Intertidal Zonation

Does Species Diversity Decrease with Tidal Height?

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Student Report
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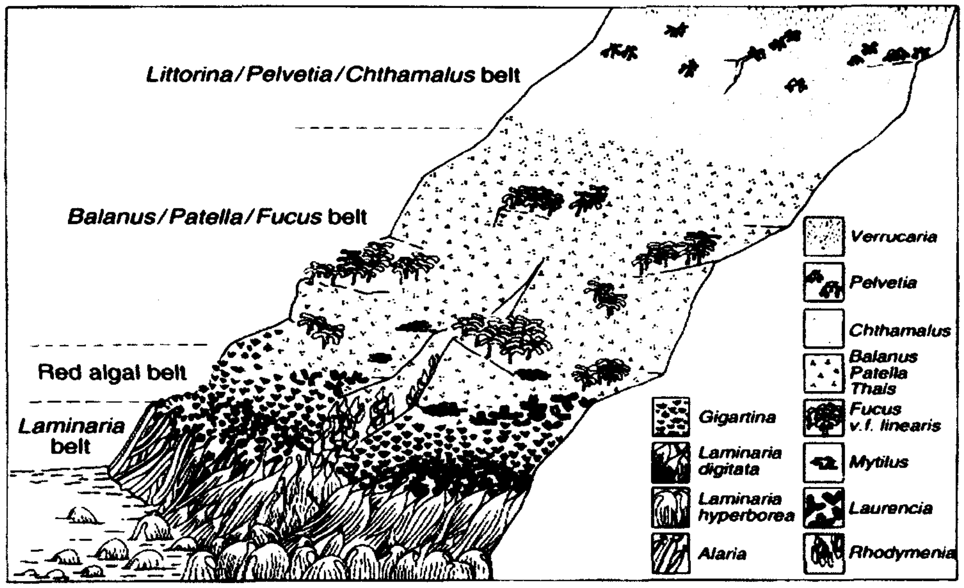
Perhaps no other community has captured the attention of field ecologists like the rocky intertidal zone. This fascinating transition zone between land and sea allows ecologists to study patterns of species distributions, abundance and diversity. The most striking observation one makes when visiting a rocky seashore is that organisms are distributed in horizontal bands. From the low to the high tide mark one can readily identify zones dominated by the brown kelp *Laminara*, pink encrusting coralline algae, dark blue mussel beds, white barnacles, littorine snails, and finally black lichens (Figure 1).



(a)

Figure 1. Typical Pattern of intertidal zonation of organisms.

Intertidal zonation, just like altitudinal and latitudinal zonation, is a reflection of organisms' responses to physical gradients and biological interactions (Merriam 1894, Whittaker 1975). Intertidal zonation is unique in that the physical gradients are very steep (e.g. a 12 ft. tidal range versus hundreds of miles in latitudinal zonation). Organisms living in the low tidal zone spend over 80% of their time in the benign and constant marine environment, while the reverse is true for organisms living in the high zone (Figure 2). At Mean Sea Level organisms spend equal amounts of time being immersed in seawater and exposed to air. Since intertidal organisms (with some exception such as mites and insects) originated in the sea, species diversity decreases up the shore. Environmental stress from desiccation, temperature extremes, and inundation by rain, becomes increasingly more important with tidal height. The higher an organism is found on the shore, the more tolerant it is to these environmental factors (Schonbeck and Norton 1978, 1980). As a general rule, desiccation sets the upper limit to a species distribution (Connell 1961, Wolcott 1973, Suchanek 1978). The factors responsible for setting the lower limit are not as easily defined. Intertidal organisms photosynthesize, grow and reproduce better lower than higher on the shore (Hayes 1929, Johnson et al. 1974., Schonbeck and Norton 1980, Behrens Yamada and Mansour 1987). There they are immersed longer, have a longer time to feed or photosynthesize, and spend less energy in protecting themselves from environmental stress. The benefits from living in this more benign environment, however, are counteracted by a higher mortality rate from space competition or predation (Connell 1961, 1970, Paine 1966, Menge 1976, 1978).

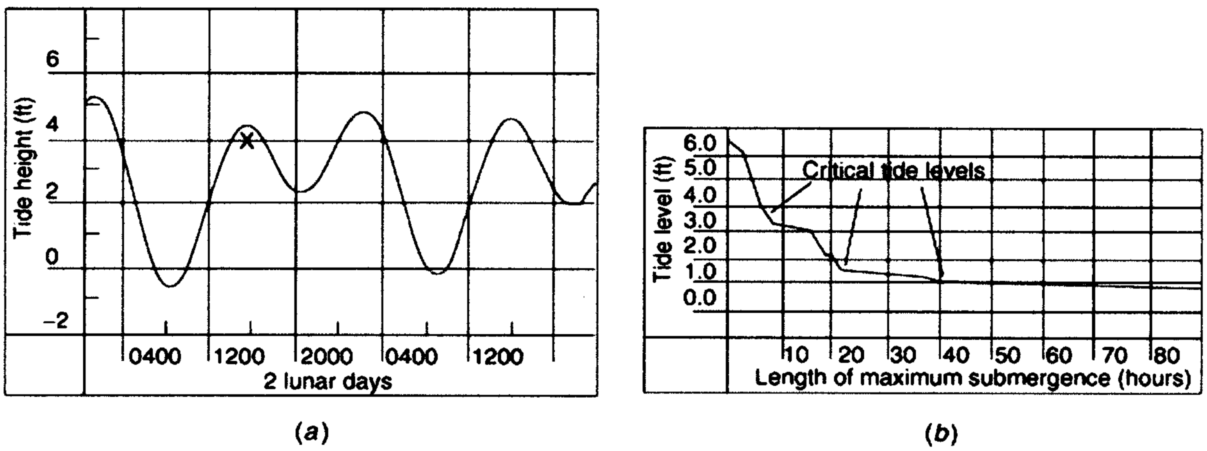


Figure 2. (a) Mixed tidal patterns, with two high and two low tides of unequal height per day, result in a discontinuous exposure gradient (b) with critical tidal levels.

While gradients in physical and biotic factors contribute to intertidal zonation, the nature of our tidal patterns tends to sharpen the zones. Mixed tides (two high and two low tides of unequal height per day) are a characteristic of the Oregon coast (Figure 2). The consequence of this tidal pattern is that the gradation of physical factors with tidal height is not smooth, but step-like, depending on the time a certain area is covered by water. For example, an organism living just below "Mean Lower High Water" (marked X in Figure 2) is immersed twice a day, versus only once a day for an organism living just above this tidemark. The sharp zonation of algal species and some sessile animals is well correlated with such critical tidal levels (Doty 1946). Mobile animals such as limpets, drilling snails, starfish and crabs can move with the changing water levels and consequently are not as nicely zoned as sessile organisms (Behrens Yamada and Boulding 1996).

Description of Zones

Five distinct zones can be identified on the Oregon coast: (Tide levels are expressed in relation to Mean Lower Low Water (MLLW) = 0 ft.). A good reference to the zonation and ecological roles of the various species is Mohler et al. 1997.

1. The spray zone (+9 ft.) is technically outside the daily tidal range. However, it is covered during storm tides and receives wash and spray from breaking waves. Very few organisms are adapted to living in this zone. Black lichens (*Verrrucaria* sp.) are characteristic of this zone. Littorine snails (*Littorina scutulata*), and finger limpets (*Lotia digitalis*) inhabit the lower portion of this zone. The rock louse (*Ligia pallasi*) hides in cracks during the day and comes out at night to forage.
2. The high zone (+6 to +9 ft.) is usually uncovered except during higher high tides. Barnacles (*Balanus glandula* and *Chthamalus dalli*) are found in crevices. The dominant grazers are finger limpets and littorine snails.
3. The upper mid tidal zone (+4 to +6 ft.) is covered and uncovered by the tide twice a day, but is inundated less than 50% of the time. Acorn barnacles (*Balanus gladula*), and drilling snails (*Nucella emarginata*) are the dominant organisms in the upper portion, while mussel beds (*Mytilus californianus*), drilling snails and gooseneck barnacles (*Pollicipes polymerus*) are abundant in the lower portion of this zone.
4. The lower mid tidal zone (+1 to +4 ft.) is covered and uncovered by the tide twice a day, but is inundated for over 50% of the time. Mussels and gooseneck barnacles are abundant in the upper portion, while giant green sea anemones (*Anthopleura xanthogrammica*), purple urchins (*Strongylocentrotus purpuratus*), black chitons (*Katharina tunicata*) and starfish (*Pisaster ochraceus*) dominate the lower portions of this zone.
5. The low tide zone (-3 to +1 ft.) is covered by water except during the lowest tides of the month. The upper limit of pink coralline algae roughly corresponds to +1 ft. MLLW. Characteristic species include the brown alga *Laminaria*, sea grasses (*Phyllospadix*), the giant barnacle (*Balanus nubilus*), sponges, tube worms, tunicates, and bryozoans.

Variation in Zonation Patterns

It must be noted that organisms do not respond to tide level, per se, but to the intensity of physical and biotic factors. It is thus not surprising to find geographic and local variations in zonation patterns. For example, the lower limit of mussel beds on the central Oregon Coast ranges from +0.5 ft to +5.5 ft, depending on starfish abundance, wave exposure and sand scouring (Menge at al. 1992). Since desiccation is less of a factor at higher latitudes, many algal species that inhabit the subtidal zone in California will penetrate the low intertidal zone in Oregon. Likewise, zones of organisms on north-facing slopes are higher than on south-facing slopes. Crevices, pools, caves, and surge channels are less affected by desiccation than adjacent habitats. Consequently, these damper microhabitats will harbor species that are characteristic of a lower tidal zone. Wave surge and spray also have an ameliorating effect on desiccation. While on very wave exposed shores all zones tend to be displaced upward, the effect of splash and spray has the most dramatic effect on the black lichen zone. In fact, the width of the black lichen zone has been used as an index of wave exposure (Ballentine 1961).

Class Sampling Exercise

Hypothesis: Since most intertidal species evolved in the stable and benign ocean environment, we would expect more species to live in the lower zones than in the physically harsh upper zones. We tested the hypothesis that species diversity increases down the shore by sampling the distribution and abundance of intertidal organisms at four tidal levels from the low zone, below the mussel band to the high zone dominated by *Littorina*, black lichens and barnacles.

Materials and Methods

In order to test the hypothesis that intertidal species diversity decreases with tidal height, we identified four distinct tidal levels on a sloping sandstone bench bordering the southern extension of North Cove, Cape Arago. The biota found on this sloping bench is typical of most rocky beaches on the Oregon coast. The presence of a band of the wave-tolerant sea palm, *Postelsia palmaeformis*, at the lowest tidal level would characterize this beach as wave-exposed. The four distinct tidal levels we sampled were:

1. High Barnacle Zone
2. Lower Barnacle Zone
3. Middle of Mussel Zone.
4. Low, Starfish Zone.

At each level, we stretched a tape parallel to the shore and sampled 16 quadrats (25 x 25 cm^2). Quadrats were evenly spaced every 2 meters (Figure 3). All individuals within a quadrat were identified to species and counted. Algae and black lichen that could not be counted as individual plants were recorded as "present". These plants were recorded in the species count as Species Richness, but were not used to calculate the Shannon-Wiener Diversity Index (Appendix 1). Percent dominance for each tidal level was calculated by adding the proportional representation of the two most common species (Appendix 1).

Figure 3. A meter tape was stretched parallel to the shore at each tidal level and 16 quadrats placed 2 meter intervals.

Results

High Barnacle Zone

With a Shannon Wiener index of 0.754, the high barnacle zone showed the lowest species diversity out of the four sampled intertidal areas (Table 1). There was a mean of 5.8 species, with ± 3.1 95% confidence index at this level. The two most dominant organisms were *Littorina scutulata* and *Balanus glandula*, accounting for 83.3% of the individuals at this level.. *B. glandula* composed the majority of the species present, having 3,648 individuals out of a total number of 4,581 individuals overall. *Lottia digitalis* and *Chthamalus dalli* were also found in high abundance. Four types of algae were found in this high intertidal area.

Low Barnacle Zone

The Low Barnacle zone was characterized by a total species richness of 21. There was a mean of 7.0 species with ± 0.9 95% confidence interval. The Shannon-Wiener Diversity index was calculated as 1.258. (Table 1, and Appendix 1 for calculations.) Although *Balanus glandula* and *Mytilus californianus* were the two most abundant species (with 73.1% dominance), *Lottia* limpets, *Chthamalus dalli*, and *Littorina scutulata* were also notable at this level. We did examine some of the microhabitats present underneath the barnacles and mussels during this zonation. This is where organisms such as amphipods and lined shore craps were identified, and may account for the unexpected high abundance of species at this level.

Mussel Zone

The species richness of the Mussel Zone totals thirteen separate species with 4,270 individuals. The mean number of species, and 95% confidence interval, is 6.9 ± 1.2. The most abundant species in this zone are *Semibalanus cariosis* with 1,760 individuals, and *Balanus glandula* with 982 individuals. Percent dominance of these two species is 62.2%. The Shannon-Wiener diversity at this tidal level is 1.462 (refer to Table 1). The salinity at this level is 30% (refer to Appendix 1).

Starfish Zone

In the Starfish Zone mean species richness was 5.68 with a ±1.81 95% confidence interval. *Semibalanus cariosi* (N=113) and *Chthamalus dalli* (N=103), contributed to a total dominance of 51.4%. This included area shared by four identified species of algae. The Shannon-Wiener Diversity index of 1.950 was the highest of all four zones examined.

Table 1. Species Richness, Dominance and Shannon Wiener Diversity at four Tidal Levels at North Cove, Cape Arago.

Tidal Level	Richness Total # Species	Mean # Species ± 95% CI	Most Abundant species	Dominance	Shannon-Wiener Diversity
High, Barnacle	15	5.8 ± 3.1	*Littorina scutulata* *Balanus glandula*	88.3%	0.754
Low Barnacle	21	7.0± 0.9	*Balanus glandula* *Mytilus californianus*	73.1%	1.258
Mussel	13	6.9± 1.2	*Semibalanus cariosis* *Balanus glandula*	62.2%	1.462
Starfish	19	5.7± 0.9	*Semibalanus cariosis* *Chthamalus dalli*	51.4%	1.950

Discussion

Our hypothesis that species diversity decreases with tidal elevation was supported by the Shannon-Wiener Index and by Dominance, but not by Species Richness. As predicted, a few tolerant species dominated the higher zone whereas a number of species were more evenly represented in the lower zones. Increased competition for space, predation and disturbance by waves is thought to contribute to fewer individuals per species in the low zone.

While the Shannon-Wiener Index and Dominance support the view that diversity increases toward the water's edge, Species Richness was similar across the four tidal levels. Possible reasons for this unexpected result include:

1. We did not sample the harshest black lichen zone, which would have yielded a low density of only a few desiccation-resistant species such as *Littorina scutulata.*
2. Some quadrats in the higher zones fell on depressions in the sandstone shelf and thus harbored species that were characteristic of lower zones. This high degree of habitat heterogeneity, combined with the high wave exposure at this site, would ameliorate any desiccation effects and thus would allow more species to coexist with the more tolerant *Balanus glandula* and *Littorina scutulata.*
3. The unexpected high number of species (21) in the lower barnacle zone was due to some students carefully examining the fauna and flora within the mussel bed rather than just scoring species visible on the surface.

In conclusion, we observed the general pattern of intertidal zonation: a few tolerant species dominating the high zones and a number of more evenly distributed species occupying the lower zones.

Acknowledgments

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Appendix 1. Pooled data from 16 quadrats at each tidal level.

Location: North Cove, Cape Arago , Samplers: ________ Date: June 24, 2004

Air Temperature ___°C	Tide level: **High, Barnacle Zone**	
Water Temperature _____°C		Substrate___sandstone
Salinity 30‰	Quadrat size:16 @ 25-25 cm^2	Slope 5-11 degrees

Species	Total #/m^2	Proportion p	ln p	p ln p
Verrucaria maura (black lichen)	p			
Littorina scutulata	399	**0.87**	-2.44	-.21
Lottia digitalis	269	0.0587	-2.83	-1.664
Balanus glandula	3648	**0.7961**		
Chthamalus dalli	229	0.0499		
Endocladia muricata	p			
Cladophora columbiana	p			
Mytilus californianus	22	0.0048		
Semibalanus cariosis	8	0.0017		
Pollicipes polymerus	6	0.0013		
Pachygrapsus cassipes	1	0.00022		
Mastocarpus	P			
Red corraline	P			
Red stringy	P			
Leafy alga	P			
Number of species	15			
% Dominance		79.6 +8.7%	88.3%	
$\hat{H} = -\sum p \ln p$				0.7540

Species Diversity Measurements on the Oregon Coast

Location: North Cove, Cape Arago, Samplers: ______________ Date: June 24, 2004

Air Temperature ___ °C
Water Temperature _____ °C
Salinity 30 ‰
Tide level: **Lower Barnacle Zone**
Substrate: sandstone
Quadrat size: 16 @ 25x 25 cm^2
Slope: 5-11 degrees

Species	Total #/m^2	Proportion p	ln p	p ln p
Verrucaria maura (black lichen)	P			
Littorina scutulata	230	0.0445		
Lottia sp.	587	0.1135		
Balanus glandula	3147	**0.6084**		
Chthamalus dalli	472	0.0912		
Semibalanus cariosis	43	0.00831		
Fucus gardneri	p			
Mastocarpus papillatus	p			
Endocladia muricata	p			
Mytilus californianus	637	**0.123**		
Nucella emarginata	2	0.00038		
amnipods	1	0.00018		
Coraline algae	p			
Pollicipes polymerus	51	0/00986		
Pelvetiopsis	p			
Stringy red	P			
Fleshy red	P			
Branched red	p			
Lined shore crab	3	0.00058		
	5173			
Number of species	21			
% Dominance		60.8 +12.3=	73.1%	
$\hat{H} = -\sum p \ln p$				1.258

Species Diversity Measurements on the Oregon Coast

Location: North Cove, Cape Arago Samplers: ________ Date: June 24, 2004

Air Temperature ___°C
Water Temperature ___°C
Salinity 30 ‰
Quadrat size: 16@ 25x25 cm^2
Tide level: **Mussel Zone**
Substrate: sandstone
Slope 5-11 degrees

Species	Total $\#/m^2$	Proportion p	ln p	p ln p
Littorina scutulata				
Lottia sp.	102	0.02389		
Balanus glandula	982	**0.229988**		
Semibalanus cariosus	1760	**0.412178**		
Pollicipes polymerus	317	0.074239		
Endocladia muricata	p			
Mytilus californianus	940	0.220141		
Nucella emarginata	5	0.001171		
Anthopleura xanthogrammica	7	0.001639		
Katherina tunicate	1	0.00023419		
Strongylocentrotus purpuratus	2	0.00046838		
Chthamalus dalli	154	0.03606		
Total Individuals	4270			
Number of species	13			
% Dominance		22.9=41.2	65.2%	
$\hat{H} = -\sum p \ln p$				1.4626

Species Diversity Measurements on the Oregon Coast

Location: North Cove, Cape Arago Samplers: ________ Date: June 24, 2004

Air Temperature ___°C Tide level: **Low, Starfish Zone**
Water Temperature _____°C Substrate: sandstone
Salinity 30 ‰ Quadrat size: 16@ 25x25 cm^2 Slope 5-25 degrees

Species	Total #/m^2	Proportion p	ln p	p ln p
Lottia sp.	8	0.0179		
Balanus glandula	54	0.121		
Chthamalus dalli	103	**0.231**		
Pollicipes polymerus	10	0.0224		
Mytilus californianus	30	0.0672		
Mytilys trossulus	31	0.0695		
Semibalanus cariosis	113	**0.253**		
Anthopleura elegantissima	2	0.0044		
Anthopleura Xanthogrammica	2	0.0044		
Pisaster	4	0.0089		
Coralline	P			
Isopod	6	0.0134		
Purple urchin	80	0.179		
Red fleshy	p			
Red fluffy	P			
Chiton	3	0.0067		
Endocladia	p			
Orange sponge	P			
Yellow sponge	P			
Total Individuals	446			
Number of species	19			
% Dominance		23.1+25.3=	51.4%	
$\hat{H} = -\sum p \ln p$				1.9507