeographic patterns of abundance through underwater visual census at 39 sites spanning a major portion of the species range (southern California, USA, to Baja California, Mexico) and made collections from seven focal sites to investigate geographic differences in demography and life histories. California sheephead densities were

significantly greater in the southern part of their range and at offshore islands than along the mainland coast. At the focal sites, we found significant spatial variation in density, fecundity, size structure, growth rates, annual survivorship, and the timing of maturation and sex change. Density- and temperature-dependent effects helped to explain the intraspecific differences in these parameters. Studies such as this one will allow for demographic plasticity to be incorporated into future stock assessments. Management of temperate reef fishes may best be achieved on smaller spatial scales as we increase our understanding of geographic variation among populations.

- ❖ Denny, M. W. and L. Benedetti-Cecchi (2011). "Scaling up in ecology: Mechanistic approaches." Annual Review of Ecology, Evolution, and Systematics 42 (Expected final online publication date for the Annual Review of Ecology, Evolution, and Systematics Volume 42 is November 2, 2011). <http://dx.doi.org/10.1146/annurev-ecolsys-102710-145103>

Ecologists have long grappled with the problem of scaling up from tractable, small-scale observations and experiments to the prediction of large-scale patterns. Although there are multiple approaches to this formidable task, they share a common underpinning in the formulation, testing, and use of mechanistic response functions to describe how phenomena are related across scales. Here, we review the basics of response functions to illustrate how they provide a means to quantify our understanding of the world, guide research when our understanding is inadequate, extrapolate beyond measured data, and simplify our conceptual grasp of reality. We illustrate these conclusions with examples of how mechanistic responses functions can contribute to accurate large-scale, long-term predictions through their implementation in theories of scale transition, self-organization, random walks, and environmental bootstrapping.

- ❖ Doney, S. C., M. Ruckelshaus, J. E. Duffy, J. P. Barry, F. Chan, C. A. English, H. M. Galindo, J. M. Grebmeier, A. B. Hollowed, N. Knowlton, J. Polovina, N. N. Rabalais, W. J. Sydeman and L. D. Talley (2011). "Climate change impacts on marine ecosystems." Annual Reviews of Marine Science 4. <http://www.annualreviews.org/doi/pdf/10.1146/annurev-marine-041911-111611>

In marine ecosystems, rising atmospheric CO₂ and climate change are associated with concurrent shifts in temperature, circulation, stratification, nutrient input, oxygen content, and ocean acidification, with potentially wideranging biological effects. Population-level shifts are occurring because of physiological intolerance to new environments, altered dispersal patterns, and changes in species interactions. Together with local climate-driven invasion and extinction, these processes result in altered community structure and diversity, including possible emergence of novel ecosystems. Impacts are particularly striking for the poles and the tropics, because of the sensitivity of polar ecosystems to sea-ice retreat and poleward species migrations as well as the sensitivity of coral-algal symbiosis to minor increases in temperature. Midlatitude upwelling systems, like the California Current, exhibit strong linkages between climate and species distributions, phenology, and demography. Aggregated effects may modify energy and material flows as well as biogeochemical cycles, eventually impacting the overall ecosystem functioning and services upon which people and societies depend.

- ❖ Figsurski, J. D., D. Malone, J. R. Lacy and M. Denny (2011). "An inexpensive instrument for measuring wave exposure and water velocity." Limnology and Oceanography: Methods 9: 204-214. <http://dx.doi.org/10.4319/lom.2011.9.204>

Ocean waves drive a wide variety of nearshore physical processes, structuring entire ecosystems through their direct and indirect effects on the settlement, behavior, and survivorship of marine organisms. However, wave exposure remains difficult and expensive to measure. Here, we report on an inexpensive and easily constructed instrument for measuring wave-induced water velocities. The underwater relative swell kinetics instrument (URSKI) is a subsurface float tethered by a short (<1 m) line to the seafloor. Contained within the float is an accelerometer that records the tilt of the float in response to passing waves. During two field trials totaling 358 h, we confirmed the accuracy and precision of URSKI measurements through comparison to velocities measured by an in situ acoustic Doppler velocimeter and those predicted by a standard swell model, and we evaluated how the dimensions of the devices, its buoyancy, and sampling frequency can be modified for use in a variety of environments.

- ❖ Gouhier, T. C., B. A. Menge and S. D. Hacker (2011). "Recruitment facilitation can promote coexistence and buffer population growth in metacommunities." *Ecology Letters* **online**. <http://dx.doi.org/10.1111/j.1461-0248.2011.01690.x>

Although positive species interactions are ubiquitous in nature, theory has generally focused on the role of negative interactions to explain patterns of species diversity. Here, we incorporate recruitment facilitation, a positive interaction prevalent in marine and terrestrial systems, into a metacommunity framework to assess how the interplay between colonisation, competition and facilitation mediates coexistence. We show that when subordinate species facilitate the recruitment of dominant species, multi-species metacommunities can persist stably even if the colonisation rate of the dominant species is greater than that of the subordinate species. In addition, recruitment facilitation can buffer population growth from changes in colonisation rates, and thus explain the paradoxical mismatch between patterns of abundance and recruitment in marine systems. Overall, our results demonstrate that recruitment facilitation can have profound effects on the assembly, dissolution and regulation of metacommunities by mediating the relative influence of local and regional processes on population abundance and species diversity.

- ❖ Hamilton, S. L., J. E. Caselle, C. A. Lantz, T. L. Egloff, E. Kondo, S. D. Newsome, K. Loke-Smith, D. J. Pondella II, K. A. Young and C. G. Lowe (2011). "Extensive geographic and ontogenetic variation characterizes the trophic ecology of a temperate reef fish on southern California (USA) rocky reefs." *Marine Ecology Progress Series* **429**: 227-244. <http://dx.doi.org/10.3354/meps09086>

Interactions between predator and prey act to shape the structure of ecological communities, and these interactions can differ across space. California sheephead *Semicossyphus pulcher* are common predators of benthic invertebrates in kelp beds and rocky reefs in southern California, USA. Through gut content and stable isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) analyses, we investigated geographic and ontogenetic variation in trophic ecology across 9 populations located at island and mainland sites throughout southern California. We found extensive geographic variation in California sheephead diet composition over small spatial scales. Populations differed in the proportion of sessile filter/suspension feeders or mobile invertebrates in the diet. Spatial variation in diet was highly correlated with other life history and demographic traits (e.g. growth, survivorship, reproductive condition, and energy storage), in addition to proxies of prey availability from community surveys. Multivariate descriptions of the diet from gut contents roughly agreed with the spatial groupings of sites based on stable isotope analysis of both California sheephead and their prey. Ontogenetic changes in diet occurred consistently across populations, despite spatial differences in size structure. As California sheephead increase in size, diets shift from small filter feeders, like bivalves, to larger mobile invertebrates, such as sea urchins. Our results indicate that locations with large California sheephead present, such as many marine reserves, may experience increased predation pressure on sea urchins, which could ultimately affect kelp persistence.

- ❖ Hamilton, S. L., J. R. Wilson, T. Ben-Horin and J. E. Caselle (2011). "Utilizing spatial demographic and life history variation to optimize sustainable yield of a temperate sex-changing fish " *PLoS ONE* **6**(9): e24580. <http://dx.doi.org/10.1371/journal.pone.0024580>

Fish populations vary geographically in demography and life history due to environmental and ecological processes and in response to exploitation. However, population dynamic models and stock assessments, used to manage fisheries, rarely explicitly incorporate spatial variation to inform management decisions. Here, we describe extensive geographic variation in several demographic and life history characteristics (e.g., size structure, growth, survivorship, maturation, and sex change) of California sheephead (*Semicossyphus pulcher*), a temperate rocky reef fish targeted by recreational and commercial fisheries. Fish were sampled from nine locations throughout southern California in 2007–2008. We developed a dynamic size and age-structured model, parameterized separately for each location, to assess the potential cost or benefit in terms of fisheries yield and conservation objectives of changing minimum size limits and/or fishing mortality rates (compared to the status quo). Results indicate that managing populations individually, with location-specific regulations, could increase yield by over 26% while maintaining conservative levels of spawning biomass. While this local management approach would be challenging to implement in practice, we found statistically similar increases in yield could be achieved by dividing southern California into two separate management regions, reflecting geographic similarities in demography. To maximize yield, size limits should be increased

by 90 mm in the northern region and held at current levels in the south. We also found that managing the fishery as one single stock (the status quo), but with a size limit 50 mm greater than the current regulations, could increase overall fishery yield by 15%. Increases in size limits are predicted to enhance fishery yield and may also have important ecological consequences for the predatory role of sheephead in kelp forests. This framework for incorporating demographic variation into fisheries models can be exported generally to other species and may aid in identifying the appropriate spatial scales for fisheries management.

- ❖ Iles, A. C., T. C. Gouhier, B. A. Menge, J. S. Stewart, A. J. Haupt and M. C. Lynch (2011). "Climate-driven trends and ecological implications of event-scale upwelling in the California Current System." Global Change Biology. <http://dx.doi.org/10.1111/j.1365-2486.2011.02567.x>

Eastern boundary current systems are among the most productive and lucrative ecosystems on Earth because they benefit from upwelling currents. Upwelling currents subsidize the base of the coastal food web by bringing deep, cold and nutrient-rich water to the surface. As upwelling is driven by large-scale atmospheric patterns, global climate change has the potential to affect a wide range of significant ecological processes through changes in water chemistry, water temperature, and the transport processes that influence species dispersal and recruitment. We examined long-term trends in the frequency, duration, and strength of continuous upwelling events for the Oregon and California regions of the California Current System in the eastern Pacific Ocean. We then associated event-scale upwelling with up to 21 years of barnacle and mussel recruitment, and water temperature data measured at rocky intertidal field sites along the Oregon coast. Our analyses suggest that upwelling events are changing in ways that are consistent with climate change predictions: upwelling events are becoming less frequent, stronger, and longer in duration. Additionally, upwelling events have a quasi-instantaneous and cumulative effect on rocky intertidal water temperatures, with longer events leading to colder temperatures. Longer, more persistent upwelling events were negatively associated with barnacle recruitment but positively associated with mussel recruitment. However, since barnacles facilitate mussel recruitment by providing attachment sites, increased upwelling persistence could have indirect negative impacts on mussel populations. Overall, our results indicate that changes in coastal upwelling that are consistent with climate change predictions are altering the tempo and the mode of environmental forcing in nearshore ecosystems, with potentially severe and discontinuous ramifications for ecosystem structure and functioning.

- ❖ Kim, S. and J. A. Barth (2011). "Connectivity and larval dispersal along the Oregon coast estimated by numerical simulations." Journal of Geographical Research-Ocean **116**: C06002. <http://dx.doi.org/10.1029/2010JC006741>

Key Points

- Cape Perpetua is a place for highest self recruitment
- Heceta Bank region has high probabilities as source/destination for settlement
- Best timing for larvae settlement is correlated with averaged alongshore wind

Connectivity and larval dispersal is explored off the Oregon coast during the summer upwelling season of 2001 using numerical ocean circulation simulations. The study region, with strong wind-driven currents and variable topography, is modeled using the Regional Ocean Modeling System (ROMS) forced by the Coupled Ocean Atmosphere Mesoscale Prediction System. A large number of passive particles as models of planktonic larvae are released daily for 120 days from 1 May to 28 August at depths of 1, 7, 15, 20, 50, and 75 m at every grid point shoreward of the 200 m isobath (on average 32 km offshore). The particles are transported by the three-dimensional currents of the model simulation. The competency time window for larval settlement is assumed to be in between days 15 and 35 after larvae are released. Larval settlement occurs at the shallowest location during the competency time window. Connectivity matrices reveal that some of the places of highest retention are similar to the proposed Oregon marine reserve sites, especially Cape Perpetua. The Heceta Bank region has high probabilities as both a source and a destination for settled larvae. Larvae released in the Heceta Bank region often settle at higher latitudes than their release location. There are strong correlations between the number of settled larvae shallower than the 50 m isobath and a 6 to 8 day running mean of the alongshore wind stress. Larvae are retained near the shore when the winds, averaged over the previous 6 to 8 days, are relaxed or downwelling favorable.

- ❖ Lockwood, B. L. and G. N. Somero (2011). "Invasive and native blue mussels (genus *Mytilus*) on the California coast: The role of physiology in a biological invasion " Journal of Experimental Marine Biology & Ecology **400**: 167-174. <http://dx.doi.org/10.1016/j.jembe.2011.02.022>

The Mediterranean blue mussel, *Mytilus galloprovincialis*, is an invasive species that has displaced a congener, *Mytilus trossulus*, from its native range in central and southern California, USA. The dynamic relationship between interspecies competition and species-specific tolerances to abiotic factors, such as temperature and salinity, appears to have facilitated the success but has also imposed limits on the spread of this biological invasion. Here, we review the literature and present new data that document physiological differences between *M. galloprovincialis* and *M. trossulus*. In all comparisons, *M. galloprovincialis* is more warm-adapted than *M. trossulus*. Higher activities of enzymes involved in ATP generation show that the native *M. trossulus* is better adapted to colder conditions than *M. galloprovincialis*. Higher metabolic capacity (temperature compensation) in the native species may, however, lead to higher metabolic costs at sites where the two species co-occur. In addition, *M. trossulus* has a lower thermal tolerance of cardiac function and substrate binding by enzymes than *M. galloprovincialis*. The higher thermal tolerance of the invasive species is likely due in part to its enhanced ability to induce changes in the expression of particular genes and proteins in response to acute heat stress. Taken together, these data predict that *M. galloprovincialis* will continue to be the dominant blue mussel species along the warmer range of the California Current. Because the northern biogeographic limit of *M. galloprovincialis* is not stable, but rather shifts to lower or higher latitudes in concert with oceanographic variability, it is important to further characterize the physiological constraints of *M. galloprovincialis*, related to its sensitivity to cold temperatures and low salinities.

- ❖ Lockwood, B. L. and G. N. Somero (2011). "Transcriptomic responses to salinity stress in invasive and native blue mussels (genus *Mytilus*)." Molecular Ecology **20**: 517-529. <http://dx.doi.org/10.1111/j.1365-294X.2010.04973.x>

The invasive marine mussel *Mytilus galloprovincialis* has displaced the native congener *Mytilus trossulus* from central and southern California, but the native species remains dominant at more northerly sites that have high levels of freshwater input. To determine the extent to which interspecific differences in physiological tolerance to low salinity might explain limits to the invasive species' biogeography, we used an oligonucleotide microarray to compare the transcriptional responses of these two species to an acute decrease in salinity. Among 6777 genes on the microarray, 117 genes showed significant changes that were similar between species, and 12 genes showed significant species-specific responses to salinity stress. Osmoregulation and cell cycle control were important aspects of the shared transcriptomic response to salinity stress, whereas the genes with species-specific expression patterns were involved in mRNA splicing, polyamine synthesis, exocytosis, translation, cell adhesion, and cell signalling. Forty-five genes that changed expression significantly during salinity stress also changed expression during heat stress, but the direction of change in expression was typically opposite for the two forms of stress. These results (i) provide insights into the role of changes in gene expression in establishing physiological tolerance to acute decreases in salinity, and (ii) indicate that transcriptomic differences between *M. galloprovincialis* and *M. trossulus* in response to salinity stress are subtle and involve only a minor fraction of the overall suite of gene regulatory responses.

- ❖ Logan, C. A. and G. N. Somero (2011). "Effects of thermal acclimation on transcriptional responses to acute heat stress in the eurythermal fish *Gillichthys mirabilis* (Cooper)." American Journal of Physiology, Regulatory, Integrative and Comparative Physiology **300**(6): R1373-R1383. <http://dx.doi.org/10.1152/ajpregu.00689.2010>

The capacities of eurythermal ectotherms to withstand wide ranges of temperature are based, in part, on abilities to modulate gene expression as body temperature changes, notably genes encoding proteins of the cellular stress response. Here, using a complementary DNA microarray, we investigated the sequence in which cellular stress response-linked genes are expressed during acute heat stress, to elucidate how severity of stress affects the categories of genes changing expression. We also studied how prior acclimation history affected gene expression in response to acute heat stress. Eurythermal goby fish (*Gillichthys mirabilis*) were acclimated to 9 ± 0.5 , 19 ± 0.5 , and $28 \pm 0.5^\circ\text{C}$ for 1 mo. Then fish were given an acute heat ramp ($4^\circ\text{C}/\text{h}$), and gill tissues were sampled every $+4^\circ\text{C}$ to monitor gene expression. The average onset temperature for a significant change in expression during acute stress increased by $\sim 2^\circ\text{C}$ for each $\sim 10^\circ\text{C}$ increase in acclimation

temperature. For some genes, warm acclimation appeared to obviate the need for expression change until the most extreme temperatures were reached. Sequential expression of different categories of genes reflected severity of stress. Regardless of acclimation temperature, the gene encoding heat shock protein 70 (HSP70) was upregulated strongly during mild stress; the gene encoding the proteolytic protein ubiquitin (UBIQ) was upregulated at slightly higher temperatures; and a gene encoding a protein involved in cell cycle arrest and apoptosis, cyclin-dependent kinase inhibitor 1B (CDKN1B), was upregulated only under extreme stress. The tiered, stress level-related expression patterns and the effects of acclimation on induction temperature yield new insights into the fundamental mechanisms of eurythermy.

- ❖ Mach, K. J., S. K. Tepler, A. V. Staaf, J. C. Bohnhoff and M. W. Denny (2011). "Failure by fatigue in the field: a model of fatigue breakage for the macroalga *Mazzaella*, with validation." *The Journal of Experimental Biology* **214**: 1571-1585. <http://dx.doi.org/10.1242/jeb.051623>

Seaweeds inhabiting the extreme hydrodynamic environment of wave-swept shores break frequently. However, traditional biomechanical analyses, evaluating breakage due to the largest individual waves, have perennially underestimated rates of macroalgal breakage. Recent laboratory testing has established that some seaweeds fail by fatigue, accumulating damage over a series of force impositions. Failure by fatigue may thus account, in part, for the discrepancy between prior breakage predictions, based on individual not repeated wave forces, and reality. Nonetheless, the degree to which fatigue breaks seaweeds on wave-swept shores remains unknown. Here, we developed a model of fatigue breakage due to wave-induced forces for the macroalga *Mazzaella flaccida*. To test model performance, we made extensive measurements of *M. flaccida* breakage and of wave-induced velocities experienced by the macroalga. The fatigue-breakage model accounted for significantly more breakage than traditional prediction methods. For life history phases modeled most accurately, 105% (for female gametophytes) and 79% (for tetrasporophytes) of field-observed breakage was predicted, on average. When *M. flaccida* fronds displayed attributes such as temperature stress and substantial tattering, the fatigue-breakage model underestimated breakage, suggesting that these attributes weaken fronds and lead to more rapid breakage. Exposure to waves had the greatest influence on model performance. At the most wave-protected sites, the model underpredicted breakage, and at the most wave-exposed sites, it overpredicted breakage. Overall, our fatigue-breakage model strongly suggests that, in addition to occurring predictably in the laboratory, fatigue-induced breakage of *M. flaccida* occurs on wave-swept shores.

- ❖ Menge, B. A., T. C. Gouhier, T. Freidenburg and J. Lubchenco (2011). "Linking long-term, large-scale climatic and environmental variability to patterns of marine invertebrate recruitment: Toward explaining "unexplained" variation." *Journal of Experimental Marine Biology and Ecology* **400**: 236-249. <http://dx.doi.org/10.1016/j.jembe.2011.02.003>

The rate of input of new individuals into communities is a key component of community dynamics. Detection of ecosystem responsiveness to climatic perturbations such as El Niño-Southern Oscillation (ENSO), Pacific Decadal Oscillation (PDO) and North Pacific Gyre Oscillation (NPGO) can provide insight into how ecosystems will respond to climate change. Although these climate patterns are ocean-based, understanding of their influences on key ecosystem processes in temperate coastal marine ecosystems is limited. Recent analyses documented orders-of-magnitude increases in mussel recruitment in the 2000s relative to the previous decade. To evaluate the generality of this pattern across other intertidal species with planktotrophic dispersive larvae, and determine the extent to which variation in recruitment was explained by climatic and environmental (upwelling) variation, we analyzed patterns of barnacle and mussel recruitment across space (at up to 10 sites across 250 km) and through time (up to 20-years). Compared to mussel recruitment, barnacle recruitment varied far less interdecadally, and showed minimal change in seasonality. Using three analytical approaches, multiple regression, quantile regression and wavelet analysis, we found that recruitment of the barnacles *Balanus glandula* and *Chthamalus dalli* and mussels *Mytilus* spp. varied in generally similar ways with climate variation as expressed in ENSO, NPGO, and PDO indices, and with upwelling, as expressed in the Bakun upwelling index. In regression approaches, NPGO and upwelling had the strongest associations with recruitment of all species, with MEI and PDO also having an influence on *C. dalli*. The strength of the association with the environment varied with recruitment magnitude, however, being generally stronger at intermediate and in some cases high recruitment densities and weak at low recruitment densities. Time series (wavelet) analysis showed that with all environmental indices, the most

consistent strong relationships occurred at annual periodicities, but multi-year periodicities were also important with PDO and upwelling indices. Patterns were complex, however, with periods of strong and weak associations at different time periodicities varying differently among the different environmental measures, and in some cases varying from strongly positive to strongly negative associations at the same periodicities through time. These relatively consistent relationships between large-scale climate and upwelling, and recruitment explained a substantial fraction of the variance (37–40%). The ~ 60% of the variance in recruitment not explained in our analyses is likely due to myriad other factors such as shorter-scale variation in upwelling, internal tidal bores, sea breezes, wave forces, larval behavior, and post-settlement processes. Thus, our analysis adds insights into potential influences on recruitment that occur at ocean basin- to regional scales, and complements the body of work that focuses on the more local-scale and shorter-term mechanistic influences that also help determine the pace at which larvae recruit to the adult habitat.

- ❖ Menge, B. A., S. D. Hacker, T. Freidenburg, J. Lubchenco, R. Craig, G. Rilov, M. Noble and E. Richmond (2011). "Potential impact of climate-related changes is buffered by differential responses to recruitment and interactions." *Ecological Monographs* **81**(3): 493-509. <http://dx.doi.org/10.1890/10-1508.1>

Detection of ecosystem responsiveness to climatic perturbations can provide insight into climate change consequences. Recent analyses linking phytoplankton abundance and mussel recruitment to the North Pacific Gyre Oscillation revealed a paradox. Despite large increases in mussel recruitment beginning in 2000, adult mussel responses were idiosyncratic by site and intertidal zone, with no response at one long-term site, and increases in the low zone (1.5%/yr) and decreases in the mid zone (1.3%/yr) at the other. What are the mechanisms underlying these differential changes? Species interactions such as facilitation by barnacles and predation are potential determinants of successful mussel colonization. To evaluate these effects, we analyzed patterns of barnacle recruitment, determined if predation rate co-varied with the increase in mussel recruitment, and tested facilitation interactions in a field experiment. Neither magnitude nor season of barnacle recruitment changed meaningfully with site or zone from the 1990s to the 2000s. In contrast to the relationship between NPGO and local-scale mussel recruitment, relationships between local-scale patterns of barnacle recruitment and climate indices were weak. Despite differences in rates of prey recruitment and abundance of sea stars in 1990-91, 1999-2000, and 2007-2008, predation rates were nearly identical in experiments before, during and after 1999-2000. The facilitation experiment showed that mussels *M. trossulus* only became abundant when barnacle recruitment was allowed, when abundance of barnacles reached high abundance of ~50% cover, and when mussel recruitment was sufficiently high. Thus, in the low zone minimal changes in mussel abundance despite sharply increased recruitment rates are consistent with the hypothesis that change in adult mussel cover was buffered by the relative insensitivity of barnacle recruitment to climatic fluctuations, and a resultant lack of change in facilitation strength. Facilitation of mussels is likely important in the mid zone as well, but the dynamics of the longer-lived *M. californianus* at our two long-term sites appeared to be driven primarily by differential regimes of disturbance. Although rocky intertidal ecosystems may be sensitive to major climatic perturbations, predicting community responses will be difficult due to complex individualistic responses of key taxa during the recruitment stage and their influences on subsequent species interactions.

- ❖ Miller, L. and M. W. Denny (2011). "The importance of behavior and morphological traits for controlling body temperature in littorinid snails." *Biological Bulletin* **220**(3): 209-223. <http://www.biolbull.org/content/220/3/209.long>

For organisms living in the intertidal zone, temperature is an important selective agent that can shape species distributions and drive phenotypic variation among populations. Littorinid snails, which occupy the upper limits of rocky shores and estuaries worldwide, often experience extreme high temperatures and prolonged aerial emersion during low tides, yet their robust physiology--coupled with morphological and behavioral traits--permits these gastropods to persist and exert strong grazing control over algal communities. We use a mechanistic heat-budget model to compare the effects of behavioral and morphological traits on the body temperatures of five species of littorinid snails under natural weather conditions. Model predictions and field experiments indicate that, for all five species, the relative contribution of shell color or sculpturing to temperature regulation is small, on the order of 0.2-2 °C, while behavioral choices such as removing the foot from the substratum or reorienting the shell can lower body temperatures by 2-4 °C on average.

Temperatures in central California rarely exceeded the thermal tolerance limits of the local littorinid species during the study period, but at sites where snails are regularly exposed to extreme high temperatures, the functional significance of the tested traits may be important. The mechanistic approach used here provides the ability to gauge the importance of behavioral and morphological traits for controlling body temperature as species approach their physiological thresholds.

- ❖ Reed, D. C., A. Rassweiler, M. H. Carr, K. C. Cavanaugh, D. P. Malone and D. A. Siegel (2011). "Wave disturbance overwhelms top-down and bottom-up control of primary production in California kelp forests " *Ecology* 92: 2108-2116. <http://dx.doi.org/10.1890/11-0377.1>

We took advantage of regional differences in environmental forcing and consumer abundance to examine the relative importance of nutrient availability (bottom-up), grazing pressure (top-down), and storm waves (disturbance) in determining the standing biomass and net primary production (NPP) of the giant kelp *Macrocystis pyrifera* in central and southern California. Using a nine-year data set collected from 17 sites we show that, despite high densities of sea urchin grazers and prolonged periods of low nutrient availability in southern California, NPP by giant kelp was twice that of central California where nutrient concentrations were consistently high and sea urchins were nearly absent due to predation by sea otters. Waves associated with winter storms were consistently higher in central California, and the loss of kelp biomass to winter wave disturbance was on average twice that of southern California. These observations suggest that the more intense wave disturbance in central California limited NPP by giant kelp under otherwise favorable conditions. Regional patterns of interannual variation in NPP were similar to those of wave disturbance in that year-to-year variation in disturbance and NPP were both greater in southern California. Our findings provide strong evidence that regional differences in wave disturbance overwhelmed those of nutrient supply and grazing intensity to determine NPP by giant kelp. The important role of disturbance in controlling NPP revealed by our study is likely not unique to giant kelp forests, as vegetation dynamics in many systems are dominated by post-disturbance succession with climax communities being relatively uncommon. The effects of disturbance frequency may be easier to detect in giant kelp because it is fast growing and relatively short lived, with cycles of disturbance and recovery occurring on time scales of years. Much longer data sets (decades to centuries) will likely be needed to properly evaluate the role of disturbance relative to other processes in determining patterns of NPP in other systems.

- ❖ Standish, J. D., J. W. White and R. R. Warner (2011). "Spatial pattern of natal signatures in the otoliths of juvenile kelp rockfish, *Sebastes atrovirens*, along the California coast." *Marine Ecology Progress Series* 437: 279-290. <http://dx.doi.org/10.3354/meps09241>

The natal origin of a post-dispersal marine fish may be determined by examining the trace elemental signatures present in the core (i.e. the pre-dispersal region) of the otolith. We found distinct spatial differences in the natal elemental signatures in the core region of the otoliths of post-dispersal juvenile kelp rockfish *Sebastes atrovirens* collected along the coast of California, USA. Laser ablation inductively coupled plasma mass spectrometry of individual otolith cores revealed detectable levels of Mn, Mg, Ba, and Sr. Using a Bayesian classification model, 2 unique elemental signature types were identified in both 2001 and 2002, and the signatures were chemically similar across years. In both years, locations received a mixture of natal types ('A' and 'B'), indicating the contribution of at least 2 chemically distinct sources to recruitment. The spatial pattern of the natal types varied among sites for both years. In 2001, Type A was nearly absent from the northernmost location, suggesting a southern origin and a limitation in the dispersal and contribution of this chemically identified natal type. In 2002, most locations had a mix of Types A and B, but Type A was most abundant in the south and least abundant in the central part of the spatial domain. However, it was not possible to specify the full extent of dispersal of either natal type. We demonstrated use of elemental signatures in the otolith core of post-dispersal individuals to evaluate larval dispersal patterns which may document the extent to which kelp rockfish populations along the California coast receive recruits from different chemically distinct sources.

- ❖ Suanda, S. H., J. A. Barth and C. B. Woodson (2011). "Diurnal heat balance for the northern Monterey Bay inner shelf." Journal of Geophysical Research **116**: C09030, 13 PP. <http://dx.doi.org/10.1029/2010JC006894>

Key Points:

- Diurnal temperature fluctuations in northern Monterey Bay are sea breeze driven
- Heating is due to along-shelf advection of a temperature gradient
- Cooling is due to cross-shelf heat flux

In the summer of 2007, physical measurements including velocity from acoustic Doppler current profilers, surface gravity wave heights measured acoustically, and temperature from thermistor chain arrays were collected along- and across- the mid to inner shelf (water depths from 10–60 m) in northern Monterey Bay. The oceanic response to a strong (8–15 m s⁻¹ daily maximum) along-shelf sea breeze is examined by evaluating the diurnal heat budget over a cross-shelf section of the inner shelf. The diurnal heat budget closes to within the 95% confidence level with daily warming and cooling periods explained by two separate, but related processes. During evening/early morning warming period, 77% of the observed temperature increase is due to along-shelf advection of a temperature gradient within the upwelling shadow zone, a process which is arrested during the period of wind-forcing. In contrast, 75% of the afternoon cooling period is explained by the cross-shelf heat flux driven by diurnal along-shelf winds. In this study, diurnal tides are found to contribute less than 10% of the observed temperature variability and surface gravity waves do not show any significant diurnal variability. Richardson number estimates show that, on average, wind-induced shear is not strong enough to erode the strength of water column stratification within the upwelling shadow.

- ❖ Watson, J. R., C. G. Hays, P. T. Raimondi, S. Mitarai, C. Dong, J. C. McWilliams, C. A. Blanchette, J. E. Caselle and D. A. Siegel (2011). "Currents connecting communities: nearshore community similarity and ocean circulation." Ecology **92**: 1193-1200. <http://dx.doi.org/10.1890/10-1436.1>

Understanding the mechanisms that create spatial heterogeneity in species distributions is fundamental to ecology. For nearshore marine systems, most species have a pelagic larval stage where dispersal is strongly influenced by patterns of ocean circulation. Concomitantly, nearshore habitats and the local environment are also influenced by ocean circulation. Because of the shared dependence on the seascape, distinguishing the relative importance of the local environment from regional patterns of dispersal for community structure remains a challenge. Here, we quantify the "oceanographic distance" and "oceanographic asymmetry" between nearshore sites using ocean circulation modeling results. These novel metrics quantify spatial separation based on realistic patterns of ocean circulation, and we explore their explanatory power for intertidal and subtidal community similarity in the Southern California Bight. We find that these metrics show significant correspondence with patterns of community similarity and that their combined explanatory power exceeds that of the thermal structure of the domain. Our approach identifies the unique influence of ocean circulation on community structure and provides evidence for oceanographically mediated dispersal limitation in nearshore marine communities.

- ❖ Woodson, C. B., J. A. Barth, O. M. Cheriton, M. A. McManus, J. P. Ryan, L. Washburn, K. N. Carden, B. S. Cheng, J. Fernandes, L. E. Garske, T. C. Gouhier, A. J. Haupt, K. T. Honey, M. F. Hubbard, A. Iles, L. Kara, M. C. Lynch, B. Mahoney, M. Pfaff, M. L. Pinsky, M. J. Robart, J. S. Stewart, S. J. Teck and A. True (2011). "Observations of internal wave packets propagating alongshelf in northern Monterey Bay." Geophysical Research Letters **38**: L01605. <http://dx.doi.org/10.1029/2010GL045453>

Internal waves of depression were observed propagating along-shelf and into northern Monterey Bay, California (CA) on the inner shelf. These waves had amplitudes approximately equal to the thermocline depth (~4 m), and were unstable to shear and mix the thermocline. Isopycnal gradient spectra showed that the wave packets lead to an elevated mean dissipation rate of $\epsilon = 2.63 \times 10^{-5} \text{ m}^3 \text{ s}^{-2}$ for up to 2 hours after wave passage. The proximity to the surface created strong surface convergences that can actively transport buoyant material, such as plankton, back into the bay. The wave packets were observed regularly over the upwelling season across multiple years suggesting they may have large effects on the documented spatial variation of phytoplankton and larvae on the inner shelf. The timing of the waves suggests they are not formed by tides interacting with bathymetry, but are generated by buoyant plume propagation.

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