Community Structure and Diversity:

Evaluating biotic interactions and oceanographic effects on NE Pacific Rocky intertidal communities using a large-scale, data-intensive survey.

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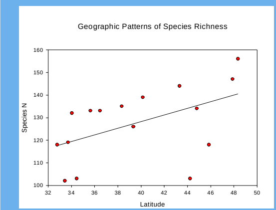
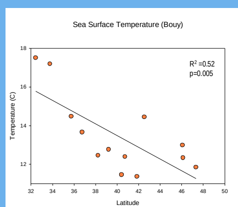
Introduction

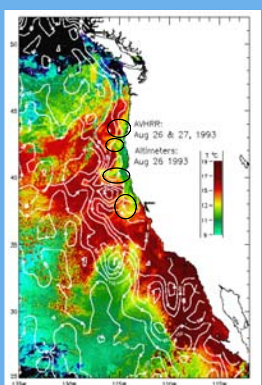
A major hindrance in understanding how marine communities respond to larger-scale perturbations has been a lack of information of natural patterns at appropriate scales. Most survey results are limited in spatial and/or temporal scope to one or a few sites and sample dates. To overcome these limitations the Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO) has been quantifying community structure of rocky intertidal communities along the US west coast from Cape Flattery, WA to San Diego, CA since 1999. The project employs a spatially nested design that provides geographically dense sampling within 16 areas (10-100km). Abundance data are collected on both invertebrates and macrophytes at four standardized elevations. Thus we are able to extrapolate our understanding of local experimental results as well as explore oceanographic factors at relevant scales.

The California Current System: Our Study Area

Do latitudinal variations of physical parameters exist? Factors such as water and air temperture certainly do exhibit a latitudinal trend increasing equatorward. Also, overall tidal range decreases as one moves south. Our initial findings of an inverse species richness could be due to the influence of these effects. However, factors such as nutrient or phytoplankton availability due to upwelling as well as larval retention zones and times are not so straightforward. Seasonal variation in these factors further complicates their effects.

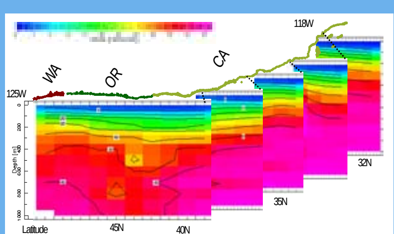






- Identified on the left are areas along the coastline with seasonal eddy formation
- The strength/distinctness varies with different seasons
- The effects of mesoscale eddies are still mostly unknown but... .
- Scale (temporal and spatial) and strength will affect retention time.

Figure derived from: http://www.oce.orst.edu/po/research/strub/index.html

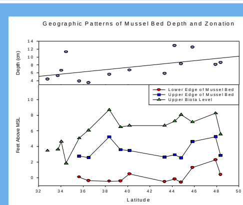


There is a slight general trend of greater Nitrate concentrations at higher latitudes; this however will vary seasonally. The figure above shows nitrate concentrations (1 degree longitude offshore) from 0-1000 m for our entire study area. Note the interesting feature at approx. 43 N. This could be indicative of greater productivity in this region, increased mixing at depth, or both.

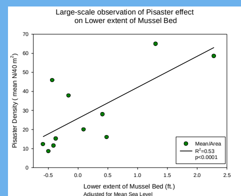
Figure derived from: LEVITUS 94 http://ingrid.ldeo.columbia.edu/SOURCES/.LEVITUS94/.ANNUAL/.NO3/

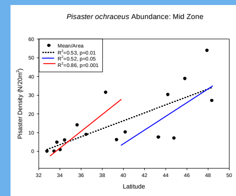
Extrapolating Local Results

Much of what we know about the biotic interactions occuring in the intertidal zone come from localized experiments. In the seventies, Paine conducted a series of experiments in northern Washington that showed that the lower extent of the mussel bed in largely controlled by the main predater, Pisaster ochraceus, while the upper extent is controlled largely due to physiological constraints (Paine, 1974).



The adjacent figures depict first the elevations of the lower and upper extents of the mussel bed and the heights of the upper edge of intertidal biota (all adjusted for the change in Mean Sea Level) and the correlation between Pisaster and the lower extent of the mussel bed for most of our study area.

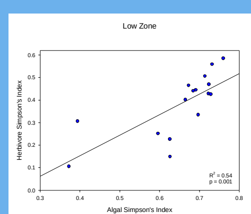


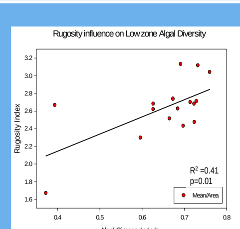


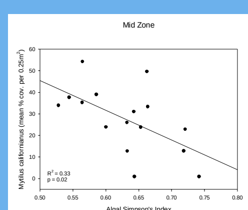
Our observations support Paine's findings though there is much variation to be explained. Looking at both Pisaster abundances and mussel bed depths, there appears to be potential for Pisaster saturation in the north thus suggesting at least two regions of different predator prey interaction. This is not supported however, when looking at North/ South differences in mussel bed heights; in fact there appears to be stronger correlation between Pisaster abundances and mussel bed heights above 39-40N. Further analysis of the abundance of food source alternatives as well as encorporating local physical variations, such as temperature anomalies and significant wave force, should lend further insight however.

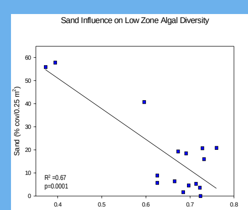
Biotic and Abiotic interactions affecting species diversity.

The figures below depict the trends of algal diversity across all of our sites (approx. 17 degrees of latitude). Diversity indices were derived using the Simpson index which combines both the numbers of species in plots and their relative abundances. Algal and herbivore diversity have a positive correlation with respect to latitude and each other in the low zone. This could be the result of a large-scale herbivore effect but more likely due to changes in substrate complexity (algal morphology). Low zone algal diversity is also correlated with two physical factors: sand abundance and substrate rugosity. In the mid zone, algal diversity does not have a significant relationship with either herbivore diversity or total invertebrate diversity. It is possible that the greater occurrence of mussels as one moves north provides competition with algal species for space and limiting the mid zone algal community to one or a few species that can invade gaps quickly. There is no significant relationship in the midzone between algal diversity and Pisaster abundance perhaps indicating different meso-scale mechanisms for gap formation.



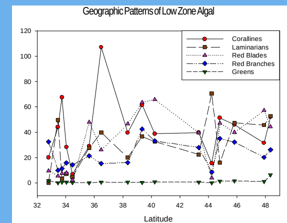


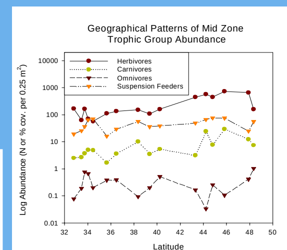




Trends of functional and trophic groupings

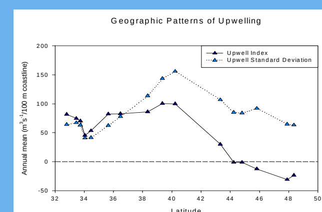
When exploring regional patterns that cover different species ranges, it is helpful to employ functional or trophic groupings. This allows insight into the subtleties that large-scale analysis of species richness or diversity patterns may not reveal. Furthermore, looking at the relative abundances of groups allows us to tease out the environmental variation that won't be confounded by evolutionary factors that affect the diversity of individual groups (e.g. kelps).





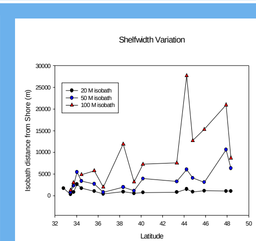
The adjacent figures depict the abundances of algal functional groups and invertebrate trophic groups over latitude. Also shown are both the mean upwell index (monthly totals averaged for the year 2000) and the standard deviation of the annual index (Bakun Index: http://www.pfeg.noaa.gov/products/PFEL/modeled/indices/upwelling/NA/upwell_menu_NA.html).

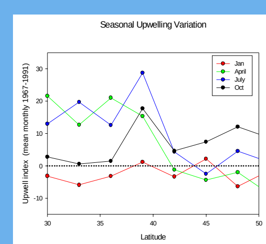
This is a coarse measure of periods of upwelling and relaxation: the higher the standard deviation, the greater the inter-month oscillation between upwelling and relaxation and or downwelling. Models depicting areas typical of upwelling suggest that macroalgae communities will predominate over sessile filter feeders in areas of persistent upwelling whilst filter feeders require periods of relaxation to bring phytoplankton populations close to shore.



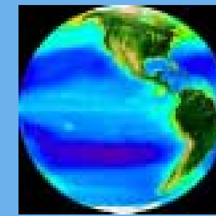
Meso-scale variation

Within the Californa Current System, there is a significant degree of mesoscale variation that can contribute to differences between intertidal communities. The sources of these variation can be geographic, such as regional differences in continental shelfwidth, and temporal, or both such as the seasonal patterns in upwelling.





Much effort is needed to determine the scale of variation, temporal and spatial, in order better understand the underlying mechanisms. For instance, the timing of upwelling and nutrient availability could effect species at different latitudes simply due to the geographic variation of low tide exposure.



Global comparisons

In a recent MEPS paper (2001), Broitman et al characterized the Chilean coast through a series of intertidal surveys in order to document broad patterns of functional and trophic group abundance and to evaluate the relevant scale of oceanographic forcing. Although there are differences in the methodologies between studies, there are some striking similarities.

1) Differences in the abundances of algal functional groups in relation to upwelling indices or upwelling variation provides evidence for the importance of mesoscale oceanographic features.

2) There are abrupt changes in the mid-zone mussel bed abundance (Chile:32S; US 34N) as one moves equatorward. These community compositional changes in the intertidal may reflect sensitive environmental gradients. However, more extensive surveying at both the northern and southern-most part of Mytilus californianus' range may be necessary to provide ample evidence.

Continued research, international collaboration, and the employment of large-scale spatially explicit protocols for intertidal community monitoring will certainly help to bridge the gap between the nearshore ocean typical of eastern boundary currents and the ecological communities on the shore.

Conclusions

Latitudinal gradients in physical conditions do exist: temperature and tidal range (e.g.). This is accompanied by a decreasing gradient in species richness as one moves equatorward. But:

Mesoscale variation in oceanographic conditions allow for variations in abundance of groups that is not immediately apparent when looking at the largest scale. Local and regional topography can effect upwelling. Seasonal eddies can contribute to propagule retention.

Between zone variation is possibly forced by both: a decrease in tidal range as one moves southward as well as mesoscale variation in physical pressures such as retention zones and upwelling. Upwelling not only can change bottom-up factors such as nutrient delivery but also top-down factors such as changing pisaster feeding rates when exposed to colder waters (Sanford, 1999).

When attempting to extrapolate local results with observational data it is important to consider mesoscale factors to explain between site variation, the seasonal strengths of these factors and their resultant effect on biological interactions.

Analyses determining the scales of variation for single species to trophic interactions when coupled with relevant oceanic processes are of the utmost of importance when attempting to understand such a variable system as that connected to the California current. Finally, integration of this dataset with results from small scale experiments, recruitment monitoring and large-scale climate observations are likely to yield further insights into the forces, both biotic and abiotic, that shape temperate intertidal communities.

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