16 - The Tidelands
Rocky Shores, Soft-Substratum Shores, Marshes, Mangroves, and Estuaries

Notes for Marine Biology: Function, Biodiversity, Ecology
By Jeffrey S. Levinton
VERTICAL ZONATION - universal feature of intertidal zone
- strong on rocky shores,
- also true of soft sediments but not as distinct
  (3-dimensional nature, owing to presence of burrowing organisms and others within the sediment)
Vancouver Island, British Columbia
Tatoosh Island, Washington
zonation
Nova Scotia
Stephenson and Stephenson, 1972
Example of zonation on rocky shore, along a gradient of wave exposure on a site in the United Kingdom
Tidepool, Tatoosh Island, Washington State
Strong physiological gradient

Ushakov 1968
Vertical Gradients

- Higher intertidal organisms - more resistant to heat and desiccation stress than lower intertidal organisms
- Higher intertidal - less time to feed. Sessile forms therefore grow more slowly than lower intertidal organisms
- Mobile carnivores (seastars, carnivorous snails can feed only at high tide, usually feed more effectively at lower tide levels, which are immersed a greater proportion of the day
Oxygen consumption

• Intertidal animals usually cannot respire at time of low tide
• Respiratory organs (gills of polychaetes, bivalves) must be moist to acquire oxygen, and therefore are usually withdrawn at low tide
• Some animals - reduce metabolic rate at time of low tide
• Some high intertidal animals can respire from air (e.g., some mussels) even at low tide, as long as air is not too dry
Pacific sand bubbler crab, *Scopimera inflata*, has membrane on each leg (shaded green), which exchanges gas from air into arterial blood.
Behavior and zonation
Wave shock

- Abrasion - particles in suspension scrape delicate structures
- Pressure - hydrostatic pressure of breaking waves can crush compressible structures
- Drag - impact of water can exert drag, which can pull organisms from their attachments to surfaces, erode particles from beaches and carry organisms from their burrows or living positions
- Lift – also caused by moving water
Causes of Vertical Zonation

• Physiological tolerance of different species at different levels of the shore
• Behavior - selective movement
• Larval and adult preference - larvae may settle at time of high tide at high levels, mobile juveniles/adults have a series of behavioral responses that keep them at certain levels of shore
• Competition - species may be capable of excluding others from certain levels of the shore
• Predation - mobile predators more effective usually on the lower shore: affects distributions of vulnerable prey species
A rocky shore in the U.K. At the time of low tide on hot dry days, the gastropod *Nucella lapillus* retreats into the crack where it is moist and cool. Note the areas cleared of mussels adjacent to the cracks.
Interspecific Interactions and Zonation

• Why are there vertical zones, with dominance often of single sessile species within a zone?
  
• (1) Differences in tolerance of species at different tidal heights (2) Competitive interactions (3) Predation changes with tidal level
**Rocky Shores of Scotland - Key Species in Joseph Connell’s study**

- *Chthamalus stellatus* - acorn barnacle, ranging from subtropical latitudes to northern British isles
- *Semibalanus balanoides* - acorn barnacle, ranging from Arctic to southern British isles, overlapping in range with *C. stellatus*
- *Nucella lapillus* - carnivorous gastropod, drills and preys on barnacles

Connell, J.H. 1961 *Ecological Monographs*
Semibalanus balanoides (northern)

Chthamalus stellatus (southern)

Nucella lapillus (predator)
Connell Field Experiment

- transplant newly settled *Chthamalus* to all tidal levels
- caged some transplants, excluded *Nucella*
- allow *Semibalanus* to settle and cleaned *Semibalanus* cyprids off some rocks
Chthamalus stellatus

Semibalanus balanoides

Nucella lapillus
Results of Connell Experiment

• *Chthamalus* survival
  • (1) poorer in presence of *Semibalanus*
  • (2) poorest where *Semibalanus* grew the fastest
  • (3) increased in high intertidal due to its resistance to desiccation, and the absence of *Semibalanus*

• Predation by *Nucella*: very high in lower shore, not on higher shore
MHWN

Chthamalus stellatus

Semibalanus balanoides

Nucella lapillus
Conclusions from Connell Experiments

• Predation important in lower intertidal
• Biological factors control lower limit of species occurrence
• Physical factors control upper limit
• Community structure a function of very local processes (larval recruitment not taken into account as a factor)
Nucella lapillus

Mytilus “byssing” Nucella
Dense population of the barnacle *Semibalanus balanoides*

Barnacles first settle in cracks

Dense population of the barnacle *Semibalanus balanoides*
Soft Sediments

- Zonation not as distinct as on rocky shores - burrowing in sediment
- Competition – also demonstrated by experiments
Sediment Competition Mechanisms

- Spatial interference
- Chemical interference - allelopathy
- Food exploitation - feeding rapidly on microalgae and detritus
SIMPLE EXPERIMENT

*Armandia brevis*  
Larva of burrowing worm

*Lumbrinereis inflata*  
Larva of tube worm

**SIMPLE EXPERIMENT**

Screen, tube makers intercepted

No screen, let tube makers through to sediment

**Conclusion:** tube builders limit burrowers – space limitation. Expt. works with soda straws.

Hemichordate *Saccoglossus bromophenolosus*

Some burrowing species produce Br-poisons
Soft Sediments - Vertical Stratification

- Dominant species found at different levels below sediment-water interface
- Experimentally reduce density of deep-dwelling clams, remaining individuals grow faster - demonstrates effect of density
- Removal of shallow dwelling species of bivalves has no effect on growth of deeper-dwelling species
Occurrence of various bivalves at different burrowing depths in a sand flat in southern California

Soft Sediment Intertidal: Food sources of non-carnivores

- Suspended phytoplankton for suspension feeders (e.g., bivalves, polychaetes)
- Microalgae and bacteria for deposit feeders (mud snails)
- Decomposing organic matter (phytodetritus and decomposing seaweeds) for deeper feeding deposit feeders
Effects on annelid assemblages

Localized food input dominance

Food input

Near surface feeders

Deeper feeders

Mobile consumer dominance

Food input

mudsnails move to food input

Near surface feeders

Deeper feeders
EXPOSED BEACHES: VERY STRESSFUL - TURBULENCE

Swash Riding - found in Mole Crab *Emerita*, some species of the bivalve *Donax*
The mole crab, *Emerita talpoida*, burrowing into an exposed beach in North Carolina.
Predation and Species Interactions

• Predators reduce prey density
• Prey species compete
• Conclude: predation may promote coexistence of competing prey species
Field Experiment of Robert Paine

- Rocky shores of outer coast of Washington State
- Principle predator - starfish *Pisaster ochraceus*
- *Pisaster* preys on a wide variety of sessile prey species, including barnacles, mussels, brachiopods, gastropods
Pacific coast starfish *Pisaster ochraceus*, flipped over
Left: eating a mussel,  Right: eating barnacles
Paine Field Experiment and Results

- Removal of *Pisaster ochraceus*
- Successful settlement of recruits of mussel *Mytilus californianus*
- Other species greatly reduced in abundance, *Mytilus californianus* became dominant
- Conclude: *Pisaster ochraceus* is a **keystone species**, a species whose presence has strong effects on community organization mediated by factors such as competition and predation
INTERTIDAL EXPERIMENTS AND STUDIES

ICONIC INTERACTIONS

1. COMPETITION (SPACE, FOOD)
2. PREDATION (VERTICAL GRADIENT)
3. DISTURBANCE (STORMS, SOME MAJOR BIOLOGICAL PLAYERS LIKE HORSESHOE CRABS)
Disturbance as a Factor in Intertidal Community Structure

- Disturbances are physical events that influence the distribution and abundance of organisms
- Disturbances may reduce abundance of competing species
- Disturbances may therefore allow coexistence of competitively inferior species, or may allow colonization of species adapted to disturbance
Postelsia palmaeformis, the palm seaweed, invades rocks that have been severely disturbed by storms. Spores are released and travel just a few cm from the plant, allowing local spread of a colonizing individual.

Blanchette, C.A. 1996, JEMBE 197:1-14
Disturbance patch size is important

See Suchanek 1981 *Oecologia*
Alternative local intertidal regimes - Maine

Petraitis and Latham 1999 *Ecology*
Alternative Stable States: Maine Rocky Shore

Seaweed-dominated patches
- Algae harbor predators of barnacles and mussels
- Algae dominate
- Long-lived algae regenerate from holdfasts

Destabilizing transitions
- Ice scour

Regular high recruitment of mussels, barnacles

Barnacle-mussel patches
- Gregarious settlement
- Barnacles and mussels dominate
- Mussels move laterally
- High recruitment

Rare high recruitment of algae

Alternative local intertidal regimes - Maine

Mussel-Barnacle

Fucus - seaweed
Spartina Salt Marshes
Herring Creek, Harwich, Cape Cod
**FIG. 14.37** Vegetational zonation in a southern New England salt marsh. (From Bertness et al. 2002, Copyright National Academy of Sciences, U.S.A.)

**Tall form**

**Short form**

- High marsh forbs
  - Aster tenuifolius
  - Atriplex patula
  - Limonium nashii
  - Salicornia europaea
  - Solidago sempervirens

- Phragmites australis

- Spartina alterniflora Zone
- Spartina patens Zone
- Juncus gerardi Zone
- Iva frutescens Zone
Subhabitats of the *Spartina* salt marsh environment. A tall form of *Spartina alterniflora* is associated with the high nutrient supply of flowing creeks. (After Redfield, 1972.)
**Salt Marshes dominated by Spartina spp.**

- Salt marshes are *accretionary* environments.
- Colonization of sediment by salt marsh plants is followed by trapping of fine particles, accretion of sediments.
- Marsh *Spartina* spp. plants spread by means of a *rhizome* system *below surface* - plants are interconnected and often consist of broad stands of the same genotype.
SA = *Spartina alterniflora*
SAS = *S. alterniflora*, short form
SP = *S. patens*
Spartina sediment and adaptations

- Sediment is often anoxic
- Aerenchymal tissue allows Spartina to exchange gases, even when surrounded by anoxic soil
- Presence of fiddler crab burrows enhances Spartina growth, perhaps owing to aeration of the soil
- Marsh ribbed mussels also enhance growth - nutrient addition?
Cross-section of *Spartina* below sediment - note aerenchymal tissue - allows gas exchange
Marsh invertebrates enhance *Spartina* growth

Marsh mussel *Geukensia demissa*  
Fiddler crab at burrow
Grazing on Spartina spp.

- Grazing by invertebrates appears to be relatively slight - possible exceptions
- This may be a response to the tough leaves, rich in cellulose, which also has silica
- Grazing on flowers, however, may be far greater, resulting in frequent failures of seed set
- Southerly areas - snail *Littorina irrorata* does damage while feeding on fungi, allows further colonization of more fungi
Trophic Cascade, southeastern salt marshes

Carnivorous crabs

$Littoraria$

$Spartina spp.$

Silliman 2001

Ecology
Fungal invasion of wound in *Spartina* – snails attack!

Silliman, B. 2001, *Ecology*
Vertical zonation

• Salt marshes exhibit the intertidal phenomenon of vertical zonation
• From low to high intertidal one often finds: *S. alterniflora*, *S. patens*, *Distichlis spicata*, and *Juncus gerardi*
• The borders between zones are often quite sharp
Salt tolerant

Less tolerant of salt
Competitively superior,
Dense rhizome system
Vertical zonation

• Lower intertidal species such as *Spartina alterniflora*, are more salt tolerant than high intertidal forms, but low intertidal forms are not physiologically limited from growing in high intertidal area

• High intertidal species are competitively superior to lower intertidal forms, but are not able to survive the longer exposure lower down to salt
SALT MARSHES IN RETREAT

- FILLING IN TO BUILD SUBURBAN HOUSING
- NUTRIENT ADDITION – INCREASES SHOOTS DECREASES RHIZOMES
- SEA LEVEL RISE?
- HERBIVOROUS CRABS?
- POISONED SALT MARSH SOIL/PEAT?
- HUMAN TRAMPLING
Mangrove Forests

- Dominated by species of mangroves, common in subtropical and tropical protected shores around the world
- Mangroves broadly rooted but only to shallow depth, in quite anoxic soils
- Underground roots have projections into air that allow gathering of oxygen
Tropical-subtropical distribution
Mistletoe and mistletoebird

Casuarina cunninghamiana

Amyema cambagei

Dicaeum hirundinaceum
Roots types, leaves, fruits and seedlings of a mangrove

FIG. 14.43 (a) A typical mangrove tree, showing the root systems. (b) Fruits and seedling. (b after Tomlinson, 1986.)
Salinity: Differential Effects on Species - Zonation
Mangroves are very salt-tolerant plants, and leaves of some spp have a salt gland (left), which can excrete salt from cell cytosol to the leaf surfaces (right).
Mangrove Forests: Important Features

- High primary productivity
- High supply of particulate organic matter, especially falling leaves, which subsidize animal growth
- Zonation of mangrove species
- Roots support a rich assemblage of sessile marine invertebrates
Mangrove forest along a salt creek in Mexico
Oyster Reefs –

Range from estuarine subtidal to more
Open coast intertidal

**FIG. 16.52** An intertidal oyster mound of the eastern oyster *Crassostrea virginica* in South Carolina (left) with a closer look at a cluster of oysters (right). (Photos by Loren Coen)
East and Gulf coasts –
Eastern oyster *Crassostrea virginica*

West coat
Olympia oyster, *Ostrea lurida*
Plus invasive asian oyster *Crassostrea gigas*

Oyster reefs greatly depleted around the world
Less than 20 percent left

Aquaculture is now main source of oysters for food
Intertidal Oyster Farm, East Sound Washington
Focus on eastern oyster *Crassostrea virginica*

**Low salinities:** slow growth, but no oyster disease

**High salinities:** fast growth, but disease, predators (oyster drill)
Oyster Reefs:

1. **Require steady bed of shell** – allows larvae to settle on shell and not die in mud

2. **Dredging removes shell faster than it can be replenished by oyster growth** – bad management in Chesapeake Bay (most oyster reefs gone) much better in Delaware Bay (oysters better managed)

3. Oysters in serious need of restoration to bring back reefs.
Oyster reefs benefit environment:

1. In shallow water – clear water of phytoplankton and enhance
   Water clarity for sea grasses

2. Oyster reefs attract many species, e.g. fish

3. Oyster reefs enhance denitrification, reduce nitrogen load in sediments of estuaries
Oyster Restoration Projects - New York Harbor and Haverstraw Bay

Factors in Successful Restoration:

1. Growth rate, survival (water quality), physiological condition, reproduction, disease

2. Sustainability - requires larval source OR establishment of new metapopulation network of reefs, retention of larvae within system

3. Habitat - Suitable bottom, use of artificial reef substrata – need shell

4. Compatibility of restoration with ecosystem function, properties of native populations (e.g., question of introduction of new genotypes, where necessary)
The End