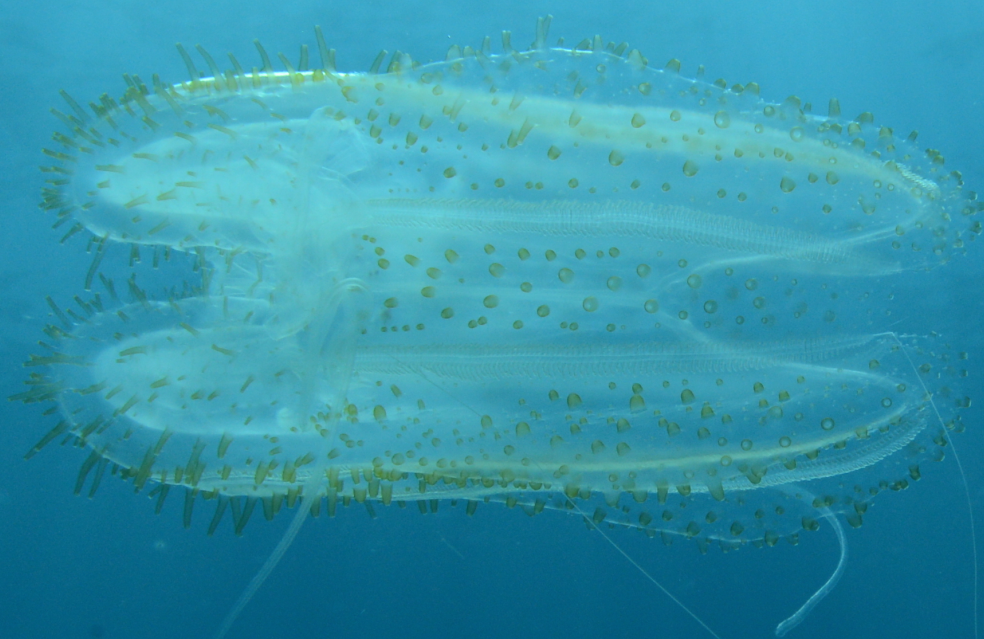


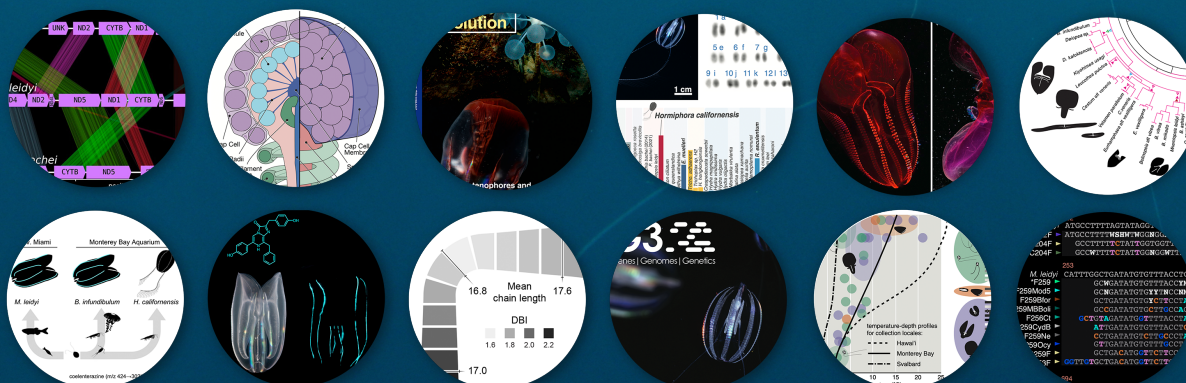
Project Outcomes Report



**Diversity, Evolution, &
EcoPhysiology of
Ctenophores**



**Co-PIs: Steven Haddock, Erik Thuesen, Joseph Ryan
2015 - 2021**



Dimensions: Collaborative Research: Life at extremes: Linking the phylogenetic and genomic diversity of ctenophores to ecophysiological adaptations in the deep sea

NSF Award numbers DEB-1542597, DEB-1542673, DEB-1542679

Overview

The deep sea is more than 90 percent of the inhabitable space on Earth, yet life there is largely a mystery to science. Ctenophores, also known as comb jellies, are marine predators found in all oceans, inhabiting both deep and shallow seas. Although fragile and difficult to study, they are ecologically important components of planktonic food webs. Also, they appear to have been the first group of animals to split off from all other organisms during evolution, even before sponges and jellyfish. Comb jellies are derived from an independent evolutionary lineage than cnidarian jellyfish, and use colloblasts ('glue cells') to capture prey instead of stinging cells. Ctenophores also use rows of cilia, arranged in bands of combs, to swim instead of rowing or jet propulsion. Over evolutionary time, many marine animals have transitioned their home ranges between shallow and deep environments despite the huge differences between these two habitats, including light, temperature, and pressure. Such habitat shifts required dramatic genetic and physiological changes to these animals. In this project, we examined the diversity of biochemical characteristics of ctenophores from around the world, with particular focus on species from representative habitats off California and Hawai'i, and in Puget Sound.

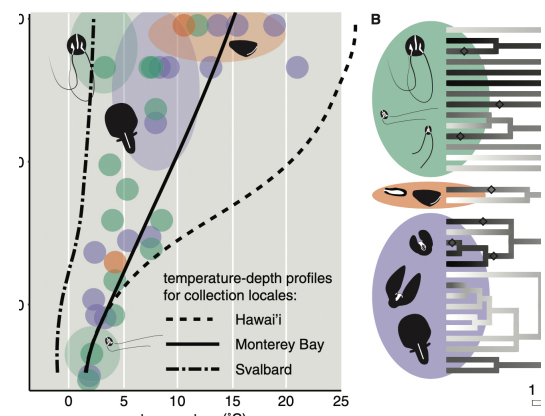
Significant project results

Transcriptome sequencing

Transcriptomes — generated by sequencing messenger RNA — provide a snapshot of all the genes that an organism is using at a given time. Once we have generated high-quality transcriptomes from rare deep-sea species, we can explore a wide diversity of adaptations without collecting more specimens. Our transcriptomes from shallow tropical and Arctic specimens as well as from species living at 4000 meters depth, enabled many of the studies that we have undertaken for the DEEPC project.

Predicting adaptive sites in a gene

Using ctenophores sampled from a range of habitats, we analyzed their genes to identify sites in metabolic enzymes which correlated with environmental parameters. These correlations were done in a phylogenetic context, meaning we could detect whether the patterns were the result of being related, or if they seemed to arise based on habitat pressure.



Metabolic enzymes

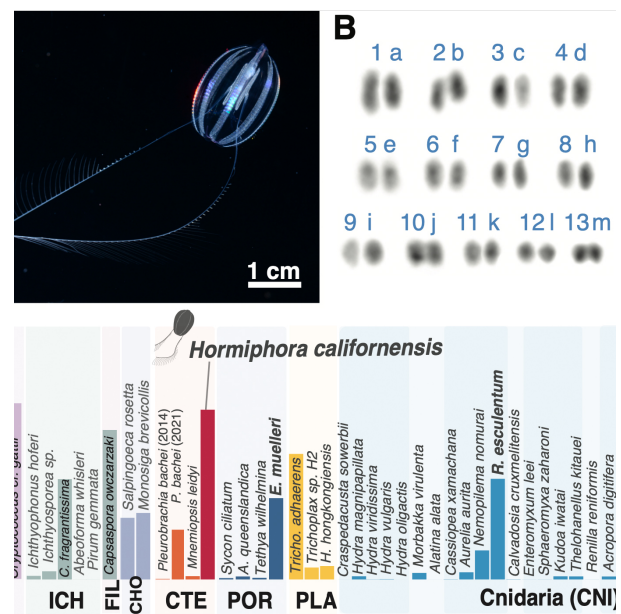
Enzymes are proteins used in metabolism and are important nearly all active processes, like feeding, locomotion, and respiration. Using 320 specimens of 39 species, we described the relationships between activities of metabolic enzymes in relation to biological and environmental parameters. We found a significant positive relationship between creatine kinase (CK) activity and comb plate density. Significant correlation of enzymatic activities to body mass were observed for ctenophore orders, but not at the whole-phyllum level. This demonstrates that the different orders have diverse strategies for coping with metabolic demands. Ctenophores did not display metabolic differences between shallow and deep species, in support of the visual-interactions hypothesis, which predicts no depth-related trend in metabolic differences for animals without vision.

Pressure effects on enzymes

Using 177 specimens from 27 species, we examined the effects of high pressure on 3 metabolic enzymes, CK, malate dehydrogenase (MDH), and pyruvate kinase (PK). Some ctenophore species displayed broad pressure tolerances, while other enzymes functioned best at the pressure of their natural habitat. After treatment, CK and PK showed an abnormal spike upon return to ambient pressure, indicating permanent damage to the protein. Of the three enzymes studied, PK was the most affected by increasing pressures while MDH activity remained relatively stable.

Genome assemblies

Working initially with the species *Hormiphora californensis*, we published the first chromosome-scale ctenophore genome, in which more than 99.7% of the sequence was assembled into 13 chromosome pairs. This was annotated with a hybrid annotation scheme (manual + automatic) to detect many gene corrections relative to previously published genomes. Another interesting feature was doubly-nested genes inserted into the non-coding spaces of entirely different genes. Having such a complete high-quality genome will enable whole new types of analyses going forward with this emerging model organism.

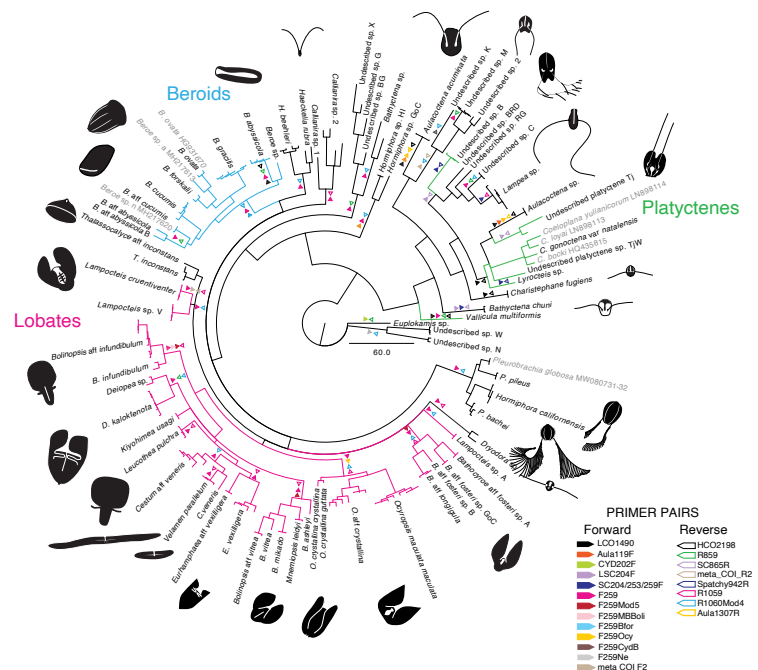
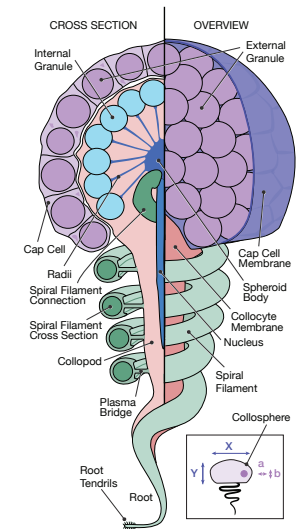


Ctenophore sticky cells

Colloblasts are sticky cellular structures found exclusively in ctenophores, mainly on their tentacles. Using electron microscopy, we prepared an extensive comparative survey of the morphology and arrangement of these fascinating structures, spanning 20 species from across the phylum.

Barcoding primers and population genetics

When people talk about DNA fingerprinting of animals, they typically employ the “barcoding” gene, cytochrome oxidase 1 (COI). Until now, this gene has been barely usable for ctenophores, because their mitochondria, where the gene resides, are so different from other animals. As a result, most “universal” DNA amplification primers are rendered useless. We developed a large set of primer pairs which work across the diversity of ctenophores. We then applied these primers to hundreds of specimens collected around the world, and increased the number of species represented in GenBank by more than 5 fold. This foundation empowers researchers to perform environmental DNA surveys as well as population genetics. We used these primers to perform population genetics on open-ocean ctenophore species, finding many cryptic species as well as surprising patterns of species delineation in the open ocean, where there few apparent barriers that could allow species to diverge.



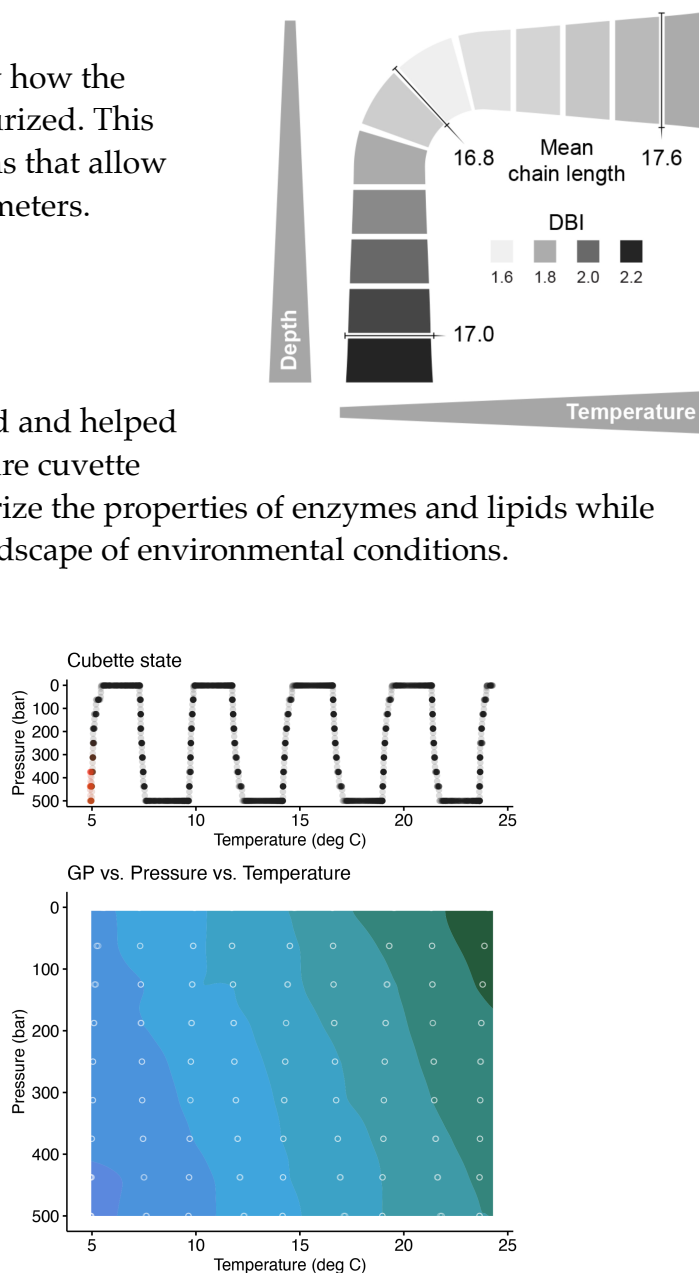
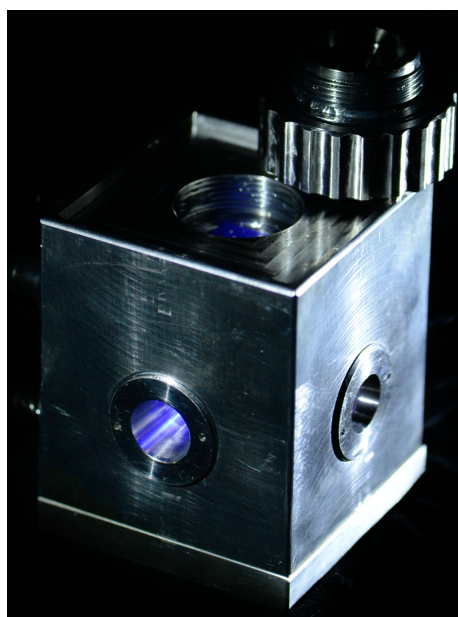
Lipids under pressure

Using samples collected from tropics to polar to deep-sea habitats, we characterized fatty acid composition of ctenophores, to see how their lipid membranes maintain function at low temperature and high pressure. Surprisingly, we found that the adaptations in chain length and number of double bonds were different for temperature and for pressure. We characterized the full diversity of ctenophore lipids using mass spectrometry. Using the synchrotron at Cornell University, we examined the x-ray scattering of lipids under high-

pressure, revealing for the first time exactly how the structures of the lipids change when pressurized. This will lead to new insights on the mechanisms that allow ctenophore cells to function down to 7000 meters.

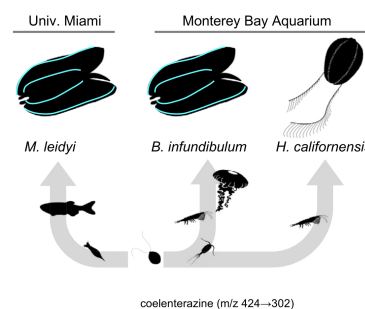
High-pressure experimentation

Graduate student Jacob Winnikoff designed and helped build a temperature-controlled high-pressure cuvette chamber. This device allows us to characterize the properties of enzymes and lipids while sweeping across a computer-controlled landscape of environmental conditions.



Origins of light-emitting molecules

Our previous work on the bioluminescence of ctenophores showed that they might have genes involved in the synthesis of the luminous substrate coelenterazine. Using ctenophores kept in culture for up to 15 generations, we were able to show that ctenophores *do* have the ability to synthesize coelenterazine, making them suitable models for revealing this important biosynthetic pathway.



Genomics and Phylogenetics

Discovered instances of horizontal gene transfer in ctenophores. Provided insights into the reproductive ecology *Mnemiopsis leidyi*, which in turn led to a husbandry resource for these ctenophores. Showed that the *Mnemiopsis leidyi* regulate gamete production via conspecific communication. Identified genes involved in tentacle-specific cell types that were lost as a result of the evolutionary loss of tentacles in a lineage of ctenophores. Produced a reconstruction of the evolution of sexual modes throughout the history of animals. Published an update of the Mnemiopsis Genome Project Portal.

Contributed to the genome annotation of a freshwater sponge (*Ephydatia muelleri*) and a sea urchin (*Echinometra* sp. EZ). Sequenced, assembled and annotated the genomes of the sea cucumber *Holothuria glaberrima*, and the tunicate *Corella inflata*.

Created the concept of **phylotocol** for transparent practices during phylogenetic analyses. Also showed that the commonly deployed six-state amino acid recoding strategy which has been applied to more than 90 published phylogenetic studies, produces suboptimal results.

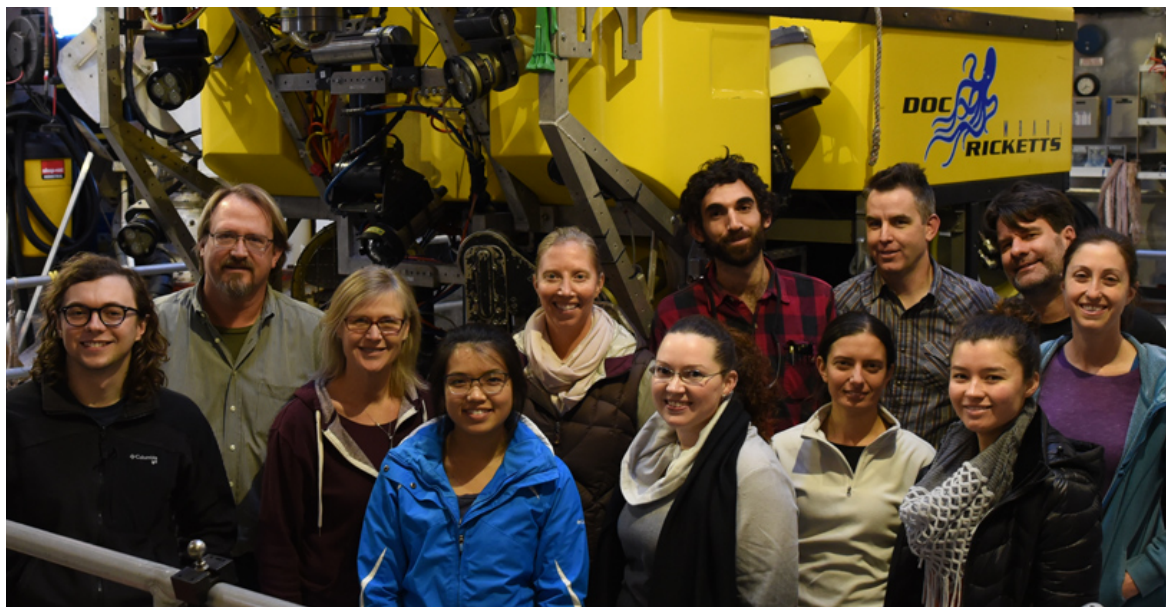
Broader Impacts, Outreach, and Communication

The DEEPC project provided research training opportunities for 21 undergraduate students and 16 graduate students. We also provided research opportunities to several dozen other collaborating scientists aboard our research expeditions locally and in Hawai'i. (Participants are listed in a supplementary table.)

Research Expeditions

We conducted 114 ROV dives in support of the project during 11 expeditions on the *R/V Western Flyer*. We also conducted two UNOLS-supported research expeditions in the waters of the Hawaiian Islands, using blue-water diving and trawls. In 2017, we were aboard the Research Vessel *Ka'imikai-O-Kanaloa*, and in 2018, we used *R/V Kilo Moana*. On the 2018 cruise we also used MBARI's miniROV submersible to collect ctenophores down to 2000 m.

These cruises provided opportunities for 55 students, scientists, and communicators to go to sea and experience deep-sea biological operations. In most cases they were able to conduct their own research projects on rare deep-living specimens.



Left to Right. Darrin Schultz, Erik Thuesen*, Lynne Christianson, Sappithah Ahmath, Susan von Thun, Leann Biancani, Jacob Winnikoff, Séverine Martini, Joseph Ryan*, Maile Prickett, Steven Haddock*, Melissa DeBiasse. Co-PIs indicated by *

Student training

At Evergreen State College, this project provided research training for 2 graduate students, who completed their master's degrees, 10 undergraduate students, 1 high school teacher and 1 high school student.

At MBARI, two graduate students completed or progressed toward their PhDs, one postdoc participated in related research, and 9 undergraduate students carried out summer internships.

At the Whitney Lab, 1 student completed a Ph.D. degree, 1 postdoc received extensive training and mentoring, and 4 undergraduates conducted research on the grant.

Scientific Meetings

We let other scientists know about our cutting edge results at many scientific meetings and through invited lectures. These included meetings of the Society for Integrative and Comparative Biology; Deep-Sea Biology Society; Smithsonian Biogenomics Conference. Association for the Sciences of Limnology and Oceanography; Western Society of Naturalists; Evolution Annual Meeting. Northern California Computational Biologists; Ocean Sciences Meeting; Extreme Biophysics Research Coordination Network Symposium; Society of

Systematic Biologists; Society for Advancement of Chicanos/Hispanics and Native Americans in Science; Smithsonian National Museum of Natural History; International Society for Bioluminescence and Chemiluminescence. PI Haddock hosted the Deep-Sea Biology Symposium and the virtual eDSBS symposium, and PI Ryan hosted the Ctenopalooza conference.

Data and Software deposition

We have posted oceanographic and biological data on the BCO-DMO site [<https://www.bco-dmo.org/project/654411>], and published tools and analytical pipelines as supplementary methods for manuscripts, as well as in dedicated software repositories, including <https://github.com/octopode/tidychrom> and <https://github.com/conchoecia/pauvre>

Public Outreach

Our exciting project has captured the interests of many different kinds of people. Below are some of the ways we taught about ctenophores and the deep sea beyond mainstream science.

Expanding Your Horizons is a nationwide STEM conference for middle school girls. In March 2018, Telissa Wilson gave a workshop on molecular biology at the Expanding Your Horizons conference in Olympia. In March 2019, Telissa Wilson and Tiffany Bachtel jointly gave the keynote address on exploring the deep sea for Expanding Your Horizons and followed up with an interactive workshop on deep-sea ctenophores.

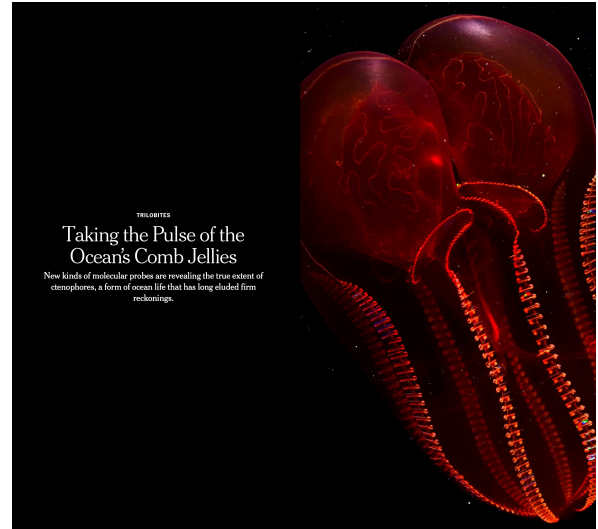
Partners in Science. Funded by the Murdock Charitable Trust, the Partners in Science program allowed Josiah Price, a teacher at Tumwater High School, to spend two summers working on the DEEPC project in the Thuesen Lab. Josiah collected ctenophores in the field, carried out high pressure spectrophotometry and joined one of the research expeditions in Hawai'i. Josiah's students followed his work through a *Ctenes for Teens* Instagram site, and DEEPC graduate students collaborated with Josiah in his classroom. Josiah presented his work to High School teachers from all over the country at two annual Partners in Science meetings.



Public exhibits. We contributed a significant amount of content to the *One Cubic Foot* exhibit at the Smithsonian National Museum of Natural History [<http://newsdesk.si.edu/photos/life-one-cubic-foot-3>]. We made contributions to the jellies exhibit at the Monterey Bay Aquarium, as well as to their upcoming deep-sea exhibit.

DEEPC in the News

Our research has been shown in the pages of *Nature*, the *Economist*, *Wired*, the *Atlantic*, the *New Yorker*, *National Geographic*, and many news outlets. Our work on ctenophore genetics was featured in a New York Times [article](#) over a dramatic two-page spread. Footage has appeared in television productions by BBC, National Geographic, and Discovery Channel.



Theses/Dissertations

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Bachtel, Tiffany S., 2020. Assessing functional diversity down the water column: the effect of hydrostatic pressure on the metabolic enzymes of ctenophores from different habitat depths (Master's Thesis), The Evergreen State College, Olympia, Washington.

Schultz, Darrin T., 2021. Chromosome-Scale Genomes, Resolving the Sister Phylum to Other Animals, and Novel Bioluminescent Systems (Ph.D. Dissertation), University of California, Santa Cruz, California.

Hernandez, Alexandra. 2021. Unraveling Ctenophorology and its Implications on Early Animal Evolution (Ph.D. Dissertation). Whitney laboratory. University of Florida.

Winnikoff, Jacob. (2022). University of California, Santa Cruz, California.

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PROJECT PARTICIPANTS

PRINCIPAL INVESTIGATORS

















 Indicates cruise participant

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 Joe Treddenick	BBC
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