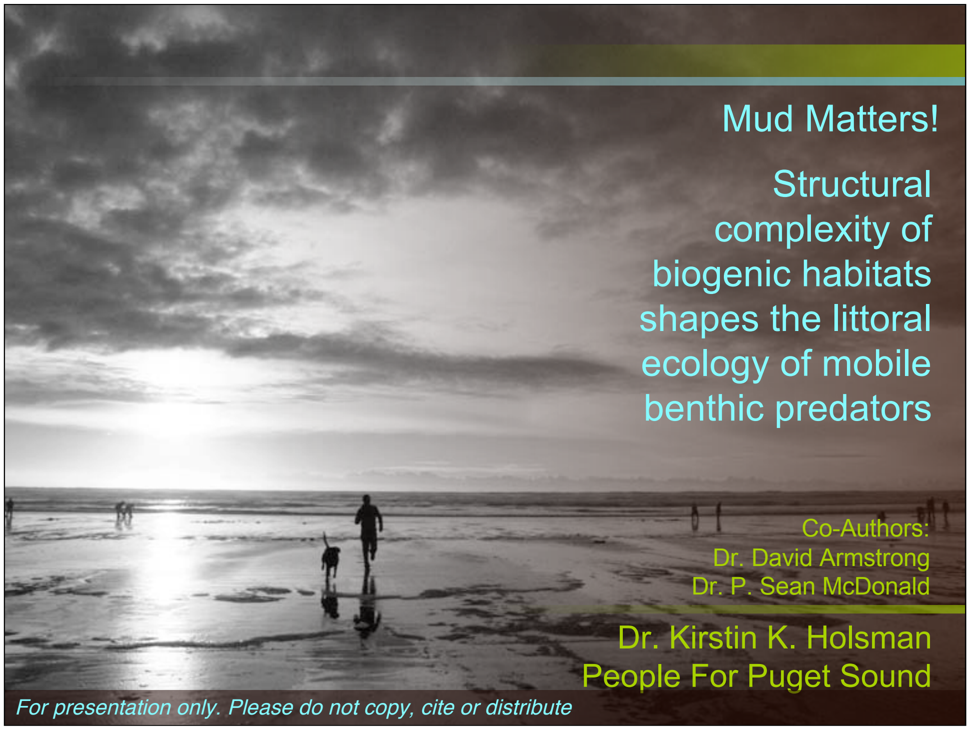
Mud Matters!
Structural complexity of biogenic habitats shapes the littoral ecology of mobile benthic predators
Co-Authors:
Dr. David Armstrong
Dr. P. Sean McDonald
Dr. Kirstin K. Holsman
People For Puget Sound
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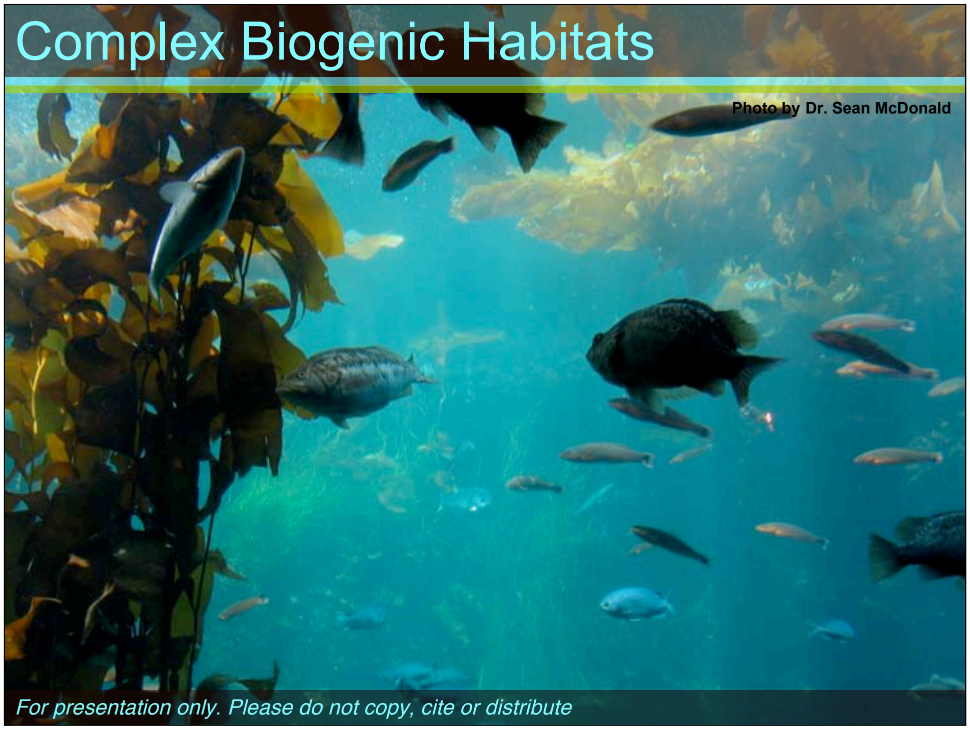
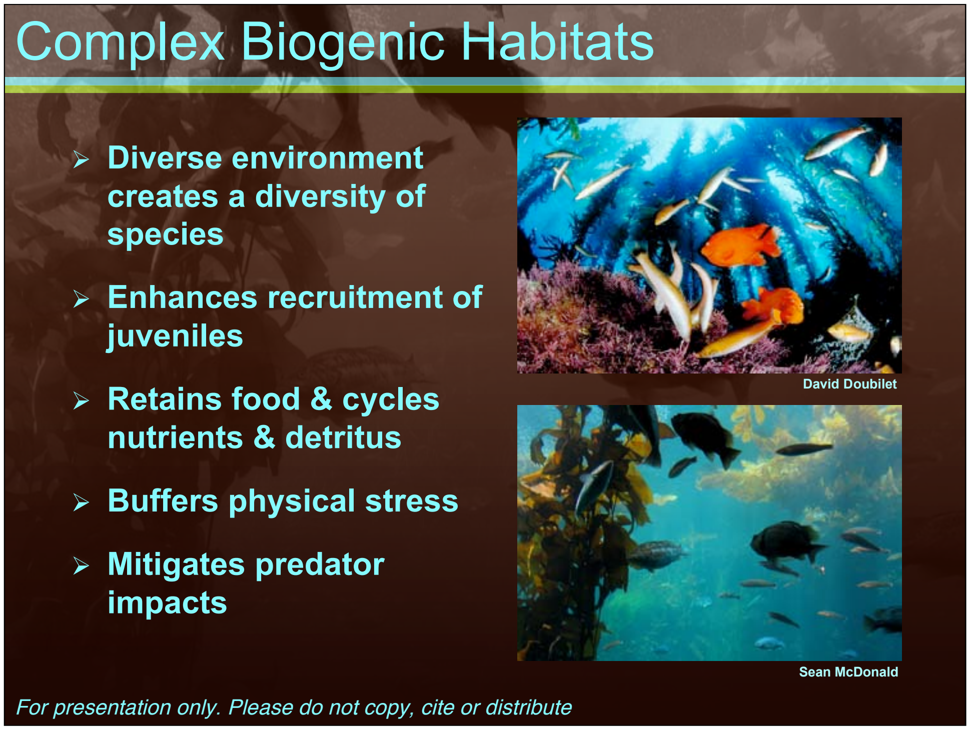


Introduction to biogenic habitats: Biogenic habitats, or “living” habitats, are areas created from the physical architecture of an organism as it grows. For example when numerous kelp plants grow up to form a kelp forest, the kelp forest they create is a type of biogeneic habitat.A relevant corollary for today’s symposium would be oyster reefs that are formed from individual oysters as they grow. The key is that these engineering organisms create three dimensional structure in areas that otherwise wouldn’t have them, and because it is a living organism that form these habitats, they are dynamic and constantly changing.



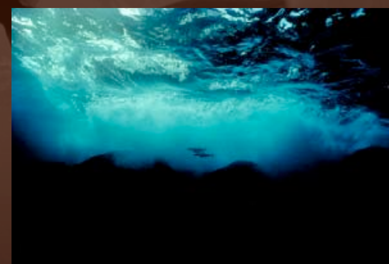
Biogenic habitats tend to be hot beds of species diversity and abundance, and so as you might expect, biogenic habitats have received a lot of attention in ecology and conservation.

What we now know is that abundance of species and organisms living in and around these habitats result from a combination of various physical properties that influence the biotic systems around these areas.

First, the architecture of biogenic habitats often alters the flow of water around these structures and especially affects boundary layer processes right along the surface of the habitat in ways that enhance the recruitment and retention of larvae and the cycling and retention of food and nutrients.

Complex Biogenic Habitats

- Diverse environment creates a diversity of species
- Enhances recruitment of juveniles
- Retains food & cycles nutrients & detritus
- Buffers physical stress
- Mitigates predator impacts

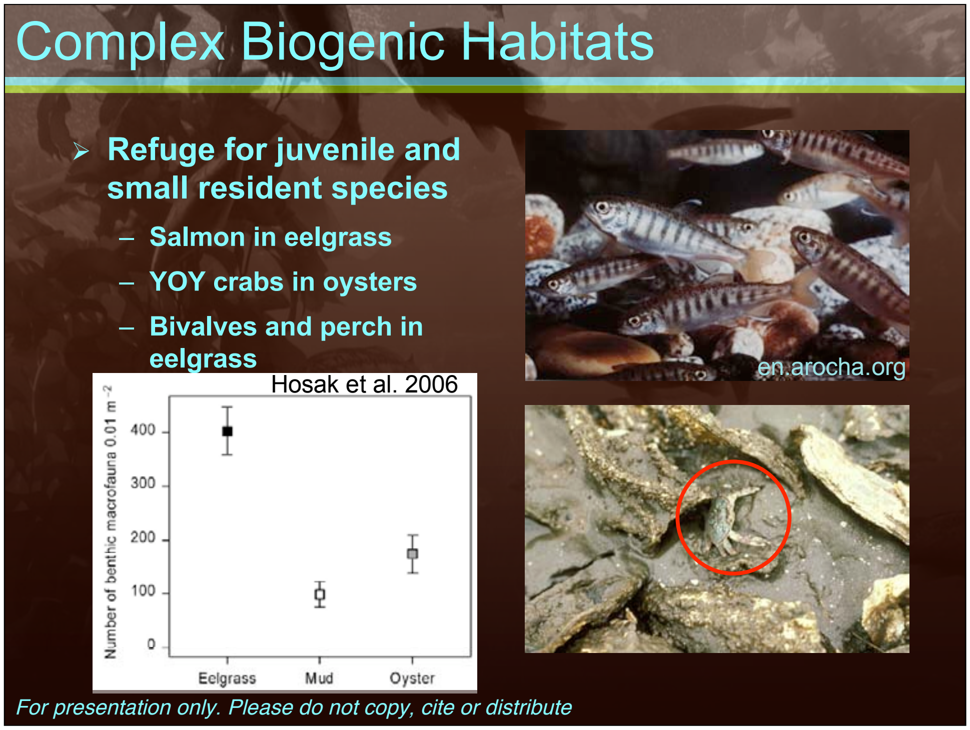


David Doubilet

David Doubilet

Complex bioegenic habitats also buffer resident species against fluctuating environmental conditions by providing them with protection from environmental stresses like wave action or desiccation.

The structure of these habitats also mitigates predator and prey interactions by providing places for prey to hide or escape predators.



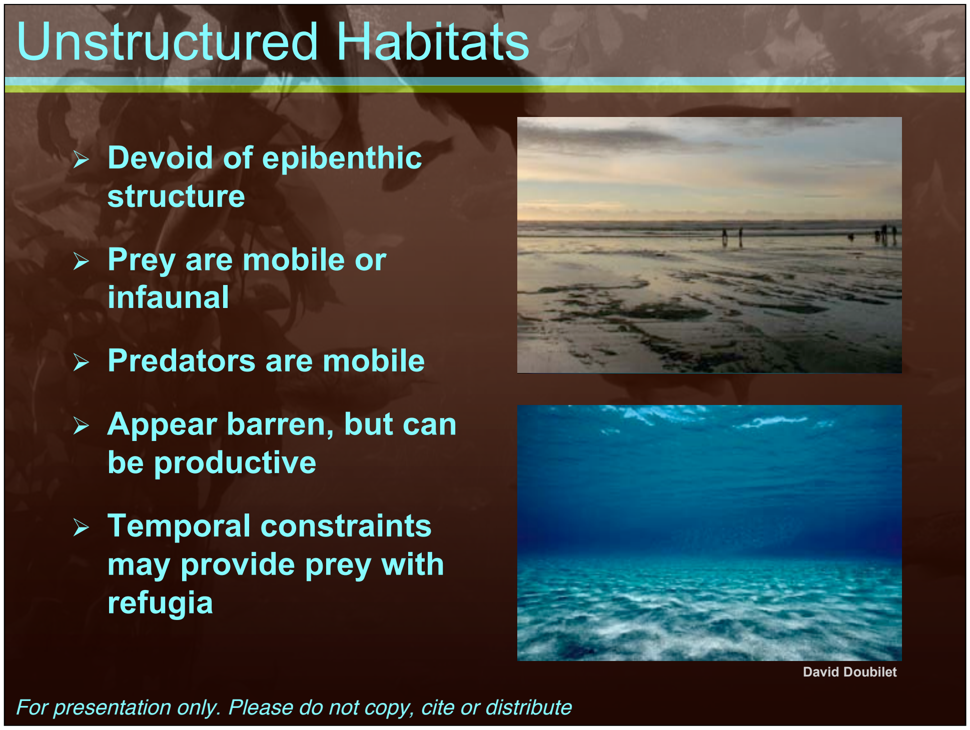
So in general biogenic habitats are considered ecologically valuable because they increase the diversity and biomass of so many species, particularly small resident and juvenile species.

A common local example is the nursery role of eelgrass beds for juvenile salmonids, and of course that relationship has become the center of salmonid management in our region.

In addition, a number of studies conducted by Dr. Armstrong and his lab showed that predation is lowest and survival is greatest for young of the year dungeness crab that settle into on-bottom oyster culture and eelgrass beds. Because juvenile survival is considered a bottleneck to adult populations, these complex shell habitats are considered critical habitats for dungeness crab.

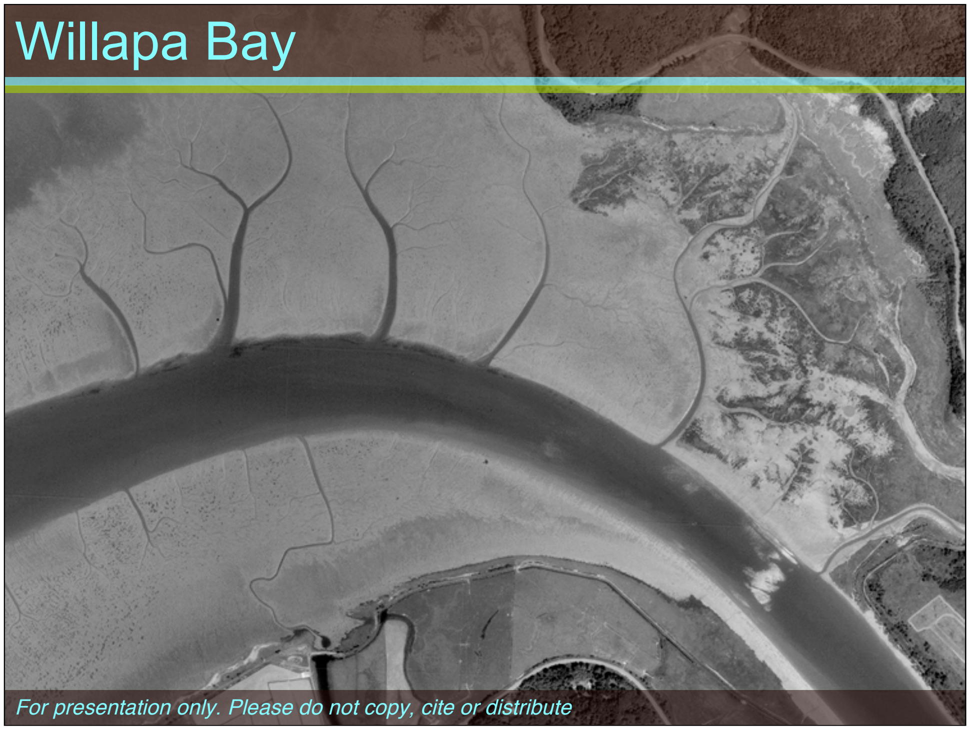
Small resident species are also often found in high abundances in biogenic habitats - this graph here by Geoff Hosak shows that density of small macrofauna in small benthic cores collected from eelgrass, mud, and oyster habitats is is highest in biogenic habitats.

Since biogenic habitats are often nursery areas for juvenile species, increasing habitat complexity is generally considered a good objective to conservation and restoration goals.



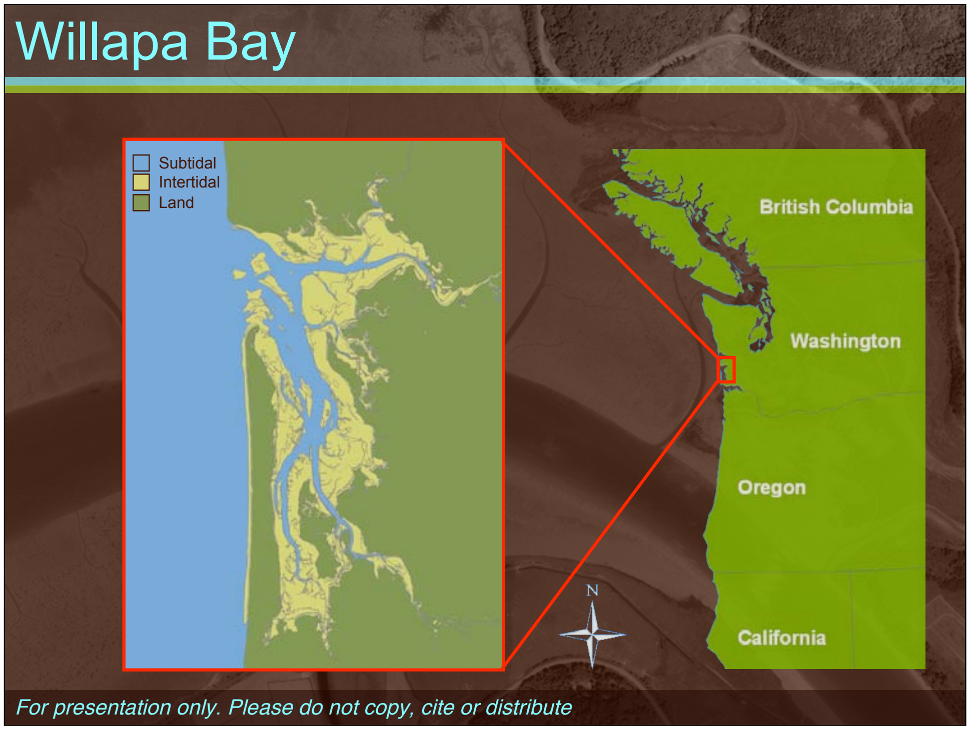
Yet the benefit of biogenic habitats to small resident prey species is at the cost of reduced foraging efficiency of migratory predators visiting these areas. Depending on the foraging constraints of these predators (for example their efficiency at locating and capturing prey) , unstructured areas that lack epibenthic, or above ground structure, may actually be more beneficial, since predators can move quickly through these areas searching for food.

Thus in these unstructured areas foraging efficiency of a predator can be higher than in structured habitats even though prey are more widely dispersed.



This relationship between predators and prey and complex habitats intrigued us, and in this study we wanted to explore how habitat use and foraging behaviors of a migratory predator might change across a range of habitat complexities.

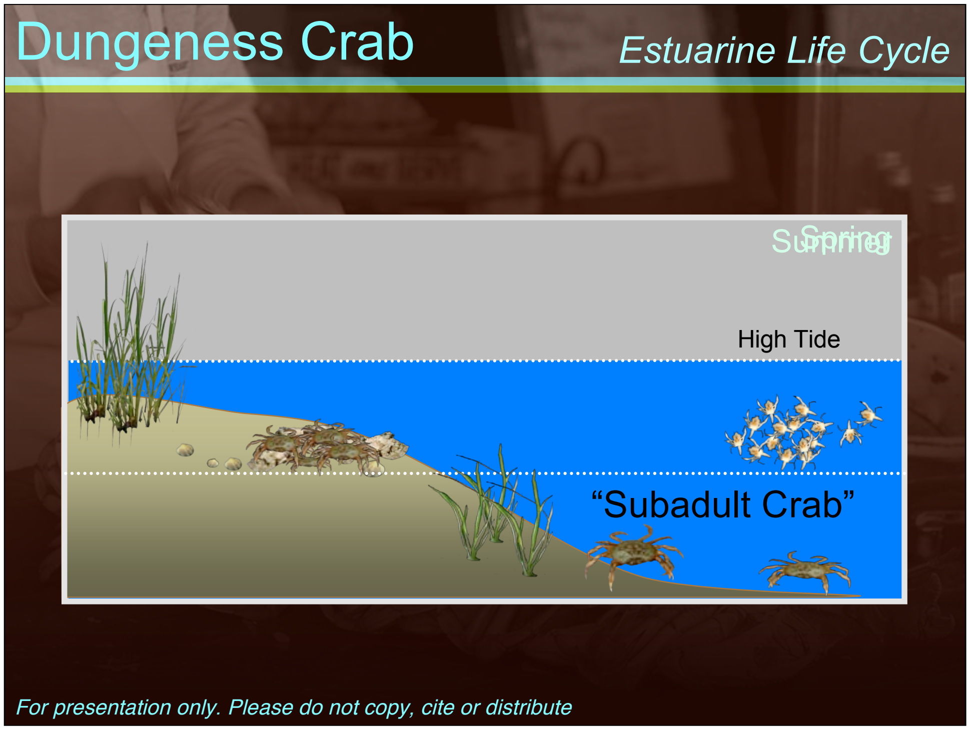
And what I want to talk about today is how unstructured littoral or intertidal habitats are important to mobile predators, especially in estuarine systems.



Most of this work I will talk about today primarily took place in Willapa Bay, WA.

Willapa Bay is located in the southwest corner of Washington, just north of the Columbia river estuary.

At 32,000 Ha at MHHW, it is a relatively large bar built system by west coast standards. About 55% of the bay is intertidal so large tides drain the system twice daily exposing a wide mosaic of intertidal habitats that range in habitat complexity.



The mobile predator we were looking at was subadult dungeness crab, so I want to take a min now and talk about the two distinct ontogenic stages of dungeness crab in coastal estuaries.

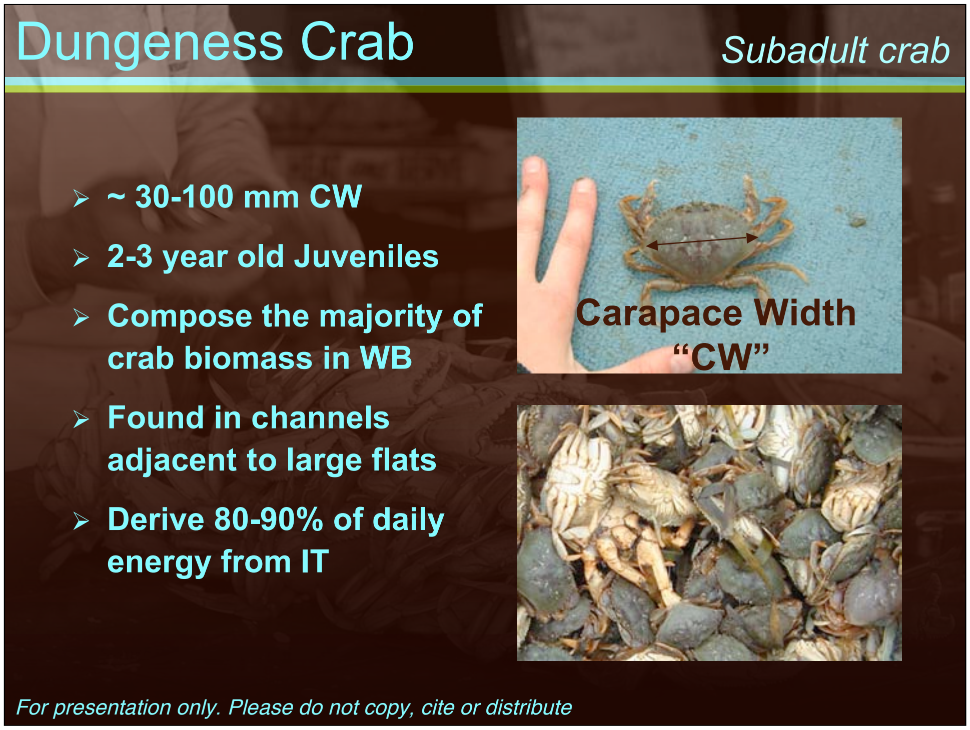
1. Late stage megalope come into coastal estuaries in late spring and settle into intertidal habitats, and as I mentioned earlier, these YOY crab really only survive in biogenic habitats like oyster or dense eelgrass.

2. They’ll spend their first summer or 3 four months in these intertidal habitats, even during lowtide - growing quickly in the protection of this habitats.

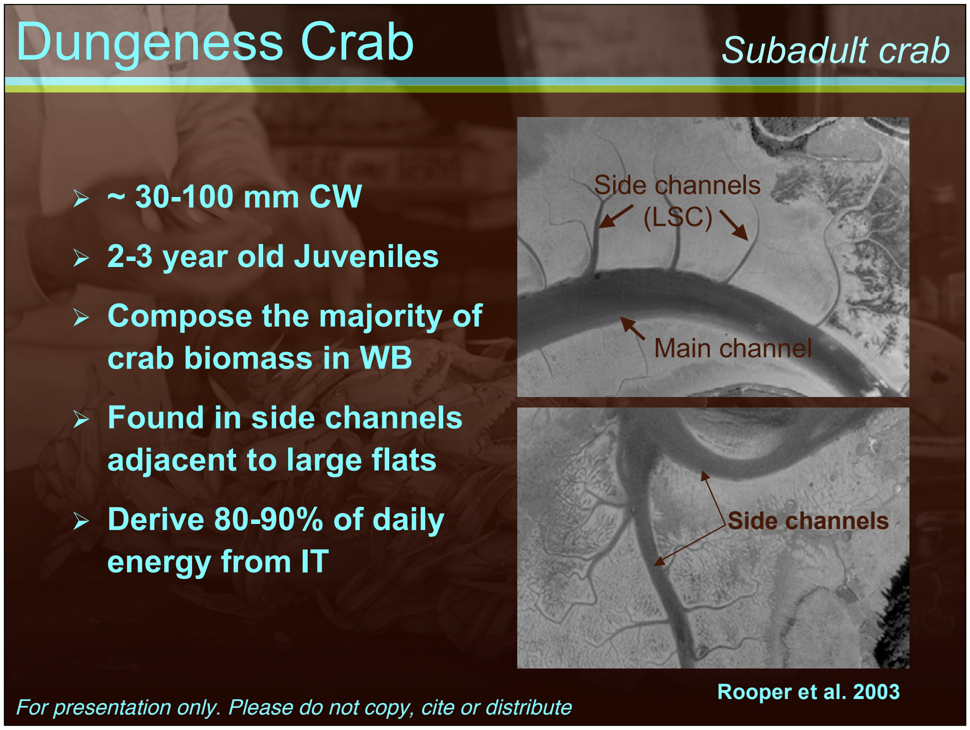
3. At the end of that first summer, once they are large enough to escape most predators, they move down into subtidal channels.

4. Now we refer to them as subadult crab - because they are still juveniles but we want to distinguish them from these younger juveniles with markedly different ecology.

Subadult crab will remain in the system for 2-3 years until they are mature and then the emigrate out of the estuary into nearshore coastal environments and we rarely find adult crabs in estuaries, they seem to leave once they are mature.

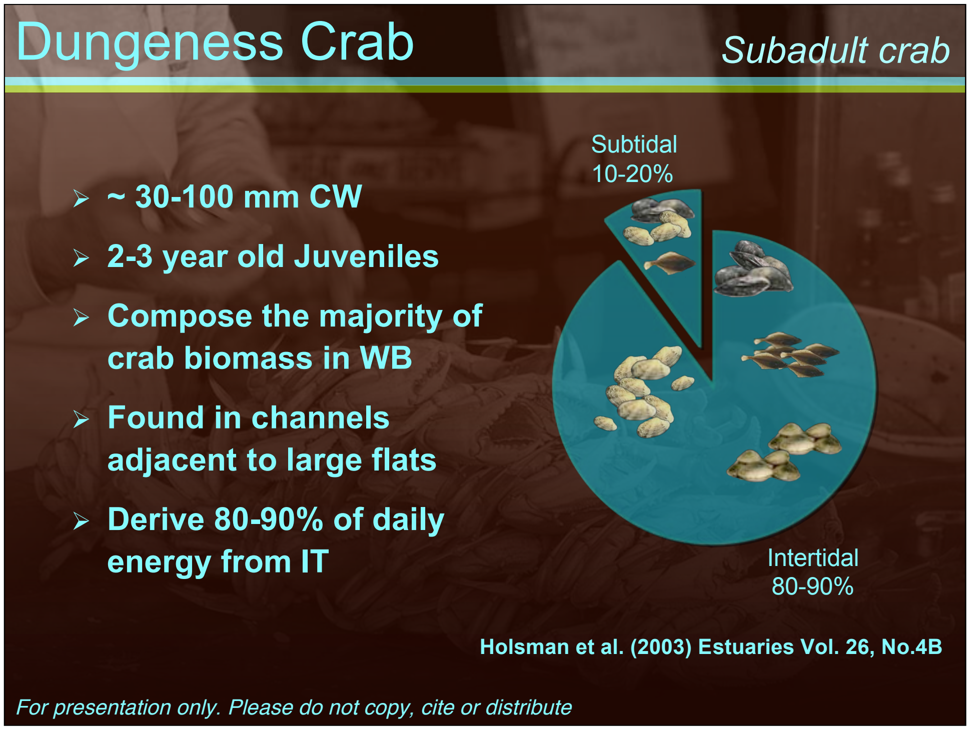


So these subadult crab these are 2,3, and 4 year old crab - not yet reproductive - and they are found in estuaries in extremely high abundances.



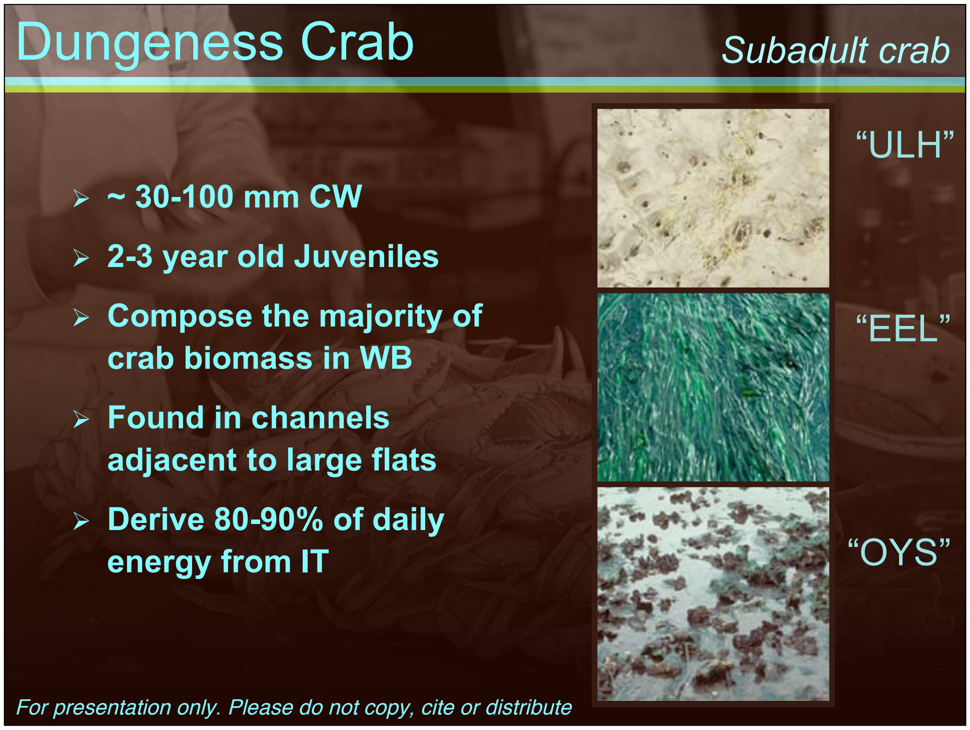
And some work that Chris Rooper and David Armstrong did showed that highest density of subadult crabs are consistently found in secondary subtidal channels of coastal estuaries.

In Willapa bay, 65% of the population of crabs are concentrated in small side channel habitats, and there are just hundreds of subadult crab packed into these channels at low tide.

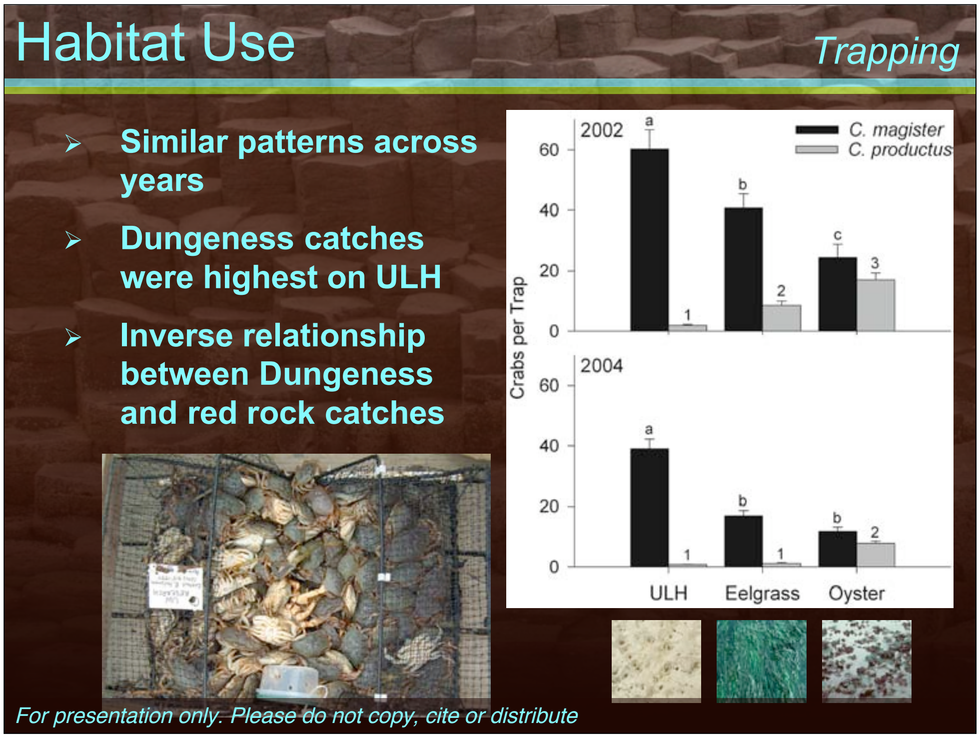


•We compared the energetic demand of crab in these areas to available prey in subtidal and intertidal areas and we essentially found that prey resources in subtidal channels were insufficient for supporting dungeness crab production rates there. Even when we included prey production into the model, and assumed that crabs were the only thing foraging on these prey in the channels, subtidal prey resources could only satisfy between 10-20% of the daily energetic needs of crabs in the area, and that meant that they were deriving the remaining 80-90%of their energetic needs from the intertidal areas.

•This formed the basis for the study that I am going to briefly talk about today, where we really wanted to get at if and when crabs were making migrations and where they were going to in the intertidal.



•And we primarily looked at differential habitat use between three dominate habitat in the system - mud and sandflats which you will hear me refer to as ULH or unstructured littoral habitats throughout today's talk, eelgrass beds, and on-bottom oyster culture.

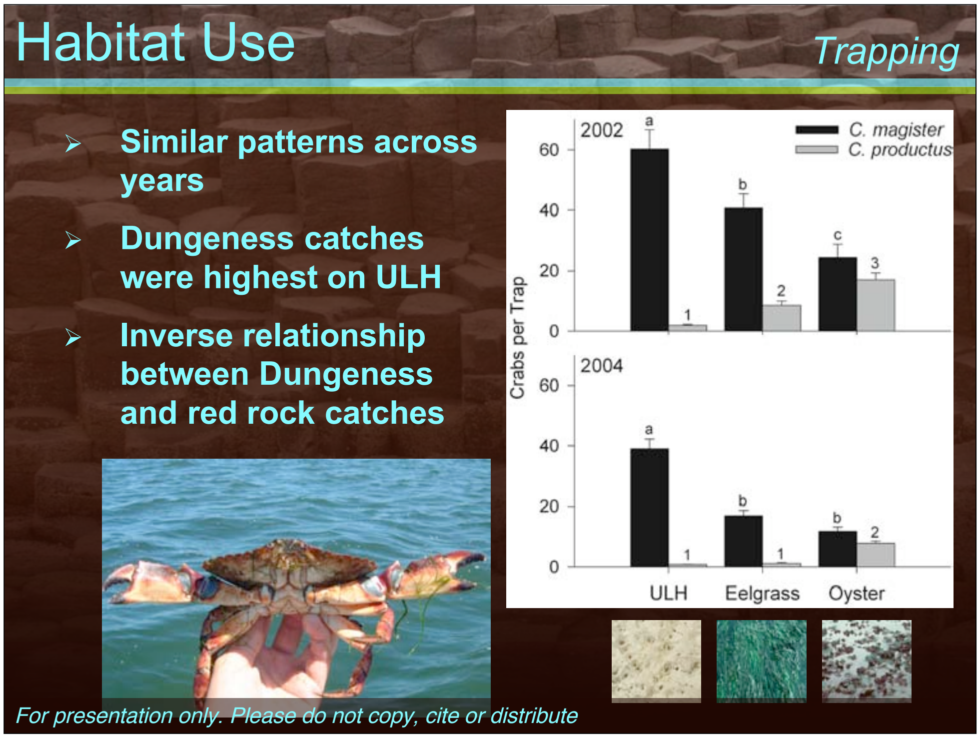


One of the first things we did was deploy trapping arrays at five sites across the bay that each had mud, eelgrass, and oyster habitats.

Shown here is a graph of the mean number of crabs we captured in traps placed on the three intertidal habitats for both 2002 and 2004. Let's focus first on the black bars first,and what you will see is that catches of crab are highest in unstructured habitats and lowest in on-bottom oyster culture.

This highlights an important ontogenetic shift in habitat use for juvenile dungeness crab, since you will recall that on- bottom oyster culture is so important to young of the year crab but these older age classes don't appear to use them as much.

It's likely that the physical structure of eelgrass and oystershell, which provide protection for many small prey species, including young of the year crab which are often cannibalized by older crab, interferes with the foraging effectiveness of migrating subdaults, by hindering their movement.

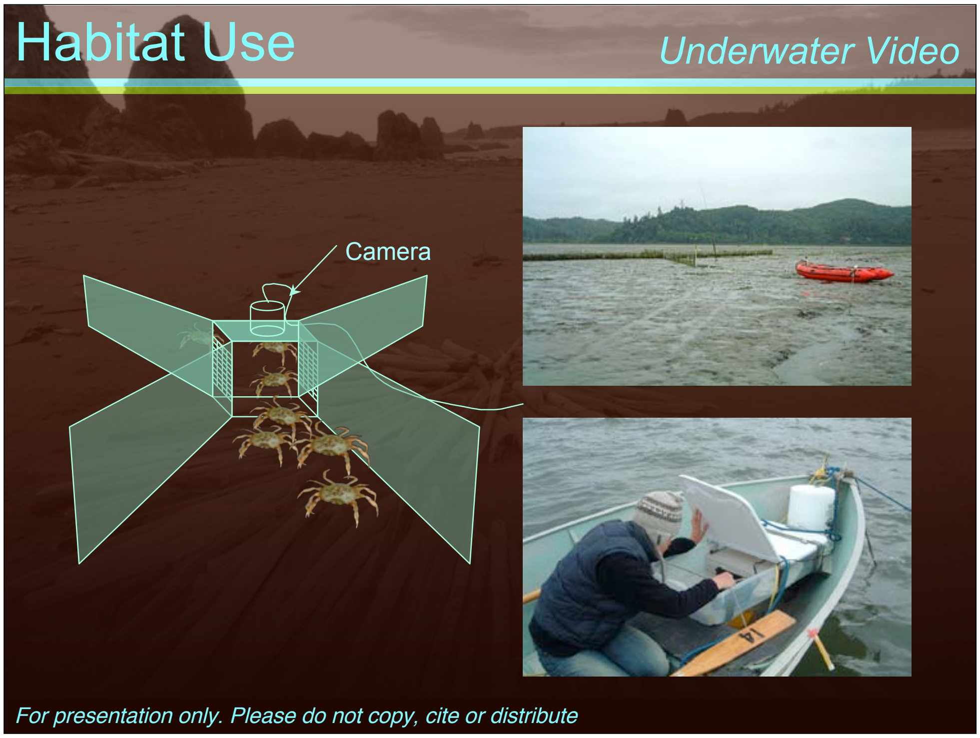


I also want to point out that we an inverse relationship between the catches of dungeness crab and this close relative the red rock crab, which are shown in the grey bars.

In contrast to Dungeness, we caught more red rock crab in oyster shell and almost none on ULH.

And anecdotally, some great research conducted by Adam Admunsen for his undergraduate thesis indicate that this species is resident in oyster beds and remains there even at low tide.

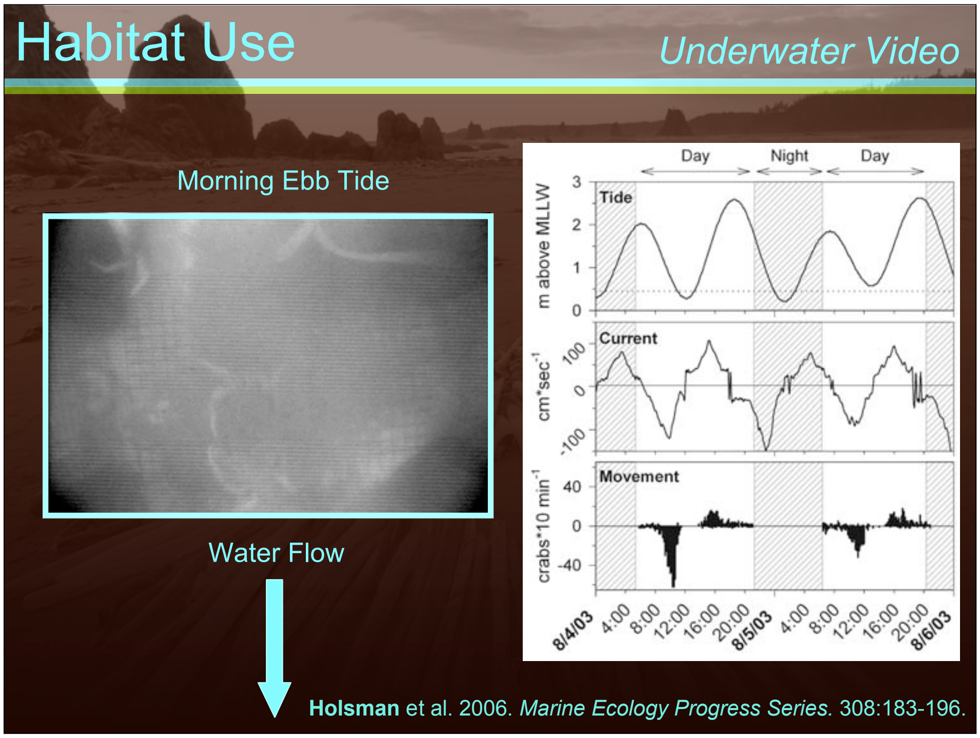
Since these are fairly aggressive crabs they could potentially be excluding dungeness from the more structured areas where they reside.



From our trapping studies alone we couldn't rule out the possibility that we were luring crabs into the intertidal with our baited traps so we also conducted some passive observations.

The first passive study I will talk about is our underwater video observations. For this we modified a design originally implemented by Dare and Edwards to examine migrations by green crab in Europe.

And what we have is a fyke or funnel shaped gate with a camera mounted at the constriction pointing downward and recording crabs as they move on and off of the flats.



On the left here we have some video showing crabs migrating off of a tide flat during a morning ebb tide.

Water is flowing from the top of the slide downward, and what you should be able to see is that crabs are moving with the tide.

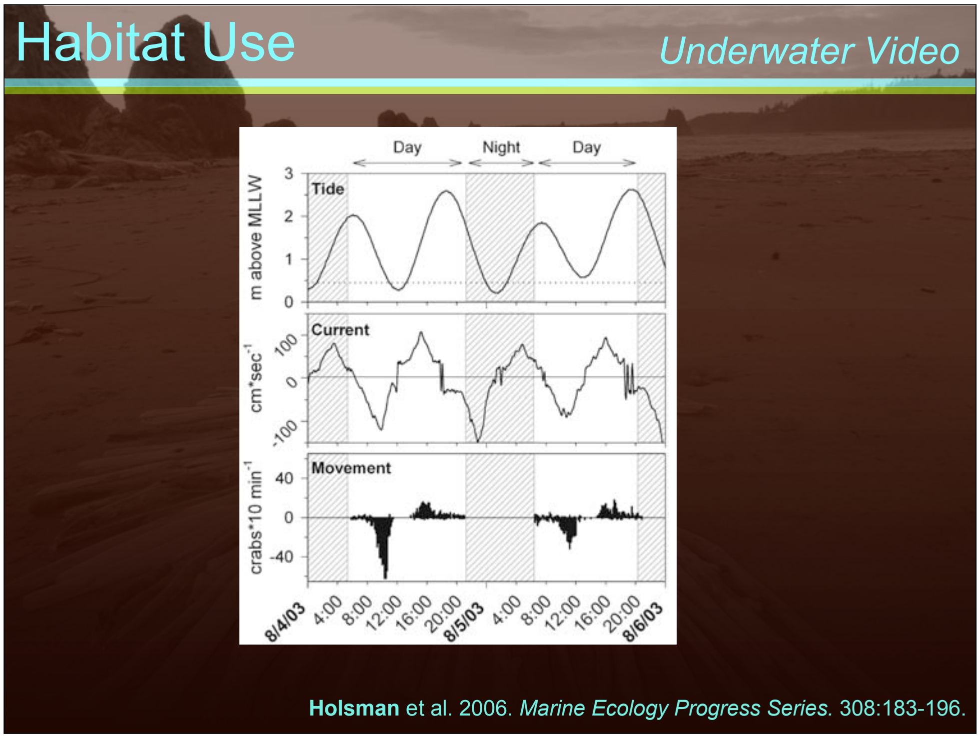
On the right we have a three panel figure which encompasses a two day snapshot of the study - gray areas indicate nighttime periods.

In the top panel we have water height in meters, showing the tidal periodicity.

Below that we have current velocity in an adjacent channel during the same time, and then lastly we have the rate of crabs moving per 10 min period.

And note that in the grey area here the visibility of the camera was severely reduced so we didn’t include the data.

And basically what we found is that migrations are tightly correlated with current velocity and direction,so crabs appear to be responding tidal cues for migration.


Habitat Use
Underwater Video
Day
Night
Day
Tide
m above MLLW
3
2
1
0
Current
cm*sec-1
100
0
-100
Movement
crabs*10 min-1
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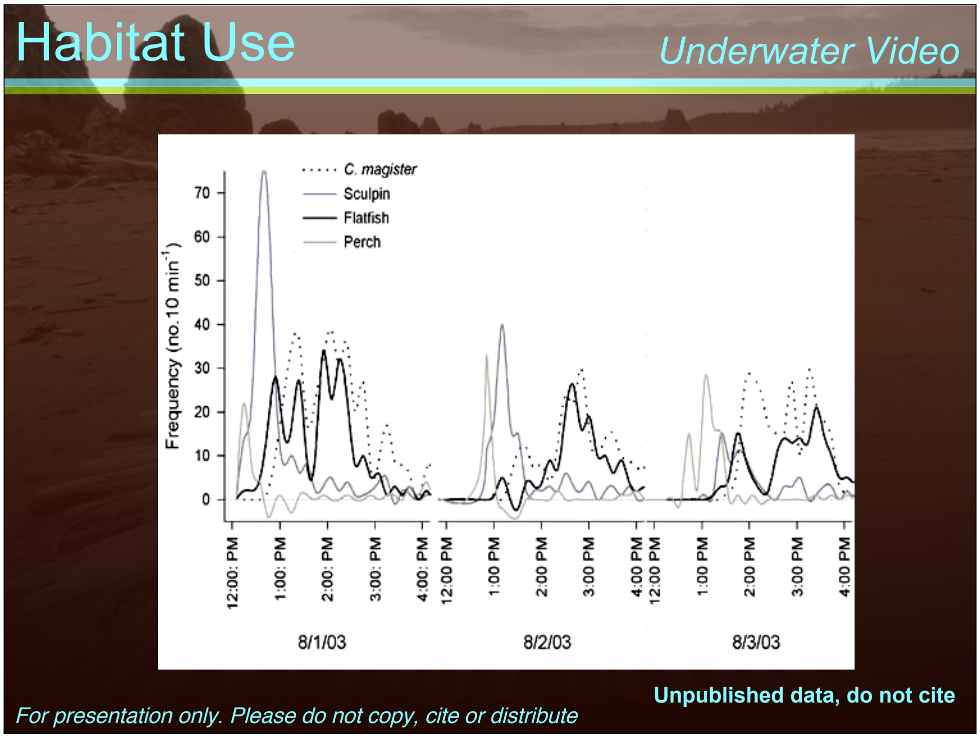
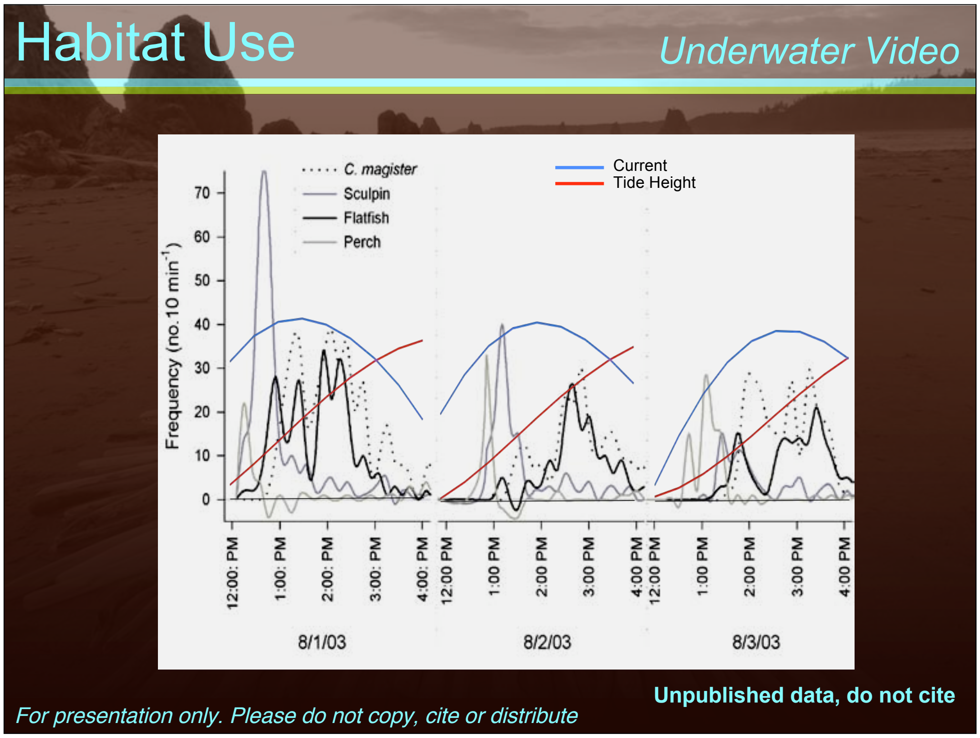
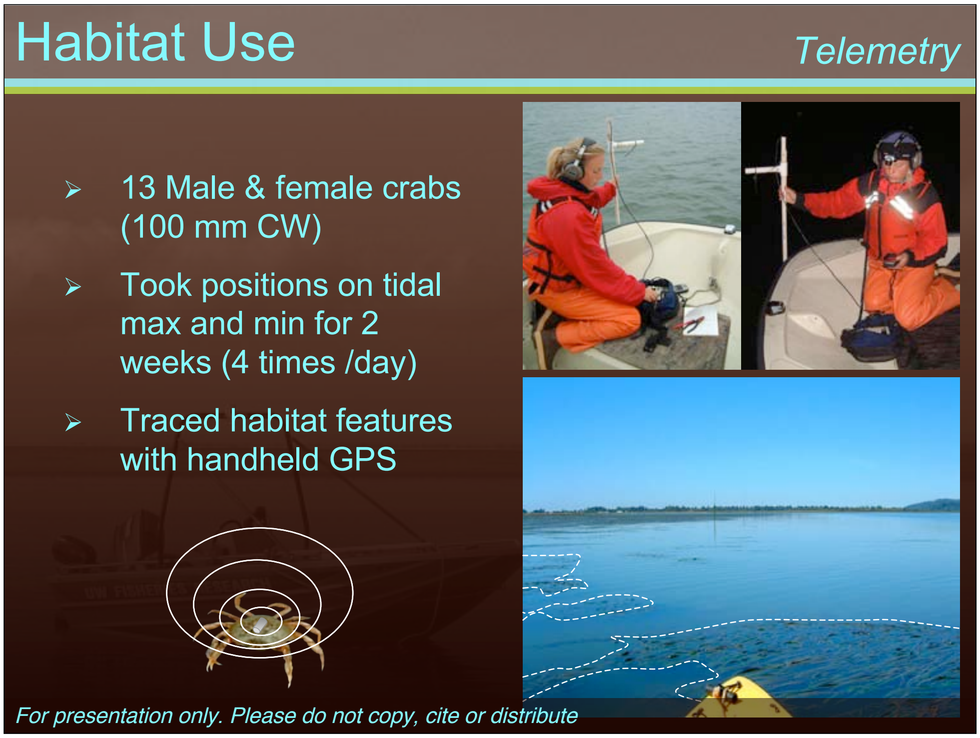
Holsman et al. 2006. Marine Ecology Progress Series. 308:183-196.



We also recorded the movement of other species on and off the flats and I want to show some data on the number of fish and crab moving onto the unstructured mudflat during a flood tide. Here we have a 4 hour snapshot of an flood tide for three consecutive days.



And when we overlay current and tide height two different patterns emerge. First, as I mentioned before you can see both crab and flatfish move up onto the flats during max current flow, and as the speed of water moving onto the flats slows down, so does the rate of their migration. In contrast, perch and sculpin are the first to go up onto the flats and they don't seem to respond to current flow, but rather seem to rush up once the water is deep enough.The other thing I want to point out is that as the tidal amplitude decreases so does the magnitude of migrations.

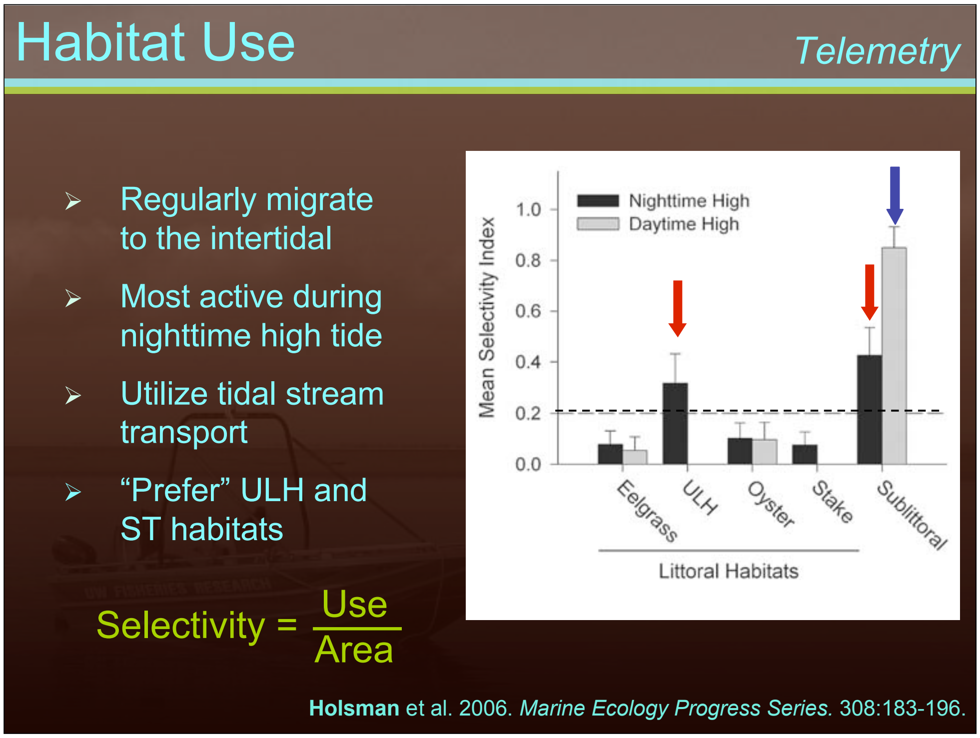


So the last thing we did was some manual acoustic telemetry on crabs

So for this we tagged and released 13 crabs and tracked them for two weeks straight, taking positions on each tidal maximum and minimum – or 4 times daily.

And we did this in order to avoid problems of autocorrelation that can accompany continuous tracking of animals.

At this time we also mapped habitat features in the area on foot or by kayak -with a handheld GPS.



Now we also did selectively analysis on the frequency of observations in each habitat - and essentially this corrects habitat use for variation in habitat availability.

All other things being equal, if a crab is randomly wandering into a habitat then selectivity would be equal for all 5 habitats and the value of the index would be 0.2, or 1 over 5.

So anything below this 0.2 threshold indicates avoidance, anything above it indicates preference.

So here are our mean indices for crabs during nighttime and daytime high tides.

So what should jump out here is that during daytime high tides (blue) crabs prefer subtidal channels, despite access to other habitats.

And during NH tides (red) some crabs prefer subtidal channels as well as ULH, again avoiding the other more structured biogenic habitats.

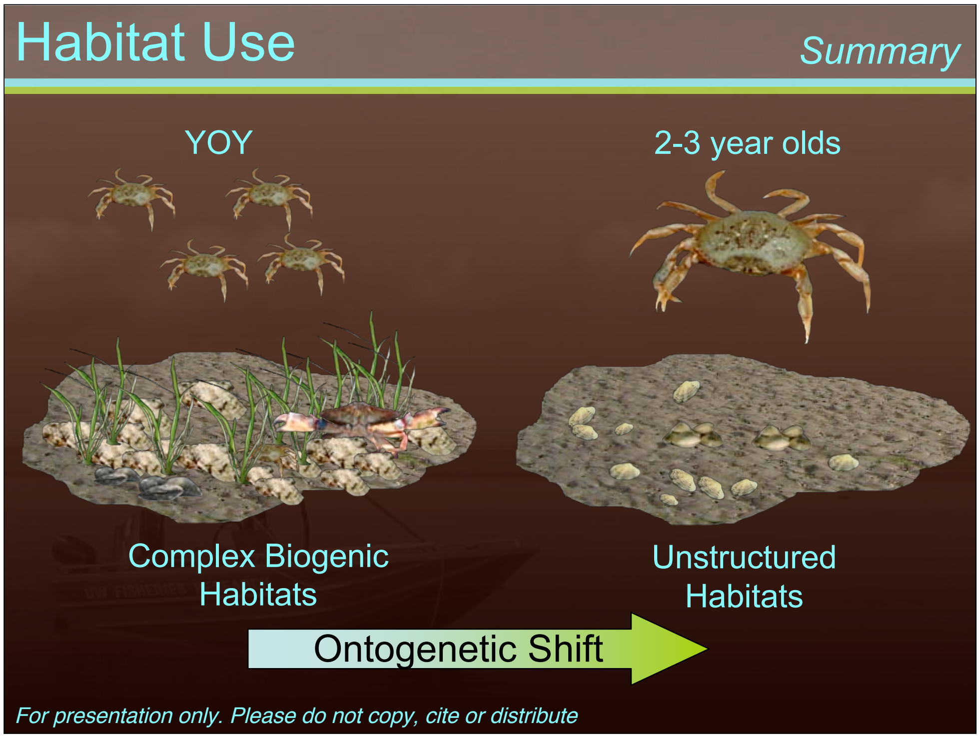
Habitat Use

Summary

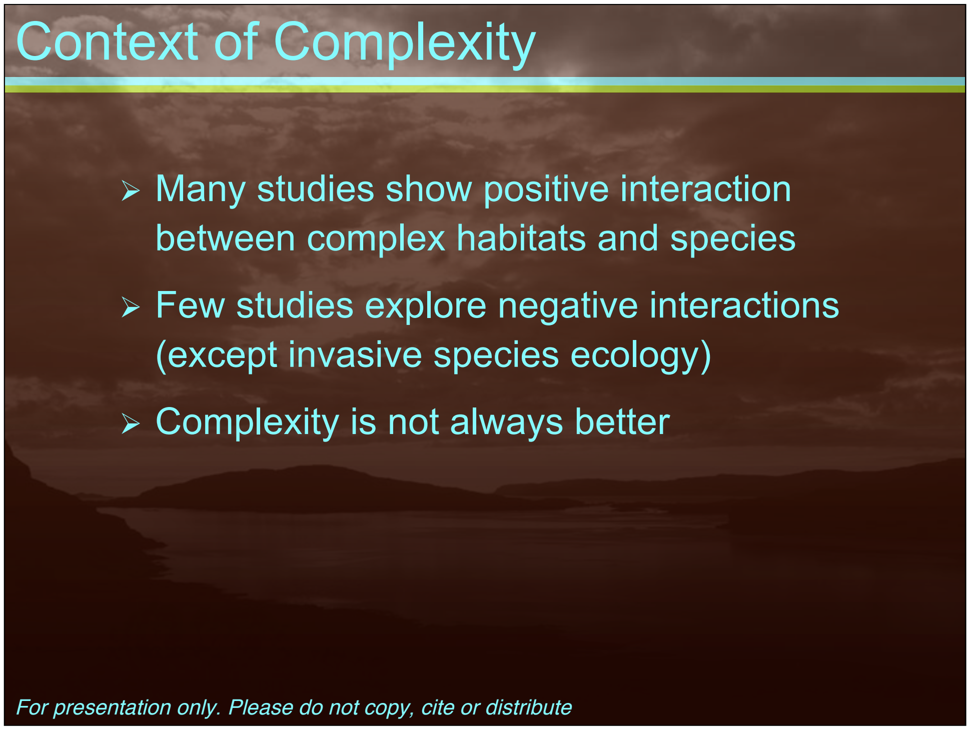
- Field studies showed that crabs regularly migrate to the intertidal to forage
  - Migrate with the tide, possibly utilizing tidal stream transport
  - Nocturnal migrations are greatest
  - Most often utilize unstructured intertidal habitats
  - Crabs avoid structured biogenic habitats

Holsman et al. 2006. *Marine Ecology Progress Series.* 308:183-196.

In summary, we saw that crabs regularly migrate into the intertidal during nighttime high tides, and they mostly move into unstructured habitats.



And what we were seeing is an otogenetic shift in habitat use, where young small crab use structured habitats for a short period of time and then primarily use unstructured areas. And this is something that Lipcius and others have seen in blue crab on the east coast, and has been observed for many commercial fish species. I just want to reiterate that these subadult crab have few predators in this system, and thus the patterns in their habitat use is likely driven by trying to avoid inter- and intra- specific competition, physical interference with structure (which may reduce foraging efficiency), and stranding during lowtide which can often result in mortality. And all of this is intensified by the temporal constraint of the tides, they only have a narrow window of time to forage and so they move into ULH because their efficiency is highest there. From that habitat they can locate prey in ULH or forage along the edges of structured habitats.



I'd like to end today with talking for a min about the context of habitat complexity. In contrast to all of the investigations of the positive interactions between complexity and species, far fewer studies have explored the negative interactions between species and complex habitats.In fact, really the few studies that do illustrate negative interactions are investigations of invasive ecosystem engineers which alter habitat structure and often increase complexity thus excluding native fauna. This paradox of habitat complexity is debated in invasive ecology, and illustrates how even ecologist have difficulty putting aside the belief that complex biogenc habitats are beneficial even when they're not naturally occurring. And in closing I just want to emphasize that the blanket assumption that complex habitats are ecologically good for all species is not entirely appropriate, it depends on the context of habitat complexity under the modifier of temporal constraint. What is important is the mosaic of structured and unstructured habitats, it is the mix of both that is important. We heard earlier from the other panelists that we need to have a landscape perspective towards habitat management, and that is absolutely true - many species need the mix of structured and unstructured areas throughout their life-history.

Photo Credit: Protect Our Shoreline 4/29/06

How does adding artificial structure to the intertidal affect mobile predators?

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Yet ULH are often overlooked and very few studies demonstrate the importance of ULH, and as a consequence there is little to no protection of unstructured littoral habitats in coastal estuaries. And in Puget Sound there are a number of activities, including aquaculture, that are increasingly altering intertidal unstructured areas and we really can't evaluate what the ecological consequences of these alterations might be because there is little work exploring the mechanistic relationships between unstructured habitats and marine species that use them.

I think we really need to move away from only conducting low-tide quadrate or infaunal core surveys; these tell us a lot about the small resident species in these areas but don't give us any idea about large mobile predators and prey that move through intertidal habitats. We need to really design studies that can quantify both daytime and nighttime abundances of species in structured and unstructured habitats so that we can appropriately asses the impacts of human mediated alterations on marine systems.

“But almost always the essence of the lives - the finding of food, the hiding from enemies, the capturing of prey, the producing of young, all that makes up the living and dying and perpetuating of the sand-beach fauna-is concealed from the eyes of those who merely glance at the surface of the sands and declare them barren.”

Rachel Carson

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