Sunflower Sea Star (*Pycnopodia helianthoides*) 1834-2023

Bibliography

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Background & Scope

The sunflower sea star (*Pycnopodia helianthoides)* is a large sea star and fills the role of a keystone mesopredator. It is native to waters of the Pacific coast, from Alaska, through British Columbia and the West Coast of the U.S., and into northern Mexico. This species exhibits top-down predatory control of kelp predators in these regions. Prior to 2013, the global population of *P. helianthoides* was estimated to be in the billions. Since then, it is estimated that sea star wasting syndrome (SSWS), also called sea star wasting disease (SSWD), has eradicated over 90% of the population.[1] In some areas these losses are estimated to be over 98%.

The National Marine Fisheries Service (NMFS) Alaska Regional Office initiated a literature review on *P. helianthoides* with the NOAA Central Library in 2023. This bibliography is intended as a reference resource for staff within NMFS Alaska Regional Office, Protected Resources Division, who are conducting Endangered Species Act (ESA) Section 7 consultations that involve this, and other, species.

The search parameters for this bibliography included all literature, including non-English literature, published on *P. helianthoides* since the species was first described in 1834, up until September 2023. The majority of the literature was published between 1960 and the present. Resources in this bibliography are primarily from peer-reviewed publications but also include books, theses, and agency reports.

Section I – General Biology and Life History

Section one provides an overview of the species and basic biological information. Literature in this section discusses reproduction, growth, genetics, physiology, morphology, and mortality.

Section II – Diet and Feeding

Section two provides information on the diet and feeding habits of *P. helianthoides*, as well as foraging and hunting behaviors.

Section III – Defense Responses of Prey

Section three discusses the defense and avoidance response behaviors of other species that are typical prey for *P. helianthoides*. Literature in this section primarily focuses on gastropods and sea urchins. In these studies, *P. helianthoides* was used to induce behavioral and chemical responses.

Section IV – Ecology

Section four provides information on how *P. helianthoides* functions in its larger ecosystems. Literature in this section discusses interactions with other species, habitat use, and regime shifts.

Section V – Distribution and Abundance

Section five includes literature with population estimates and survey data. Some of the literature in this section provides insight into *P. helianthoides* abundance prior to the occurrence of SSWS.

Section VI – Threats and Conservation

Section six focuses on the major threats to *P. helianthoides'* survival, as well as recovery and conservation efforts for the species. Much of the literature in this section discusses SSWS.

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[1] National Marine Fisheries Service (2022). Endangered Species Act Status Review Report: Sunflower Sea Star (*Pycnopodia helianthoides*). https://media.fisheries.noaa.gov/2023-03/pycnopodia-helianthoides-status-review-draft-2022.pdf

Sources Reviewed

The following databases were used to identify sources: Aquatic Science and Fisheries Abstracts, Dimensions, Lens.org, Clarivate Analytics' Web of Science: Science Citation Index Expanded, Wiley Online Library, ProQuest's Earth-Atmospheric & Aquatic Science Database, Science Direct, JSTOR, Google Scholar, Department of Fisheries and Oceans Canada, and NOAA's Institutional Repository. Additionally, gray literature was collected from a variety of online sources, including numerous Department of Fish and Wildlife/Game websites and university repositories.

Section I: General Biology and Life History

Ahearn, G. A., & Behnke, R. D. (1991). L-Proline Transport Systems of Starfish Pyloric Caeca. *JOURNAL OF EXPERIMENTAL BIOLOGY, 158*(1), 477-493. https://doi.org/10.1242/jeb.158.1.477

Purified brush-border membrane vesicles (BBMV) of starfish [*Pycnopodia helianthoides* (Brandt)] pyloric caecal epithelium were prepared by magnesium precipitation in order to characterize the possible role of this organ in amino acid transport. L-[3H]proline uptake by these vesicles was Na+-dependent and greater at pH7.5 than at pH5.5. L-Pipecolate was a competitive inhibitor of L-proline influx into these BBMV, exhibiting a Ki value of 0.02 mmol l−1. The amino acid inhibitors, L-pipecolate, L-alanine and L-leucine were used as test substrates to block L-proline influx by the IMINO, NBB and L transport systems, respectively, in order to estimate the contribution of each process to total L-proline entry into pyloric caecal cells. The carrier-mediated transport constants for L-proline transfer by these three systems were: Kt=0.18mmoll−1 (IMINO), 0.13mmoll−1 (NBB) and 0.21 mmol T1 (L); Jmax= 1310 pmol mg−1 protein 30 s −1 (IMINO), 360 pmol mg−1 protein 30 s−1 (NBB) and 470pmolmg−1protein30s−1 (L). L-Proline influxes through both the IMINO and NBB systems were sigmoidal functions of the external [Na+], while transfer by the L system was Na+-independent. Multiple sodium ions (e.g. 2 or 3 Na+/L-proline) appear to be associated with L-proline transport by both Na+-dependent transport systems, but the nature of this association (i.e. activation or energization) is unclear. Results suggest that starfish pyloric caecal epithelium possesses a similar array of L-proline transport proteins to those found in similar cell types of mammalian intestine or kidney, providing tentative support for an absorptive function for this organ.

Ahearn, G. A., & Franco, P. (1991). Electrogenic 2na+/H+ Antiport in Echinoderm Gastrointestinal Epithelium. *JOURNAL OF EXPERIMENTAL BIOLOGY, 158*(1), 495-507. https://doi.org/10.1242/jeb.158.1.495

Purified brush-border membrane vesicles (BBMV) of starfish (*Pycnopodia helianthoides*) pyloric caecal epithelium were prepared by a magnesium precipitation technique in order to compare the properties of Na+/H+ exchange in this invertebrate tissue with those of an apparently unique recently described crustacean electrogenic antiporter. In starfish BBMV 22Na uptake was markedly enhanced by an outwardly directed pH gradient and membrane potential (inside negative) compared to control short-circuited vesicles. External amiloride abolished the stimulatory capacity of the proton gradient and membrane potential as driving forces for sodium transport. Sodium influx, in the presence of an outwardly directed proton gradient, was a sigmoidal function of [Na+]o and yielded a Hill coefficient of 2.6, suggesting that more than one sodium ion was exchanged with each internal proton during the exchange event. Two additional findings were used to establish the number of external Na+ binding sites and the transport stoichiometry of the starfish antiporter. First, amiloride acted as a competitive inhibitor of Na+ binding to two external sites with markedly dissimilar apparent amiloride affinities (Kil=28µmoll−1; Ki2= I650µmol F1). Second, a static head flux ratio analysis resulted in a 2Na+/H+ exchange stoichiometry where a balance of driving forces (e.g. no net Na+ flux) was attained with a combination of a 10:1 Na+ gradient and a 100:1 H+ gradient. Results suggest that the electrogenic 2Na+/H+ exchanger previously characterized for crustacean epithelia also occurs in echinoderm cells and may be a widely distributed invertebrate antiporter.

Alexander, M. E., & Dresden, M. H. (1980). Collagenolytic Enzymes from the Starfish, *Pycnopodia helianthoides*. *Comparative Biochemistry and Physiology, Part B, 67*(4), 505-509. https://doi.org/10.1016/0305-0491(80)90407-1

Two collagenolytic proteinases have been isolated from the starfish, *Pycnopodia helianthoides* and partially characterized.2.2. The larger of these two enzymes, with a molecular weight of approx 60,000, resembles the vertebrate collagenases in that it is inhibited by ethylenediamine tetraacetate and is able to cleave the collagen triple-helix.3.3. The smaller enzyme, with a mol. wt of approximately 16,500, resembles the vertebrate chymotrypsins in its ability to hydrolyse acetyl-tyrosine-ethylester and its cleavage of collagen in the telopeptide region.4.4. Other properties of the enzymes, including alkaline pH optima, acidic isoelectric point and heat stability are similar for both proteinases.

Araki, G. S., & Giese, A. C. (1970). Carbohydrases in Sea Stars. *Physiological Zoology, 43*(4), 296-305. Retrieved from https://www.proquest.com/scholarly-journals/carbohydrases-sea-stars/docview/18542958/se-2?accountid=28258

Cellulase activity using carboxymethylcellulose as a substrate was found in the pyloric caeca of 8 spp of sea stars found on the California coast. These include *Patiria miniata, Pisaster ochraceus, P. giganteus, P. brevispinus, Pycnopodia helianthoides, Poraniopsis inflata, Luidia foliolata,* and *Dermasterias imbricata*. Both viscosimetric and reducing-sugar methods were employed. (2) The cardiac stomachs and body fluids of all 6 spp tested (*Poraniopsis* and *Luidia* were not tested) showed little or no cellulase activity. (3) The main pH optimum for cellulase in *P. miniata* was about pH 4.6 (between 45 degrees and 65 degrees C). However, another peak, at approximately pH 5.5, occurred when lower temps were tested. (4) Laminarinase, lichenase, cellobiase, amylase, glycogenase (except in *Luidia*), and maltase occurred in the pyloric caeca of *P. miniata, P. ochraceus, P. giganteus, P. inflata,* and *L. foliolata*. Fucoidinase and carrageeninase, as determined by an increase in reducing sugars, were either absent or slight in these spp. (5)The significance of the occurrence of beta-glucanases in carnivorous sea stars was discussed.

Asotra, S., Mladenov, P. V., & Burke, R. D. (1988). Polyamines and Cell Proliferation in the Sea Star *Pycnopodia helianthoides*. *Comparative Biochemistry and Physiology, Part B, 90*(4), 885-890. https://doi.org/10.1016/0305-0491(88)90349-5

Diamines (putrescine and cadaverine) and polyamines (spermidine and spermine) were extracted from tissues of the sea star *Pycnopodia helianthoides*, separated and quantitated using reversed-phase high-performance liquid chromatography (RP-HPLC). Simultaneous measurements of levels of protein and DNA and rates of incorporation of 14C-thymidine were carried out. 2. The most abundant polyamine in tissues was spermidine (0.3873-2.5282 nmol/mg tissue) followed by spermine (0.103-1.5517 nmol/mg tissue), putrescine (0.2096-0.5322 nmol/mg tissue) and cadaverine (0.022-0.6064 nmol/mg tissue). 3. An unknown molecule with derivatization and elution behaviour similar to that of polyamine standards was detected in all tissues. 4. Protein levels ranged from 20.47 mg/g tissue in the body wall to 48.44 mg/g tissue in the pyloric caecum. 5. DNA levels were lowest in the ovary (0.25 mg/g tissue) and highest in the testis (5.62 mg/g tissue). 6. Incorporation of 14C-thymidine was highest in the testis. Testicular tissue had the highest spermidine/spermine ratio (5.4). A significant correlation between the spermidine/spermine ratio and 14C-thymidine incorporation (expressed either as DPM/g tissue or

DPM/mg protein) suggests that polyamines are implicated in the regulation of cell proliferation in the sea star *P. helianthoides*.

Brandt, J.-F. (1834). *Prodromus Descriptionis Animalium Ab H. Mertensio Observatorum: Fascic. I. Polypos, Acalephas Discophoras Et Siphonophoras, Nec Non Echinodermata Continens*. St. Petersburg: L'Academie Imperiale des Sciences. Retrieved from https://www.biodiversitylibrary.org/item/40762

This document is one of the earliest academic publications of the sea star *Pycnopodia helianthoides*. Written in Latin, it discusses basic biological features of *P. helianthoides.*

Bruno, I., D'Auria, M. V., Iorizzi, M., Minale, L., & Riccio, R. (1992). Marine Eicosanoids: Occurrence of 8,11,12-Trihydroxylated Eicosanoic Acids in Starfishes. *EXPERIENTIA, 48*(1), 114-115. https://doi.org/10.1007/bf01923622

The occurrence of 8,11,12-trihydroxyeicosa-5,14,17(Z),9(E)-tetraenoic acid and 8,11,12-trihydroxyeicosa-5,14(Z),9E-trienoic acid in starfish species, i.e. *Patiria miniata*, *Dermasterias imbricata*, *Pycnopodia helianthoides*, *Culcita novaeguinea* and *Nardoa tubercolata* is reported.

Bruno, I., Minale, L., & Riccio, R. (1989). Starfish Saponins, 38. Steroidal Glycosides from the Starfish *Pycnopodia helianthoides*. *JOURNAL OF NATURAL PRODUCTS, 52*(5), 1022-1026. https://doi.org/10.1021/np50065a017

Three novel steroidal monoglycosides, pycnopodiosides A [1], B [2], and C [3], together with one novel polyhydroxysteroid[5], have been isolated from the starfish *Pycnopodia helianthoides* collected off the Gulf of California. These compounds co-occur with the common asterosaponin thornasteroside A, one known steroidal monoglycoside, coscinasteroside B, and two known polyhydroxysteroids 6 and 7. The structures of the new metabolites were determined from spectral data and comparison with those of related steroids.

Caine, G. D., & Burke, R. D. (1985). *Immunohistochemical Localization of Gonad Stimulating Substance in the Seaster Pycnopodia helianthoides.* Paper presented at the Echinodermata. https://doi.org/10.1201/9781003079224-103

Gonad stimulating substance (GSS) is a peptide extractable from radial nerves that stimulates ovarian follicle cells to release 1-methyladenine, which in turn induces oocyte maturation and spawning in seastars. Although a great deal is known about this neuroendocrine phenomenon, the precise location of GSS in the radial nerve cord, and the pathway by which GSS is transported to the ovary remain unclear. Here we report immunohistochemical localization of GSS to the perihemal epithelium of the radial nerve cord in *Pycnopodia helianthoides*. The location of GSS appears to correspond to axons containing numerous lOO nm diameter, electron-dense vesicles. We propose that GSS is released into the radial hemal sinus and transported to the ovary within the hemal system.

Chaet, A. B. (1966). Gamete-Shedding Substances of Starfishes - a Physiological-Biochemical Study. *AMERICAN ZOOLOGIST, 6*(2), 263-271. Retrieved from https://www.jstor.org/stable/3881357

A shedding substance, found in the radial nerves of 14 species of starfish, induced the release of gametes from intact animals as well as from whole or fragmented gonads. The shedding substance was not sex-specific, being present in the radial nerves of both males and females throughout the year, and, in general, was not species-specific. This neurosecretory-like polypeptide appeared to function by stimulating ovarian muscle to contract, and was calcium-dependent: it also stimulated the maturation of immature eggs. The shedding substance has been purified and its amino acid composition investigated. A second physiologically-active material, termed "shedhibin" because it inhibited shedding activity, was also found in the radial nerves of ripe sea stars. In the presence of shedhibin, normally-adequate quantities of shedding substance would not cause the release of gametes from isolated ovarian fragments. It appeared that although the level of shedding substance was constant throughout the year, the level of shedhibin fluctuated, possibly controlling the natural release of gametes from sea stars. The precise chemical nature of shedhibin has yet to be determined.

Dayton, P. K. (1973). Two Cases of Resource Partitioning in an Intertidal Community: Making the Right Prediction for the Wrong Reason. *The American Naturalist, 107*(957), 662-670. Retrieved from https://www.journals.uchicago.edu/doi/epdf/10.1086/282865

An important ecological goal is understanding patterns of coexistence and exclusion of species in the same geographic area. Because most multispecies ecological systems are extremely complex, it is probably impossible to describe all the component populations in terms of their physiological status or demographic characteristics such as age distributions and birth and death rates. One current method of studying such ecological systems is to design a generalized model, based on a few premises or simplifying assumptions, which will generate testable predictions. If, upon being tested, these predictions are falsified, the simplifying assumptions are changed accordingly; but if the predictions are verified, the assumptions are often considered to be substantiated. [Excerpt from introduction]

Desantis, M., & Cloud, J. G. (1984). Electrical Stimulation of the Starfish's Radial Nerve in Vitro Induces the Release of a Gonadotrophin. *JOURNAL OF EXPERIMENTAL ZOOLOGY, 231*(3), 423-427. https://doi.org/10.1002/jez.1402310316

In starfish a neuropeptide responsible for the induction of ovulation and the reinitiation of meiotic maturation in fully grown oocytes appears to be released from the radial nerves at the time of spawning. The objectives of this investigation were to determine if the radial nerve would release this gonadotrophin when electrically stimulated in vitro and to locate other possible sources of this factor. Electrical stimulation of radial nerves isolated from the starfish, *Pycnopodia helianthoides*, resulted in the release of the gonadotrophin. Significant amounts of this neuropeptide were detected neither in other tissues of the starfish nor in mammalian nervous tissue.

Elphick, M. R., Reeve, J. R., Burke, R. D., & Thorndyke, M. C. (1991). Isolation of the Neuropeptide Salmfamide-1 from Starfish Using a New Antiserum. *PEPTIDES, 12*(3), 455-459. https://doi.org/10.1016/0196-9781(91)90083-2

We have raised antisera in rabbits to a conjugate of thyroglobulin and Lys-Tyr-Ser-Ala-Leu-Met-Phe-NH2 (KYSALMFamide), a synthetic analog of the starfish neuropeptide S1 (Gly-Phe-Asn-Ser-Ala-Leu-Met-Phe-NH2). The sensitivity and specificity of two antisera (BL and SL) for S1 were established by testing the ability of S1 and structurally related peptides (SALMFamide-2 and various FMRFamide-related peptides) to displace iodinated KYSALMFamide from the serum antibodies in an RIA. Both antisera are sensitive to femtomolar amounts of S1. BL is highly specific for S1 but SL is not, since it is also able to detect femtomolar amounts of the FMRFamide-related peptides. We have used the BL antiserum in the RIA to monitor the purification of S1 immunoreactivity from radial nerve cord extracts of both *Asterias rubens* and *Pycnopodia helianthoides*. The partial amino acid sequence GFNSALM was obtained from automated Edman degradation sequencing of pure immunoreactive peaks from both species.

Feder, H. M., & Christensen, A. M. (1966). Aspects of Asteroid Biology. In *Physiology of Echinodermata: A Collective Effort by a Group of Experts.* R. Boolootian (Ed.), (pp. 87-127): John Wiley and Sons. Retrieved from https://discover.library.noaa.gov/permalink/01NOAA_INST/1qbesct/alma991001361739707381

This chapter discusses the following topics in relation to sea stars: influence of temperature and salinity, tidal exposure and desiccation, rate of locomotion and migration, feeding habits (including the perception of food, food & feeding mechanisms, and feeding rate), growth and age, reproduction, responses of organisms to sea stars, and toxic properties of sea stars.

Ferguson, J. C. (1971). Uptake and Release of Free Amino Acids by Starfishes. *The Biological Bulletin, 141*(1), 122-129. Retrieved from https://www.journals.uchicago.edu/doi/10.2307/1539996

Net uptake and release of dissolved free amino acids was measured in experiments with 10 species of Puget Sound starfishes, utilizing gas liquid chromatography. When specimens were placed in filtered sea water with 0.5 mM/l L-alanine, most of the amino acid was removed within a 6 hour period, and no more than trace quantities of other amino acids appeared in the media. When specimens were placed in filtered sea water with 0.5 mM/l concentrations of 12 amino acids, there was considerable net uptake of all the amino acids except glycine, which in two cases with Pteraster was further released into the media. In a similar experiment in which glycine and L-methionine were omitted from the mixture, there was significant net release of glycine but not l-methionine, simultaneously with considerable uptake of the majority of the other 10 amino acids in most cases. When the uptake mechanism for neutral amino acids was partially inhibited by including 1.0 mM/l L-alanine in the media, a fairly large efflux of glycine and occasionally a much lesser amount of l-serine and other amino acids was detected. The amino acids released by the various species appeared to correlate with those maintained free in their tissues. The results of the study support the concept that starfish can receive net benefit from dissolved nutrients in their environments. They further indicate that the transport system for taking up amino acids is also significant in the retention of those amino acids already in the metabolic pools.

Ferguson, J. C. (2020 [1994]). Madreporite Inflow of Seawater to Maintain Body Fluids in Five Species of Starfish. In *Echinoderms through Time.* B. David, A. Guille, & J.-P. Feral (Eds.), (pp. 285-289): CRC Press https://doi.org/10.1201/9781003077831

Starfish possess spacious, fluid-filled body cavities, but are often described as being both isosmotic and lacking excretory organs; seemingly, a physiological paradox. Recent work provides the answer. It indicates that seawater enters the madreporite, but is more important for perivisceral coelomic fluid balance than supplying ambulacral fluid to the tubefeet. It supplements a largely overlooked low-level hyperosmoticity as a way to maintain fluid homeostasis. A high molecular weight fluorescent tracer, fluorescein isothiocyanate dextran (FID), allowed madreporic uptake to be quantified in the Florida species, *Echinaster graminicola*. Additional work has now been carried out on 5 Pacific forms. After 24 hours of exposure to FID in their media, *Pisaster ochraceus, Leptasterias hexactis, Henricia leviuscula*, and *Luidia foliolata* all showed significant levels of it in their perivisceral and ambulacral fluids. In *Pycnopodia helianthoides* it was only detected in the latter. Loss of perivisceral fluid usually accelerates madreporic replacement. Comparison of the rates of madreporic uptake to the levels of hyperosmoticity maintained reveals different patterns of adaptation by the several species. *Pisaster*, for example, is rather impermeable, and relies almost wholly on madreporic uptake for fluid balance. *Pycnopodia* is more permeable, and depends heavily on osmotic uptake. *Luidia* makes good use of both mechanisms.

Fisher, W. K. (1911). *Asteroidea of the North Pacific and Adjacent Waters: Part 1. Phanerozonia and Spinulosa*. Washington, D.C.: Smithsonian Institution Press. Retrieved from https://library.si.edu/digital-library/book/bulletinunitedst7611911unit

This three-part publication discusses Phanerozonia, Spinulosa, and Forcipulata. This document discusses the orders Phanerozonia and Spinulosa, and families that fall under each order.

Fisher, W. K. (1928). *Asteroidea of the North Pacific and Adjacent Waters: Part 2. Forcipulata (Part)*. Washington, D.C.: Smithsonian Institution Press. Retrieved from https://library.si.edu/digital-library/book/bulletinunitedst7621928unit

This three-part publication discusses Phanerozonia, Spinulosa, and Forcipulata. This document is the first of two parts of a discussion on the order Forcipulata. It presents information on the families Brisingidae, Zoroasteridae, and four subfamilies of the Asteriidae (Pedicellasterinae, Labidiasterinae, Coscinasteriinae, and Pycnopodiinae).

Fisher, W. K. (1930). *Asteroidea of the North Pacific and Adjacent Waters: Part 3. Forcipulata (Concluded)*. Washington, D.C.: Smithsonian Institution Press. Retrieved from https://library.si.edu/digital-library/book/bulletinunitedst7631930unit

This three-part publication discusses Phanerozonia, Spinulosa, and Forcipulata. This document is the second of two parts of a discussion on the order Forcipulata. It presents information on the genera Asteriinae, Notasteriinae, and Neomorphasterinae in the Northern and Southern hemispheres.

Foltz, D. W., Bolton, M. T., Kelley, S. P., Kelley, B. D., & Nguyen, A. T. (2007). Combined Mitochondrial and Nuclear Sequences Support the Monophyly of Forcipulatacean Sea Stars. *MOLECULAR PHYLOGENETICS AND EVOLUTION, 43*(2), 627-634. https://doi.org/10.1016/j.ympev.2006.10.012

Previous molecular phylogenetic analyses of forcipulatacean sea stars (Echinodermata: Asteroidea) have reconstructed a non-monophyletic order *Forcipulatida*, provided that two or more forcipulate families are included. This result could mean that one or more assumptions of the reconstruction method was violated, or else the traditional classification could be erroneous. The present molecular phylogenetic analysis included 12 non- forcipulatacean and 39 forcipulatacean sea stars, with multiple representatives of all but one of the forcipulate families and/or subfamilies. Bayesian analysis of approximately 4.2 kb of sequence data representing seven partitions (nuclear 18S rRNA and 28S rRNA, mitochondrial 12S rRNA, 16S rRNA, 5 tRNAs and cytochrome oxidase I with first and second codon positions analyzed separately from third codon positions) recovered a consensus tree with three well-supported clades (78%-100% bootstrap support) that corresponded at least approximately to traditional taxonomic ranks: the superorder *Forcipulatacea* (*Forcipulatida* + *Brisingida*) + *Pteraster*, the *Brisingida/Brisingidae* and *Asteriidae* + *Rathbunaster* + *Pycnopodia*. When a molecular clock was enforced, the partitioned Bayesian analysis recovered the traditional *Forcipulatacea*. Five of six genera represented by two or more species were monophyletic with 100% bootstrap support. Most of the traditional subfamilial and familial groupings within the *Forcipulatida* were either unresolved or non-monophyletic. The separate partitions differed considerably in estimates of model parameters, mainly between nuclear sequences (with high GC content, low rates of sequence substitution and high transition/transversion rate ratios) and mitochondrial sequences.

Greer, D. L. (1962). Studies on the Embryology of *Pycnopodia helianthoides* (Brandt) Stimpson. *PACIFIC SCIENCE, 16*(3), 280-285. Retrieved from http://hdl.handle.net/10125/5944

The embryonic development of *Pycnopodia helianthoides*, the 20-rayed sea star, which has a small egg (120j-t), an indirect form of development, and larval metamorphosis, has not been previously reported in detail. Mortensen (1921) was able to rear only the early gastrula. No other references to the development of *Pycnopodia* have been found. Species of other multi-rayed sea stars with a yolky egg (and in consequence a more direct form of development) are much better known, e.g., *Solaster endeca* (Gemmill, 1912), *Leptasterias hexactis* (Osterud, 1918), and *Crossaster papposus* (Gemmill, 1920)... The purpose of this study is to report the continuous observation under laboratory culture of the development of *Pycnopodia* from fertilization to completion of metamorphosis. The newly metamorphosed larva has five arms. [Excerpt from introduction]

Hamilton, W. F. (1921). Coordination in the Starfish. I. Behavior of the Individual Tube Feet. *Journal of Comparative Psychology, 1*(6), 473-488. https://doi.org/10.1037/h0070484

After citing the literature on the extension and retraction of the tube feet of the starfish, Hamilton, by diagrams and by verbal exposition, presents the results of his own experiments on *Pycnopodia, Asterina*, and *Pisaster*. It was found that: (1) *Pisaster ocraceus* exhibits three well-defined physiological states,—of "locomotion," "activity without orientation," and "rigidity,"—which influence the responses of the animal's tube-feet and arms; (2) extension, in any of the three states, is spontaneous and occurs in an isolated, water-inflated tube foot; (3) attaching is a product of the physiological state, most frequently, of rigidity; (4) withdrawal is a response to contact stimulation; (5) the step-reflex intergrades with the withdrawal response stimulated by contact with the ambulacral disk and is conditioned also by the locomotor orientation of the tube-feet; (6) the tube-foot is attached much more strongly during the first part of the step-reflex; and (7) its attachment force is from 2.8 (*Asterina*) to 2.06 (*Pycnopodia*) times its pulling force.

Hotchkiss, F. H. C. (2000). On the Number of Rays in Starfish. *AMERICAN ZOOLOGIST, 40*(3), 340-354. https://doi.org/10.1093/icb/40.3.340

Multiradiate starfish evolved independently in fourteen living families. Twenty living families are strictly 5-rayed. The FIVE-PLUS hypothesis is that supernumerary rays develop separately from the five primary rays. The ontogeny of the primary rays is proposed to be highly integrated ("en bloc" hypothesis), closely timed (synchronic hypothesis) and a developmental constraint ("tamper-proof" hypothesis). The "en bloc" hypothesis postulates that the five primary rays develop as a unit. The deep structure of this unit is believed to be a 2-1-2, BA-A-BA, organization. The synchronic hypothesis postulates that there is only a brief time at metamorphosis during which the "en bloc" pathway operates. There is a pause before the development of supernumerary rays. The "tamper-proof" hypothesis postulates that the "en bloc" pathway has no heritable variation and cannot be co-opted for the production of supernumerary rays. There is diversity of timing and pattern in the development of supernumerary rays. Postgeneration of rays in the rudiment and intercalary regeneration of rays in the imago are independent ray-producing pathways that may have been co-opted variously and recurrently in the multiple origins of multiradiate starfish.

Iorizzi, M., Minale, L., Riccio, R., & Yasumoto, T. (1993). Starfish Saponins, Part 51. Steroidal Oligoglycosides from the Starfish *Distolasterias nipon*. *JOURNAL OF NATURAL PRODUCTS, 56*(10), 1786-1798. https://doi.org/10.1021/np50100a019

A reinvestigation of the extracts from the starfish *Distolasterias nipon*, collected at Mutsu Bay, Japan, has led to the isolation of six glycosides of polyhydroxysteroids and six asterosaponins. Four steroidal glycosides have been identified as distolasterosides D1 [1] and D2 [2] (previously isolated from the same organism), and pycnopodioside C [5] and pisasteroside A [6], previously found in the related species *Pycnopodia helianthoides* and *Pisaster ochraceus* (family Asteridae), respectively. Two asterosaponins have been identified as the common versicoside A [7] and thornasteroside A [7a]. The two remaining glycosides of polyhydroxysteroids, named distolasterosides D4 [3] and D5 [4], and four asterosaponins designated nipoglycosides A [8], B [9], C [10], and D [11] are new compounds, and their structures have been elucidated mainly by interpretation of spectral data and comparison with known compounds.

Juorio, A. V., & Robertson, H. A. (1977). Identification and Distribution of Some Monoamines in Tissues of the Sunflower Star, *Pycnopodia helianthoides* (Echinodermata). *JOURNAL OF NEUROCHEMISTRY, 28*(3), 573-579. https://doi.org/10.1111/j.1471-4159.1977.tb10428.x

The distribution of some monoamines in the tissues of an echinoderm, the sunflower starfish, *Pycnopodia helianthoides*, has been investigated in order to ascertain whether monoamine levels are similar to those found in other Deuterostomia. Dopamine, noradrenaline and octopamine were present in the arm nerves at concentrations of 5954 ng/g, 2133 ng/g and 260 ng/g respectively. The octopamine/ noradrenaline ratio for the arm nerve was 0.12 and thus similar to the typical mammalian (deuteros-tome) ratio rather than the higher invertebrate (protostome) ratio. Trace amounts of p-tyramine, β-phenylethylamine were also present. 5-Hydroxytryptamine was not detected but tryptamine was present in high concentrations (1251 ng/g).

Kjerschow-Agersborg, H. P. (1922). The Relation of the Madreporite to the Physiological Anterior End in the Twenty-Rayed Starfish *Pycnopodia helianthoides* (Stimpson). *Biological Bulletin Wood's Hole, 42*, 202-216. https://doi.org/10.2307/1536522

In a previous paper (1918) the writer recorded some facts concerning the bilateral tendencies and habits in *Pycnopodia helianthoides*. These were based on data gained from experimental studies and on others from observations on the behavior of the organism in its native environment. It was the writer's purpose at that time to follow the paper of 1918 with one on the physiology and histology, as well as other structural features of this species, and for this reason certain points were omitted from the paper mentioned above which might well have been included therein. Owing, however, to the writer's remoteness from the Pacific coast for the last five years and the lack of material on which to conclude this second work, it has been quite impossible for this additional contribution to appear sooner. During the last summer (1921) the writer was, however, so fortunate as to find opportunity to visit Puget Sound and gather some additional information on *Pycnopodia*. [Excerpt from introductory paragraph]

Kjerskog-Agersborg, H. P. (1918). Bilateral Tendencies and Habits in the Twenty-Rayed Starfish *Pycnopodia helienthoides* (Stimpson). *Biological Bulletin Wood's Hole, 35*, 232-253. https://doi.org/10.2307/1536379

The purpose of the investigation upon which this paper is based is to show to what extent the radial symmetry in *Pycnopodia helienthoides* is disturbed by its bilateral tendencies. The nature of the investigation has been primarily based on observations on the animal in its native home, and as little as possible have conditions been introduced during experimentations which would deviate from that of its natural abode. The carrying out of this experimental work on *Pycnopodia* was done in connection with other work at the University of Washington, during the year 1915, and during part of the summer of 1916. The experimental work was done at Bremerton, Wash., which is situated about twelve miles from Seattle. In some of the bays at Bremerton, *Pycnopodia* had congregated in super-abundance, offering a considerable inducement to perform experiments on them there, rather than anywhere else on the Puget Sound. And although much time was consumed in traveling between Seattle and Bremerton, the abundance of specimens at the latter place compensated fully for the time thus lost. Occasionally a number of specimens were brought from Bremerton and planted in Elliot Bay at West Seattle for the purpose of studying them there, but when the salinity was found to fluctuate more at the latter place than at the former, it was thought unwise to study them in the new place as under normal conditions and therefore, Bremerton was selected as the most logical place for collecting these data. [Introduction]

Knott, K. E., & Wray, G. A. (2000). Controversy and Consensus in Asteroid Systematics: New Insights to Ordinal and Familial Relationships. *AMERICAN ZOOLOGIST, 40*(3), 382-392. https://doi.org/10.1093/icb/40.3.382

Phylogenetic approaches have sparked controversy in asteroid systematics since 1987. Despite recent attempts at resolving these differences and evidence of some consensus, our understanding of relationships among asteroid taxa remains unsatisfactory. This paper presents results of an investigation into asteroid evolutionary history using DNA sequence data from mitochondrial transfer RNA and the cytochrome oxidase c subunit I genes analyzed with and without previously published ribosomal gene sequences. Analysis of these genes provides an assessment of familial relationships but does little to

elucidate ordinal relationships. A basal position for the Paxillosida is not supported. However, close relationships of some velatid and valvatid taxa are upheld. The resulting phylogenies are not a definitive answer to controversies in asteroid systematics. However, with new insights to some asteroid relationships, they highlight the need for a redirection of future systematic studies so a consensus can be made.

Lambert, P. (2000). Introduction and Family Asteriidae. In *Sea Stars of British Columbia, Southeast Alaska and Puget Sound.* (pp. 3-20; 112-145). Vancouver, Toronto: UBC Press, Royal British Columbia Museum.

A description of the species and subspecies of sea stars in the coastal waters of northwestern North America. Although it covers the coastal waters down to 200 metres below the surface, it lists 26 more species that live below 200 metres and 14 others that occur just outside the region covered.

Liu, Y., Murray, J. A., & Cain, S. D. (2018, 2018 MAR). *See through Sea Star Eyes: A Study on the Optic Cushion of Pycnopodia helianthoides.* Paper presented at the Society for Integrative and Comparative Biology 2018 Annual Meeting. Retrieved from https://sicb.org/abstracts/see-through-sea-star-eyes-a-study-on-the-optic-cushion-of-pycnopodia-helianthoides/

Starfishes possess compound eyes at the tip of each of their arms. Some species use low-resolution vision to navigate towards the reef. But the mechanisms of visual coding remain largely unknown. Here we describe the morphology and show the adaptation pattern of the eye. [Excerpt from abstract]

Low, C. J., & Beamish, R. J. (1978). *A Study of the Nesting Behavior of Lingcod (Ophiodon elongatus) in the Strait of Georgia, British Columbia.* Retrieved from https://www.proquest.com/reports/study-nesting-behavior-lingcod-ophiodon-elongatus/docview/15118018/se-2?accountid=28258

The nest guarding behaviour of male lingcod was observed from December 1 to June 10 in Dodd Narrows, south of Nanaimo, BC, and vicinity. The males appeared to establish territories as early as December 1, in area with crevice spaces of suitable sizes, and some water movement. Egg deposition first occurred January 5, with two spawning peaks January 26 and February 3, and sporadic nest deposition until February 24. Hatching was observed between March 19 and April 9 with other nests probably hatching, but not observed to do so, between March 6 and June 10. A total of 77 nests were located in the research area, in a shoreline length of 134 m. Of these, 8 were observed to hatch, 13 more may have hatched, and the remaining 58, or 74% were lost to predators. Predation on egg masses by kelp greening (*Hexagrammos decagrammus*), striped seaperch (*Embiotoca lateralis*), giant red sea urchins (*Strongylocentrotus franciscanus*), sunflower star (*Pycnopodia helienthoides*), small sculpins (*Jordania zonope* and *Artedius meanhi*), and anemones (*Tealia crassicorius*) was observed. Lingcod were observed to chase greenling and seaperch, but were not observed to show any reaction to other nest predators. When the guarding male was removed from seven nests, four of the nests were lost to predators in a short period. In the other three cases, another, smaller male replaced the removed male. One of these nests was seen to hatch, and the other two may have hatched.

Margolin, A. S. (1964). The Mantle Response of *Diodora aspera*. *Animal Behaviour, 12*(1), 187-194. https://doi.org/10.1016/0003-3472(64)90120-4

Diodora aspera, the common keyhole limpet of the North American Pacific coast, displays a characteristic response to seven species of forcipulate seastars, *Pisaster ochraceus, Pisaster brevispinus, Pisaster giganteus, Leptasterias aequalis, Evasterias troschelii, Orthasterias Koehleri,* and *Pycnopodia helianthoides*, to one seastar of the order Phanerozonia, *Hippasteria spinosa*, to one seastar of the order Spinulosa, *Patiria miniata*, to one ophiuroid, *Gorgonocephala eucnemis*, and to one echinoid, *Strongylocentrotus purpuratus*. The typical reaction consists of a protrusion of the siphon from the "keyhole", and an extension and reflexing of the middle mantle fold over the shell margin, with a movement of the mantle fold dorsomedially to cover most of the shell. Observations made on ten individuals of *D. aspera* kept in an aquarium with two *P. ochraceus* seastars for six days indicated that the reaction was effective in protecting the limpet from being eaten by this seastar, which is possibly one of its predators. The reaction was evoked by actual contact with the seastar, and also as a result of proximity without contact. The limpet reacted in a similar manner to seawater in which a seastar of a stimulating species had previously been kept; this water proved no longer effective after it was boiled for three minutes, or after standing for ten hours at 12 °C. It is assumed that the seastar produces a stimulating substance which is soluble in seawater, heat-labile, and which tests indicated did not act through a dialyzing membrane. Repeated stimulation of the same limpet, at regularly timed intervals alternating with timed rest periods in running seawater, resulted in a drop in starting reaction time for the second and third stimulation, and complete cessation of resonse after 320 to 390 minutes. The behaviour of *D. aspera* kept in the aquarium with *P. ochraceus* for six days suggested some kind and degree of adaptation.

McClintock, J. B. (1989). The Biochemical and Energetic Composition of Somatic Tissues During Growth in the Sea Star, *Pycnopodia helianthoides* (Echinodermata, Asteroidea). *Comparative Biochemistry and Physiology, Part A, 93*(4), 695-698. https://doi.org/10.1016/0300-9629(89)90486-6

The biochemical composition and energy content of the body wall (BW) and pyloric ceca (PC) tissues of *Pycnopodia helianthoides* were measured for juveniles and adults ranging from 14 to 176mm radius. 2.2. Juveniles (R = 14–22 mm) had BW tissues composed of 62.5% ash, 1.2% carbohydrate, 32.1% protein and 4.2% lipid. Medium sized adults (R =24–35 mm) had BW values of 57.8% ash, 1.1% carbohydrate, 36.9% protein and 4.2% lipid. Large sized adults (R =85–176 mm) had BW values of 48.9% ash, 1.2% carbohydrate, 44.4% protein and 5.5% lipid.3.3. The energy content (kJ/g dry wt) of the BW tissues increased 26% with increasing body size (9.4 kJ/g dry wt, R = 14–22 mm; 10.6 kJ/g dry wt, R = 24–35 mm; 12.7 kJ/g dry wt, R =85–176 mm).4.4. The biochemical composition and energy content of the pyloric ceca remained constant over different body sizes (ash = 8.4%; carbohydrate = 3.2%; protein = 73.3%; lipid = 15.1%; 25.2 kJ/g dry wt).5.5. Greater amounts of organics and energy in the total BW than the PC tissues and increases in nutrient and energy levels of the BW (kJ/g dry wt) with growth indicates that BW tissue is not biochemically static, and may not only serve a structural function, but provide a reservoir for nutrients and energy.

McGaw, I. J., & Twitchit, T. A. (2012). Specific Dynamic Action in the Sunflower Star, *Pycnopodia helianthoides*. *Comparative Biochemistry and Physiology, Part A, 161*(3), 287-295. https://doi.org/10.1016/j.cbpa.2011.11.010

The effects of meal size and meal type on specific dynamic action (SDA) were investigated in a large, active asteroid, the sunflower star, *Pycnopodia helianthoides*. When the sunflower stars were fed clam flesh totalling 5%, 10%, or 20% of their body weight there was a step-wise increase in the scope, time to peak oxygen consumption, duration of the response and total SDA. The change in the rate of oxygen consumption was slower than other organisms, and oxygen uptake remained elevated for over 12 d following consumption of the largest meal. There were also differences in the characteristics of the SDA if sunflower stars consumed a whole clam versus the shucked flesh of a clam. The time to reach peak oxygen consumption was greater for sunflower stars consuming a whole clam. This occurred because the clam had to be opened before they could digest the flesh; a smaller initial peak comprising 3.5% of the total SDA represented the energy require to open the clam valves. When the sunflower stars were fed different prey items (e.g. butter clam, purple urchin and herring) of similar wet organic mass, there was no difference in the time to peak, peak oxygen uptake or total SDA despite the fact that the prey items differed in protein, lipid and caloric content. There was an increased duration for which oxygen uptake remained elevated for sea stars that consumed the urchin meal. Five of the seven sunflower stars that consumed urchins exhibited a smaller second peak in oxygen uptake, totalling approximately 8.5% of the SDA energy budget. This likely represented the energy required to eject the urchin test from the stomach. Although the sunflower star is much larger and more active than other sea stars, it displayed similar SDA responses to other members of the Asteroidea, indicative of the low metabolic rate of this class.

Miller, R. L., & Vogt, R. (1996). An N-Terminal Partial Sequence of the 13 Kda *Pycnopodia helianthoides* Sperm Chemoattractant 'Startrak' Possesses Sperm-Attracting Activity. *JOURNAL OF EXPERIMENTAL BIOLOGY, 199*(2), 311-318. https://doi.org/10.1242/jeb.199.2.311

Freshwater extracts of starfish ovaries were used to purify the sperm-attracting peptide 'startrak' from *Pycnopodia helianthoides* using hydrophobic interaction chromatography and DEAE-high-pressure liquid chromatography. Partially purified attractant had a molecular mass of 13 kDa, estimated from gel filtration and polyacrylamide gel electrophoresis results. The purified attractant was subjected to amino acid analysis and direct sequencing, and was found to consist largely of a single peptide composed of an estimated 127 residues based on a molecular mass of 13kDa. An N-terminal sequence of amino acids from positions 3 to 34 was obtained and synthesized as:
NH2-Ala-Glu-Leu-Gly-Leu-Cys-Ile-Ala-Arg-Val-Arg-Gln-Gln-Asn-Gln-Gly-Gln-
Asp-Asp-Val-Ser-Ile-Tyr-Gln-Ala-Ile-Met-Ser-Gln-Cys-Gln-Ser-COOH. The synthetic peptide possessed sperm-attracting activity 130 times greater than the activity of partially purified startrak and showed a pattern of species-specificity of sperm chemotaxis similar to that of startrak. Antibody prepared against synthetic peptide removed the sperm-attracting activity from crude and partially purified preparations of startrak. The partial sequence of startrak was not homologous with that of any of the known echinoid sperm motility-activating peptides.

Mladenov, P. V., Igdoura, S., Asotra, S., & Burke, R. D. (1989). Purification and Partial Characterization of an Autotomy-Promoting Factor from the Sea Star *Pycnopodia helianthoides*. *The Biological Bulletin, 176*(2), 169-175. https://doi.org/10.2307/1541585

Echinoderms possess collagenous connective tissues that are capable of rapid, nervously mediated changes in their tensile strength. Arm autotomy in sea stars is facilitated by a rapid decrease in the

tensile strength of connective tissues in the arm base. In this study, an autotomy-promoting factor (APF) has been isolated from the fluids released by scalded or autotomizing sea stars (*Pycnopodia helianthoides*). When injected into the coleom, APF elicits a complex behavioral response that culminates within minutes in multiple arm autotomy and a generalized softening of the body wall. Injection of fluid from intact, untreated sea stars does not promote the autotomy response. APF is a water soluble, heat-labile substance derived from the body wall. It is ammonium sulphate precipitable and its activity is reduced or destroyed by several proteolytic enzymes. On the basis of its gel permeation elution pattern, APF has Mr of about 1200 Daltons. APF can be purified to a single peak of activity by reversed-phase HPLC. We conclude the substance is a peptide or has a peptide component.

Montgomery, E. M. (2014). Predicting Crawling Speed Relative to Mass in Sea Stars. *JOURNAL OF EXPERIMENTAL MARINE BIOLOGY AND ECOLOGY, 458*, 27-33. https://doi.org/10.1016/j.jembe.2014.05.009

Larger animals typically move faster than smaller individuals of the same species. This relationship is highly conserved across many diverse groups of vertebrates with varied modes of locomotion. But the relationship between body size and locomotion speed is much less clear among invertebrate taxa - the Asteroidea (sea stars) in particular. One sea star species crawls faster at larger body sizes, three species show no correlation between body size and crawling speed, and another sea star species actually crawls slower at larger body sizes. To further examine these unusual patterns of locomotion in sea stars, the relationship between body size and crawling speed was quantified in three unstudied species of Northeast Pacific sea star: *Pycnopodia helianthoides, Solaster stimpsoni*, and *Dermasterias imbricata*. The two multi-armed species *P. helianthoides* and *S. stimpsoni* followed the general trend: larger individuals crawled faster. But the five-armed *D. imbricata* crawled slower, like the previously reported five-armed star *Patiria miniata*. Arm number and scaling differences among species are not sufficient to explain why some sea star species crawl faster at larger body sizes. But two shape ratios relating arm length, arm width, and oral disk diameter may enable predictions of the relationship between body size and crawling speed in unstudied sea star species. Crawling speed differences within and among species could have implications for predator-prey dynamics as well as feeding mode.

Montgomery, E. M. Z. (2013). *The Size Dependence of Sea Star Locomotion: Does Bigger Mean Faster?* (M.S.), University of Alberta. https://doi.org/10.7939/R3GH9BM3F

As a general rule, larger-bodied animals within a species move at faster absolute speeds independently of locomotive mode. The relationship between body size and speed in sea stars is decidedly less clear. One species of sea star follows the general trend, three species show no correlation between body size and speed, and one species exhibits the opposite relation. To address these puzzling observations, I quantified body size, body shape, and crawling speed in four previously unstudied species of Northeast Pacific sea stars: the multi-armed stars *Pycnopodia helianthoides* and *Solaster stimpsoni*, and the fixed-arm number *Dermasterias imbricata* and *Leptasterias hexactis*. Only *L. hexactis* exhibited statistically significant allometries in arm width, arm length, and oral disk. When correlating measures body size with crawling speeds, larger individuals within the multi-armed species were faster - but larger individuals of fixed-arm species crawled slower. Crawling speed differences between plastic and fine sand differed among species.

Punnett, T., Miller, R. L., & Yoo, B. H. (1992). Partial Purification and Some Chemical Properties of the Sperm Chemoattractant from the Forcipulate Starfish *Pycnopodia helianthoides* (Brandt, 1835). *JOURNAL OF EXPERIMENTAL ZOOLOGY, 262*(1), 87-96. https://doi.org/10.1002/jez.1402620112

The sperm attractant of the forcipulate starfish *Pycnopodia helianthoides* has been isolated by sea water extraction from ripe ovaries. After concentration and purification by adsorption and desorption using an Amberlite resin followed by gel filtration chromatography, the most active fractions have been further purified by reverse-phase and hydrophobic-interaction chromatography. A relative purification of 2 × 105 was obtained. Exposure of the partially purified attractant to temperature extremes and enzymes reveals that the molecule is heat and freeze-thaw stable and that it is degraded by the proteases trypsin, chymotrypsin, and pronase. Four different procedures used to determine molecular size produce the same estimate of about 12 kD. The attractant is retarded during Sephadex G-25 chromatography and does not run as a tight band on sodium dodecyl sulfate-polyacrylamide gel electrophoresis (SDS-PAGE). These results suggest that the sperm attractant of this starfish is a small protein.

Rio, G. J., Ruggieri, G. D., Martin, S. J., Stempien, F., & Nigrelli, R. F. (1963, 1963). *Saponin-Like Toxin from the Giant Sunburst Starfish, Pycnopodia helianthoides, from the Pacific Northwest.* Paper presented at the Sixth Annual Meeting, American Society of Zoologists. Retrieved from https://www.jstor.org/stable/3881322

Toxic steroid saponins (holothurin), isolated from several species of Holothuroidea, may be widely distributed in the Echinodermata, the degree of toxicity varying with the species. A heat-stable, saponin-like principle was extracted from the sunburst starfish using the procedure described by Hashimoto and Yasumoto (Bull. Jap. Soc. Scientific Fisheries, 26:1132, 1960) for isolating a similar substance from a Japanese toxic starfish, *Asterina pectinifera*. The starfish toxins appear to differ from holothurin mainly in the sugar moieties. Rf values are similar to glucose, xylose and rhamnose; a fourth spot on the chromatogram, with an Rf value between xylose and rhamnose, has not been identified as yet. The sunburst toxin is lethal to *Fundulus heteroclitus* immersed in solutions of 1 part in a million. The symptoms are typically hemolytic and neurological; stained smears show erythrocytes with condensed nuclear material with vacuolated centers. Intraperitoneal injections are also lethal but the survival time is protracted; blood smears show a striking eosinophilia. The action of the toxin on sea urchin egg development is similar to holothurin, causing animalization and cytolytic effects. *Asterias forbesi*, the common Atlantic starfish, appears to be resistant to the sunburst toxin. Solutions in which the common starfish survived for four hours produced the cytolytic but not the characteristic animalization effects on sea urchin eggs, indicating some degradation of the toxin perhaps by an enzymatic action on the sugars. Studies on the detoxifying agent in the common starfish and comparison of the biochemistry and pharmacology of the sunburst toxin with holothurin are in progress. (Supported by a grant from the John A. Hartford Foundation, Inc.)

Rio, G. J., Stempien, M. F., Nigrelli, R. F., & Ruggieri, G. D. (1965). Echinoderm Toxins—I. Some Biochemical and Physiological Properties of Toxins from Several Species of Asteroidea. *Toxicon, 3*(2), 147-155. https://doi.org/10.1016/0041-0101(65)90008-5

Water soluble toxic fractions were isolated from five species of sea stars, *Pycnopodia helianthoides*, *Asterias forbesi, Patiria miniata, Pisaster ochraceous*, and *Pisaster brevispinus*. Each toxin is a saponin which on hydrolysis yields insoluble aglycones, and four similar sugars as determined by paper

chromatography. They give a negative Legal test and a positive sulfate test. In vivo physiological tests, with saponins in solution, caused death in *Fundulus heteroclitus* (Linnaeus) over a wide concentration range. These compounds, in low concentrations, induced hematological changes in *F. heteroclitus*. In addition, solutions of the saponins caused hemolysis of human erythrocytes in vitro. While the sugars may be similar or even identical in the different saponins, the aglycone portion of each probably differs. This may be concluded from the graded series of responses seen in the physiological studies. Indications are that the mode of action of the saponins is due to changes in membrane permeability.

Ritter, W. E., & Crocker, G. R. (1900). Papers from the Harriman Alaska Expedition, III. Multiplication of Rays and Bilateral Symmetry in the 20-Rayed Star-Fish, *Pycnopodia helianthoides* (Stimpson). *Proceedings of the Washington Academy of Sciences, 2*, 247-274. Retrieved from https://www.jstor.org/stable/24525865

Having had the good fortune to spend the early summer 1899 in Alaska, as a member of the scientific staff of the Harriman Alaska Expedition, I was able to collect a fine series Pacific coast star-fish (*Pycnopodia helianthoides*) which follows the coast northward from central California to southeastern Alaska. At Yakutat Bay, near the northern limit of its range, I found it about the middle of June in greater abundance than I have ever seen it elsewhere. The reef near the anchorage off the Indian village of Yakutat, a large area of which is exposed at extreme low tide was everywhere strewn with large specimens, and on the Laminaria, which grows here in great luxuriance, were thousands of young ones of all sizes, from a few millimeters in diameter to practically the full grown state. Observing that the smallest had only six or eight rays, it occurred to me that the study of a complete series of growing animals would probably reveal a law of their multiplication and might possibly also throw light on the important and difficult problem of the axial relations of the adult star to the larva ; a problem in which I was deeply interested from my interest in the question of the relationship between the Echinodermata and the Enteropneusta. I consequently collected and preserved a large number of specimens, the results of the study of which are recorded in the following pages. [Excerpt from introduction]

Robilliard, G. A. (1972). A New Species of Dendronotus from the Northeastern Pacific with Notes on *Dendronotus nanus* and *Dendronotus robustus* (Mollusca: Opisthobranchia). *CANADIAN JOURNAL OF ZOOLOGY, 50*(4), 421-432. https://doi.org/10.1139/z72-060

A new species of *Dendronotus*, discovered in the San Juan Islands, Washington, is described. The description is based on color, external morphology, structure of the jaws, number and shape of radula teeth, and structure of the reproductive system. In the laboratory, this species copulated and spawned in February. It showed a swimming escape response to the asteroid, *Pycnopodia helianthoides*, a potential predator in natural situations. The prey of this new species of *Dendronotus* is probably one or more species of hydroids. *Dendronotus nanus* is provisionally accepted as a valid species distinct from *D. iris.* However, the similarities between the two species are discussed and it is suggested that further studies will show that the two species are the same with the name *D. iris* taking precedence. Some features of the radula, jaw, and digestive system of *D. robustus* are discussed briefly. The reproductive system is described in detail and figured for the first time. Some aspects of ecology, especially feeding, are discussed. Although most specimens examined had eaten hydroids, some had ingested whole one or more sabellid polychaetes.

Roccatagliata, A. J. (1996). *Aislamiento Y Elucidación Estructural De Metabolitos Secundarios Polares Presentes En Equinodermos.* (Ph.D.), Universidad de Buenos Aires. Retrieved from https://digital.bl.fcen.uba.ar/collection/tesis/document/tesis_n2871_Roccatagliata

The analysis of polar extracts of the starfish *Cosmasterias lurida* Philippi (1858) led us to report the structures of two novel polyhydroxylated xylosides sulfated at C-4' of the xylosyl moiety and four new asterosaponins, two pentaglycosides, Cosmasterosides A and B, and two tetraglycosides, Cosmasterosides C and D, together with two known saponins, the major pentaglycoside Ophidianoside F, previously isolated from *Ophidiaster ophidianus*, *Linckia laevigata* and *Thromidia catalai* and small amounts of the tryglycoside Forbeside H, reported before from *Asterias forbesi*. [Excerpt from abstract]

Ruggieri, G. D. (1965). Echinoderm Toxins—II. Animalizing Action in Sea Urchin Development. *Toxicon, 3*(2), 157-160. https://doi.org/10.1016/0041-0101(65)90009-7

Lyophilized extracts of the whole sea stars, *Pisaster ochraceous, Pisaster brevispinus*, and *Asterias forbesi*, and extracts of the tube feet of *Asterias forbesi*, were tested for their effects on sperm motility, and unfertilized and fertilized eggs of the sea urchin, *Arbacia punctulata*. The effects of these toxins were compared with those previously reported for holothurin, from the Bahamian sea cucumber, *Actinopyga agassizi*, for the extracts of the Pacific sunburst sea star, *Pycnopodia helianthoides*, and for the red webbed sea star, *Patiria miniata*. Sperms were immobilized and unfertilized eggs severely cytolyzed at relatively weak concentrations. Developmental modifications, characterized as animalization (ectodermization) were obtained with all of the toxins tested. The high surface activities, structural configuration, and the presence of sugars and sulfate in these toxins contribute to their solubility, penetrability, and affinity for cellular constituents. These properties undoubtedly play important roles in provoking animalization in the developing sea urchin.

Ruiz-Ramos, D. V., Schiebelhut, L. M., Hoff, K. J., Wares, J. P., & Dawson, M. N. (2020). An Initial Comparative Genomic Autopsy of Wasting Disease in Sea Stars. *MOLECULAR ECOLOGY, 29*(6), 1087-1102. https://doi.org/10.1111/mec.15386

Beginning in 2013, sea stars throughout the Eastern North Pacific were decimated by wasting disease, also known as “asteroid idiopathic wasting syndrome” (AIWS) due to its elusive aetiology. The geographic extent and taxonomic scale of AIWS meant events leading up to the outbreak were heterogeneous, multifaceted, and oftentimes unobserved; progression from morbidity to death was rapid, leaving few tell-tale symptoms. Here, we take a forensic genomic approach to discover candidate genes that may help explain sea star wasting syndrome. We report the first genome and annotation for *Pisaster ochraceus*, along with differential gene expression (DGE) analyses in four size classes, three tissue types, and in symptomatic and asymptomatic individuals. We integrate nucleotide polymorphisms associated with survivors of the wasting disease outbreak, DGE associated with temperature treatments in *P. ochraceus*, and DGE associated with wasting in another asteroid *Pycnopodia helianthoides*. In *P. ochraceus*, we found DGE across all tissues, among size classes, and between asymptomatic and symptomatic individuals; the strongest wasting-associated DGE signal was in pyloric caecum. We also found previously identified outlier loci co-occur with differentially expressed genes. In cross-species comparisons of symptomatic and asymptomatic individuals, consistent responses distinguish genes associated with invertebrate innate immunity and chemical defence, consistent with context-dependent stress responses, defensive apoptosis, and tissue degradation. Our analyses thus highlight genomic

constituents that may link suspected environmental drivers (elevated temperature) with intrinsic differences among individuals (age/size, alleles associated with susceptibility) that elicit organismal responses (e.g., coelomocyte proliferation) and manifest as sea star wasting mass mortality.

Rutherford, J. C. (1973). Reproduction, Growth and Mortality of the Holothurian *Cucumaria pseudocurata*. *MARINE BIOLOGY, 22*(2), 167-176. https://doi.org/10.1007/bf00391780

Certain phases of the ecology of a sea cucumber (*Cucumaria pseudocurata* Deichmann, 1938) population at Shell Beach, Sonoma County, California (USA), were investigated. The sea cucumber is a brooder, lays large (1 mm diameter) yolky eggs, which undergo direct development. It forms large aggregations in the rocky intertidal zone, extending from the lower boundary of the *Mytilus californianus* beds to about zero tide-level. The gonad cycle was followed from September, 1970 to January, 1972. Spawning occurred in January, 1971 and January, 1972. The holothurians produce from 1 to as many as 340 eggs, depending on the size of the individual; they completely spawn-out in a few days. Hatching takes place about 1 month after egg laying. The main sources of mortality are predation by the sea star *Pycnopodia helianthoides* and wave action. Survival of the young is negatively correlated with density of the aggregation. *C. pseudocurata* increases in weight 10 to 30 fold in the first year, but much more slowly in later years. Individuals live perhaps 5 years or more, and do not become reproductive until about the third year. Dispersal is accomplished by the young being washed away to a suitable new habitat. The upper range of the intertidal distribution is determined by exposure to air, and the lower range by *P. helianthoides* predation.

Sanchez R., P. (2000). The Sequence of Origin of the Postmetamorphic Rays in Heliaster and Labidiaster (Echinodermata: Asteroidea). *REVISTA CHILENA DE HISTORIA NATURAL, 73*(4), 573-578. https://doi.org/10.4067/s0716-078x2000000400002

Postmetamorphic rays in *Heliaster* and *Labidiaster* originate in four `quadrants' between the five primary rays, and not normally in the madreporic interradius. The rays originate in one of two very definite sequences depending on the species. *H. kubiniji* and *H. multiradiatus* share one sequence, whereas *H. canopus, H. helianthus* and *Labidiaster* share the other sequence. *Pycnopodia, Rathbunaster*, *Heliaster* and *Labidiaster* add rays at far greater sizes and in a manner that is distinctive from other multiradiate starfish, possibly indicating a new taxonomic unit.

Sloley, B. D., & Juorio, A. V. (1990). Biogenic-Amines in the Nervous and Other Tissues of Several Species of Starfish - Presence of Relatively High-Levels of Tryptamine and Low-Levels of 5-Hydroxytryptamine. *BIOGENIC AMINES, 7*(4), 341-349.

Abstract not available.

Smith, M. J., Nicholson, R., Stuerzl, M., & Lui, A. (1982). Single Copy DNA Homology in Sea Stars. *JOURNAL OF MOLECULAR EVOLUTION, 18*(2), 92-101. https://doi.org/10.1007/bf01810827

The sequence homology in the single copy DNA of sea stars has been measured. Labeled single copy DNA from *Pisaster ochraceus* was reannealed with excess genomic DNA from *P. brevispinus*, *Evasterias*

troschelii, Pycnopodia helianthoides, Solaster stimpsoni, and *Dermasterias imbricata*. Reassociation reactions were performed under two criteria of salt and temperature. The extent of reassociation and thermal denaturation characteristics of hybrid single copy DNA molecules follow classical taxonomic lines. *P. brevispinus* DNA contains essentially all of the sequences present in *P. ochraceus* single copy tracer while *Evasterias* and *Pycnopodia* DNAs contain 52% and 46% of such sequences respectively. Reciprocal reassociation reactions with labeled *Evasterias* single copy DNA confirm the amount and fidelity of the sequence homology. There is a small definite reaction of uncertain homology between *P. ochraceus* single copy DNA and *Solaster* or *Dermasterias* DNA. Similarly *Solaster* DNA contains sequences homologous to approximately 18% of *Dermasterias* unique DNA. The thermal denaturation temperatures of heteroduplexes indicate that the genera *Pisaster* and *Evasterias* diverged shortly after the divergence of the subfamilies Pycnopodiinae and Asteriinae. The two *Pisaster* species diverged more recently, probably in the most recent quarter of the interval since the separation of the genera *Pisaster* and *Evasterias*.

Stimpson, W. (1861). *On New Genera and Species of Starfishes of the Family Pycnopodidae* (Asteracanthion Mull. And Trosch.).* Paper presented at the Proceedings of the Boston Society of Natural History. Retrieved from https://www.biodiversitylibrary.org/item/37036

This document is one of the earliest academic publications of the sea star *Pycnopodia helianthoides*. It is a reproduction of a paper presented at the Boston Society of Natural History in December 1861. It discusses basic biological features of *P. helianthoides.*

Strathmann, R. (1978). Length of Pelagic Period in Echinoderms with Feeding Larvae from the Northeast Pacific. *JOURNAL OF EXPERIMENTAL MARINE BIOLOGY AND ECOLOGY, 34*(1), 23-27. https://doi.org/10.1016/0022-0981(78)90054-0

Minimum and maximum times from fertilization to settling are reported for larvae reared in the laboratory from 12 species of echinoderms representing four classes. For the holothuroid *Parastichopus californicus* (Stimpson) the maximum time observed was 13 weeks; for the asteroids *Luidia foliolata* Grube, *Pisaster ochraceus* (Brandt), and *Pycnopodia helianthoides* (Brandt) the maxima were 20, 32, and 21 weeks, respectively; for the ophiuroid *Ophiopholis aculeata* (Linnaeus) the maximum was 31 weeks; for the echinoids *Brisaster latifrons* (A. Agassiz), *Dendraster excentricus* (Eschscholtz), *Allocentrotus fragilis* (Jackson), and *Strongylocentrotus droebachiensis* (O. F. Müller) maxima were 24, 23, 36, and 21 weeks, respectively. The maximum pelagic periods in each class of echinoderms were approximately double other estimates based on cultured larvae. The pelagic periods in these cultures suggest a capacity for extensive dispersal in nature.

Verrill, A. E. (1909). Remarkable Development of Star-Fishes on the Northwest American Coast; Hybridism; Multiplicity of Rays; Teratology; Problems in Evolution; Geographical Distribution. *The American Naturalist, 43*(513), 542-555. Retrieved from http://www.jstor.org/stable/2455607

This article discusses starfishes of the Northwest American coast, ranging from San Francisco to the Aleutian Islands. Topics include hybridism, multiplicity of rays, teratology, problems in evolution, and geographical distribution.

Verrill, A. E. (1914). Subfamily Pycnopodiinae. In *Monograph of the Shallow-Water Starfishes of the North Pacific Coast from the Arctic Ocean to California.* (pp. 197-202): Smithsonian Institution. https://doi.org/10.5962/bhl.title.25926

This section provides information on the biology of subfamily Pycnopodiinae, genus Pycnopodia Stimpson, and species *Pycnopodia helianthoides* (Brandt) Stimpson.

Wilkie, I. C., Emson, R. H., & Mladenov, P. V. (1995). *Autotomy Mechanism and Its Control in the Starfish Pycnopodia helianthoides (Brandt).* Paper presented at the Fourth European Echinoderms Colloquium, London, United Kingdom. Retrieved from https://books.google.com/books?id=Pfb3lsIjLsEC&pg=PA137&lpg=PA137&dq=%22Autotomy+Mechanism+and+its+Control+in+the+Starfish+Pycnopodia+helianthoides+(Brandt)%22&source=bl&ots=NNmAOZkBeZ&sig=ACfU3U3xSAH4LdGNFyqfmbIULkXhZbPpCA&hl=en&sa=X&ved=2ahUKEwjppPm3r7KCAxVgODQIHTmMC40Q6AF6BAgUEAM#v=onepage&q=%22Autotomy%20Mechanism%20and%20its%20Control%20in%20the%20Starfish%20Pycnopodia%20helianthoides%20(Brandt)%22&f=false

Pycnopodia helianthoides always autotomises arms at the base. In the ambulacral (lower) side of the arm there is a diffuse breakage region consisting of a number of interambulacral joints which are not distinguishable morphologically from the rest of the ambulacrum. At an autotomising joint the ligaments undergo an endogenous loss of tensile strength and the muscles rupture by means of an intrinsic contractile mechanism. Experiments on isolated preparations showed that autotomy is mediated by a specific noncholinergic neural pathway, and that the autotomy-promoting factor present in body fluids from scalded or autotomising starfish is either a parac.rine agent which activates this pathway or a neurotransmitter chemical within it.

Wobber, D. R. (1975). Agonism in Asteroids. *The Biological Bulletin, 148*(3), 483-496. https://doi.org/10.2307/1540524

Intraspecific agonistic behavior, called bouts, which involves ray interactions between individual sea stars, is reported in species from all three living orders of asteroids and described for *Patiria miniata* and *Pycnopodia helianthoides*. This behavior indicates a certain sensitivity to conspecific contact on the aboral surface, in which each individual attempts to place a ray or rays on top of its opponent, an act which may initiate opponent withdrawal. Agonistic intraspecific bouts affect the distribution and feeding of both species although bouts may take place where food is not present. 2. *Patiria* bouts may last over two hours and sometimes terminate by individuals overlapping and sharing food. Evidence suggests that *Patiria* bouts are: (a) quite common; (b) not related to sexual behavior; (c) territorial; and (d) influenced as to outcome by relative body orientation; however, when territorial behavior is involved, relative body orientation does not affect bout outcomes. *Pycnopodia* bouts are of shorter duration (up to 10 minutes), terminating with the withdrawal of one or both animals, and sometimes resulting in an extensive pursuit. 3. Two forms of intraspecific *Patiria* bouts are noted: continuous-contact and intermittent-contact. Intermittent-contact bouts appear less intensive, permitting individuals to feed and to engage in bouts with more than one opponent at a time. It is speculated that intermittent-contact bouts are a type of ritualized activity of a fairly complex nature. 4. Interspecific bouts between specimens of *Pycnopodia* and two species of *Pisaster* (*P. giganteus* and *P. brevispinus*) have been

observed only when the *Pisaster* sp. is in possession of food. *Pycnopodia* individuals approach and place rays on the aboral surface of the feeding sea star while attempting to obtain the food with other rays. The specimen of *Pisaster* sp. actively counterattacks using its pedicellariae.

Wu, Y. (1988). *Molecular Cloning and Characterization of Histone Gene Clusters in Two Sea Star Species.* (M.S.), Simon Fraser University. Retrieved from https://summit.sfu.ca/item/5289

The organization and DNA sequences of histone genes from *Solaster stimpsoni* and *Pycnopodia helianthoides* have been investigated. The sizes of major histone gene cluster elements were first determined by genomic blots. Partial genomic libraries of *Pycnopodia* and *Solaster* were constructed and screened three time with histone gene sequences from *Pisaster ochraceus* or *Dermasteria imbricata*. A recombinant bacteriophage containing a 5.4 kb histone gene cluster element was isolated from the *Pycnopodia* genomic library. Two recombinant phage carrying either a 6.2 kb or a 7.5 kb histone gene cluster element from *Solaster* genomic library were identified. The 5.4, 6.2 and 7.5 kb histone gene elements have been characterized.

Genomic blots indicate that *Pycnopodia* contains a single major histone gene cluster, whereas *Solaster* contains at least three different sizes of histone gene clusters. The histone genes isolated from either *Pycnopodia* or *Solaster* are organized in tandem repeats. Restriction enzyme mapping and Southern hybridization reveal that the arrangement and transcriptional polarity of core histone genes within each gene cluster element are identical (5'-H2B-H2A-H4-H3-3'), and are also the same as those from three other sea stars. The results suggest that there is a remarkable stability in histone gene organization in sea stars. [Excerpt from abstract]

Zhuang, Z. (1996). *Comparative Physiology of Calcium Transport in Crustacean (Homarus Americanus) and Echinoderm (Helianthoides Pycnopodia) Gastrointestinal Epithelia.* (Ph.D.), University of Hawaii at Manoa. Retrieved from https://scholarspace.manoa.hawaii.edu/handle/10125/10564

Calcium ions play a critical role in maintaining normal life activities of an organism such as in controlling enzymes and signal pathways, as a structural component in the skeleton of vertebrates and many invertebrates, etc. Knowledge of calcium regulation and transport is therefore important for an understanding of a wide array of biological processes. Elucidation of the calcium transport mechanisms of the brush border and basolateral membranes of both the lobster and the sea star will contribute important advances to our understanding of the comparative and evolutionary physiology of transport processes in invertebrates. Descriptions of ion transport by the digestive gland of Decapoda are still in their primary stages, with the 2 Na+ / H+ antiporter as the only example of a transport system which is satisfactorily explained. Understanding of the possible common occurrence and utilization of this antiporter in cation transport in invertebrates will be a significant addition to the biology of invertebrates and may also provide some insight into the evolution of transport proteins within the animal kingdom. Lastly, but not least, as the lobster is an animal with high economic value in the world, an increased knowledge of its physiology may provide some insights into improving the growth and production of this species in cultivation.

Zhuang, Z., Duerr, J., & Ahearn, G. A. (1995). *Divalent-Cations Are Transported by the Electrogenic 2na(+)/1 H+ Antiporter in the Seastar (Pycnopodia helianthoides).* Paper presented at the FASEB JOURNAL. Retrieved from https://faseb.onlinelibrary.wiley.com/toc/15306860/1995/9/3

45Ca2+ uptake by brush border membrane vesicles of seastar pyloric ceca was stimulated by an outwardly-directed H+ gradient and this stimulation was enhanced by the simultaneous presence of an induced membrane potential (inside negative; K+/valinomycin) [Excerpt from abstract]

Zhuang, Z., Duerr, J. M., & Ahearn, G. A. (1995). Ca2+ and Zn2+ Are Transported by the Electrogenic 2na+/1h+ Antiporter in Echinoderm Gastrointestinal Epithelium. *JOURNAL OF EXPERIMENTAL BIOLOGY, 198*(5), 1207-1217. https://doi.org/10.1242/jeb.198.5.1207

45Ca2+ uptake by purified brush-border membrane vesicles of starfish (*Pycnopodia helianthoides*) pyloric ceca was stimulated by an outwardly directed H+ gradient and this stimulation was enhanced by the simultaneous presence of an induced membrane potential (inside negative; K+/valinomycin). External amiloride (competitive inhibitor; Ki=660 µmol l-1) and a monoclonal antibody raised against proteins associated with the lobster (*Homarus americanus*) electrogenic 2Na+/1H+ antiporter both inhibited approximately half of the proton-gradient-stimulated 45Ca2+ uptake. These results suggested that Ca2+ might be transported by the electrogenic antiporter and that the crustacean antibody was inhibitory to the exchange function in echinoderms, as was recently shown in crustacean epithelial brush-border membrane vesicles. Carrier-mediated 45Ca2+ influx by amiloride-sensitive and amiloride-insensitive systems displayed the following kinetic constants: (amiloride-sensitive) Kt=66±2 µmol l-1; Jmax=0.173±0.002 pmol µg-1 protein 8 s-1; (amiloride-insensitive) Kt=18±0.3 µmol l-1; Jmax=0.100±0.001 pmol µg-1 protein 8 s-1. Zn2+ was a mixed inhibitor of 45Ca2+ influx by carrier-mediated transport, displaying a Ki of 920 µmol l-1. Mn2+, Cu2+, Fe2+ and Mg2+ also inhibited 45Ca2+ uptake, but the mechanism(s) of inhibition by these other cations was not disclosed. An equilibrium shift experiment showed that both Na+ and Zn2+ were able to exchange with equilibrated 45Ca2+ in these vesicles, suggesting that both monovalent and divalent cations were able to enter pyloric cecal cells through a common carrier-mediated transport system. In addition, the echinoderm electrogenic system appeared to exhibit a molecular component recognized by the crustacean antibody that may imply a similar epitope in the two animals.

Section II: Diet and Feeding

Breen, P. A. (1979). *Selective Feeding of the Sunflower Star, Pycnopodia helianthoides, in the Laboratory.* Retrieved from https://www.proquest.com/reports/selective-feeding-sunflower-star-pycnopodia/docview/15114222/se-2?accountid=28258

Six invertebrate prey were offered to *P. helianthoides* in order to measure their selective feeding rate on *Strongylocentrotus droebachiensis*. Highly selective feeding was observed, in this order from most to least selected: *Venerupis japonica, Saxidomus giganteus, Protothaca staminea, S. droebachiensis, S. franciscanus* and *Crassostrea gigas*. These results do not support the idea that *Pycnopodia* are an

important limiting predator on green sea urchins. They may limit the lower distribution of Manila clams in the intertidal zone. Feeding rates calculated from this study were estimated to be 28 kg wet wt/adult/yr.

Brewer, R. (2003). *Chemosensory Responses and Foraging Behavior of Pycnopodia helianthoides: Predator or Scavenger?* (M.S.), University of Alaska Fairbanks, Fairbanks, AK. Retrieved from https://scholarworks.alaska.edu/bitstream/11122/4895/1/Brewer.Reid.2003.pdf

Chemical cues released by damaged or dead organisms can affect how and where benthic scavengers feed, whether damage or mortality is natural or fishery-related. These cues may also cause predators to act as facultative scavengers. Experiments were performed to determine the role that the seastar *Pycnopodia helianthoides* plays in the presence of scavengable prey. The results of these experiments suggest that *P. helianthoides* preferentially scavenge in lieu of its normal predatory role. When given a choice, *P. helianthoides* choose damaged or decaying food over live prey even when live prey is encountered en route to the damaged animal. The densities and activities of *P. helianthoides* were compared between areas where food was continually introduced and areas where food was not introduced. Adding scavengable food to areas with *P. helianthoides* caused a spatial redistribution of the seastar population, a change in the foraging dynamics of the seastars, and in some cases, a change in the densities of the prey that *P. helianthoides* normally consume. The effects of introducing food appeared to result in a change in the role that *P. helianthoides* plays in the benthic community. This change in modes could have significant effects on the equilibrium of the benthic community.

Brewer, R., & Konar, B. (2005). Chemosensory Responses and Foraging Behavior of the Seastar *Pycnopodia helianthoides*. *MARINE BIOLOGY, 147*(3), 789-795. https://doi.org/10.1007/s00227-005-1608-7

Chemical cues released by damaged or dead organisms can affect how and where benthic organisms feed. These cues may cause predators to act as opportunistic scavengers in lieu of their normal predatory role. A scavenger, as defined in this study, is an organism that consumes damaged and/or dead organisms. In-situ experiments were performed to determine how the seastar *Pycnopodia helianthoides* (Brandt) reacts in the presence of chemical cues from one of its prey species, the butter clam *Saxidomus giganteus* (Deshayes), using both intact and damaged individuals. The results of these experiments suggest that *P. helianthoides* use their chemosensory abilities to locate damaged/dead prey. The role of current in propagating chemical cues was paramount in this foraging activity. *P. helianthoides* chose damaged prey over live prey even when live prey was encountered en route to the damaged individual. This study suggests that chemical cues emitted from damaged or dead individuals may cause significant changes in foraging tactics of key predators, thus altering food-web dynamics.

Dearborn, J. H., Edwards, K. C., & Fratt, D. B. (1991). Diet, Feeding-Behavior, and Surface-Morphology of the Multiarmed Antarctic Sea Star *Labidiaster annulatus* (Echinodermata, Asteroidea). *MARINE ECOLOGY PROGRESS SERIES, 77*(1), 65-84. https://doi.org/10.3354/meps077065

Labidiaster annulatus is a large, multi-armed sea star common in moderate depths along the Antarctic Peninsula and off the islands of the Scotia Arc. Analyses by frequency of occurrence and several volumetric methods of stomach contents from 194 individuals from South Georgia, the South Sandwich

Islands, and the Antarctic Peninsula show *L. annulatus* is an active and opportunistic predator and scavenger on prey from at least 10 phyla. Most common prey are euphausiids and amphipods which are caught initially by large, crossed, toothed pedicellariae arranged in wreaths on annuli along the arms and subsequently retained and passed to the oral surface and along the ambulacral groove to the mouth by the action of flexible arms and tube feet. *L. annulatus* obtains food, including actively-swimming crustaceans and small fish, directly from the water column, and to a lesser degree from within and on the substrate. Patterns of surface ciliation suggest that no methods of feeding involving cilia are utilized. Differences in the size and function of crossed pedicellariae, sources and types of prey and methods of prey capture now suggest that *L. annulatus* is not an ecological equivalent of *Pycnopodia helianthoides* from western North America.

Duggins, D. O. (1983). Starfish Predation and the Creation of Mosaic Patterns in a Kelp-Dominated Community. *ECOLOGY, 64*(6), 1610-1619. https://doi.org/10.2307/1937514

Subtidal kelps in Torch Bay, Alaska, resemble a mosaic of discrete algal patch types. This pattern reflects the patchy distribution of herbivorous sea urchins (*Strongylocentrotus* spp.) and the rapid successional dynamics of the plant association. Factors potentially causing the aggregated distribution of urchins include physical parameters, food availability, interspecific competition, and starfish predation. Each of these factors is considered, with particular emphasis on predation. The starfish *Pycnopodia helianthoides* is the only predator observed feeding on sea urchins in Torch Bay, and it elicits a strong escape response in two of the three urchin species (and the third at small size). Manipulations of *Pycnopodia* and urchins indicate that predation, by creating even short—lived herbivore—free patches, can significantly affect subtidal algal assemblages, and thus primary productivity, species richness, and species distribution in this important marine community.

Eckert, G. L. (2007). Spatial Patchiness in the Sea Cucumber *Pachythyone rubra* in the California Channel Islands. *JOURNAL OF EXPERIMENTAL MARINE BIOLOGY AND ECOLOGY, 348*(1-2), 121-132. https://doi.org/10.1016/j.jembe.2007.04.004

Pachythyone rubra is a small, direct-developing sea cucumber, with a limited geographic range in central and southern California. Surveys from 1996 to 1998 in the Santa Barbara Channel revealed spatial patchiness, with high densities immediately adjacent to low or zero densities in similar habitat. To investigate causes of this patchiness, I transplanted and followed survival and recruitment of *P. rubra* in sites that had high and low densities of *P. rubra*. This transplant experiment revealed that survival and recruitment of *P. rubra* vary spatially, along a gradient in environmental conditions, and that these differences may be caused by predation, sedimentation, and food supply. Laboratory predation experiments identified two predators: the lobster *Panulirus interruptus* and the sea star *Pycnopodia helianthoides*. Field observations and trials with freeze-dried *P. rubra* pellets suggested that fish do not eat *P. rubra*. Population growth of *P. rubra* was highest in the western region of the Channel Islands that receives cool, nutrient and phytoplankton-rich water suitable for *P. rubra* feeding and reproduction. Patchiness of *P. rubra* in this area may result from spatially variable, but intense, predation by *P. helianthoides*. The eastern region of the Channel Islands has warmer water with less nutrients and phytoplankton, which may be less suitable for *P. rubra* feeding and reproduction but lacks *P. helianthoides*, resulting in lower population growth but potentially more stable patches over space and time.

Feder, H. M., & Hoberg, M. K. (1981). *The Epifauna of Three Bays (Port Etches, Zaikof Bay and Rocky Bay) in Prince William Sound, Alaska, with Notes on Feeding Biology.* NOAA/OMPA, BOULDER, CO (USA). Retrieved from https://www.arlis.org/docs/vol1/OCSEAP2/Biological/OCSEAP-Biological-v14.pdf

Benthic trawling operations in Port Etches resulted in the collection of six invertebrate phyla and 39 species; Zaikof Bay and Rocky Bay produced 11 and 78, and 9 and 86 phyla and species, respectively. Echinoderms dominated the biomass in all three bays. The sea star, *Pyncnopodia helianthoides*, was dominant in Port Etches and Zaikof Bay, and the basket star, *Gorgonocephalus caryi*, was dominant in Rocky Bay as well as Zaikof Bay. Echinoderms made up the bulk of the epifaunal invertebrate biomass in the study areas. They may contribute pulses of high energy organic material, as gametes, into adjacent waters during their spawning periods. It is possible that the gametes shed by the large populations of echinoderms in the study areas may represent important components generally overlooked in calculations of secondary productivity. Stomach contents of the snow crab (*Chionoecetes bairde*), the sunflower sea star (*P. helianthoides*), and several fish species were analyzed. The importance of deposit-feeding bivalves in the diet of snow crab, and bivalves and predatory/scavenger gastropods as food for the sunflower sea star is demonstrated.

Freeman, A. (2006). Size-Dependent Trait-Mediated Indirect Interactions among Sea Urchin Herbivores. *BEHAVIORAL ECOLOGY, 17*(2), 182-187. https://doi.org/10.1093/beheco/arj014

Despite their importance in community interactions, nonlethal indirect effects of predators are not well understood in many marine food webs. In this study, I found that within a guild of herbivorous sea urchins, small urchins (*Strongylocentrotus droebachiensis* and small *Strongylocentrotus franciscanus*) altered grazing rates in the presence of the predatory sea star (*Pycnopodia helianthoides*) and were highly preferred by the predator. In contrast, large urchins (adult *S. Rranciscanus*) did not significantly alter grazing in the presence of cues from the sea star and, when immobile, were less frequently attacked by the predator. However, the sea star's preference (active predator choice) was obscured by sea urchin mobility, that is, small *S. Rranciscanus* was only most preferred when unable to escape. These results suggest that by identifying the relative threat of predation facing guild members and the degree to which individuals transmit trait-mediated indirect interactions, these indirect effects may be predictably incorporated in community interactions.

Galloway, A. W. E., Gravem, S. A., Kobelt, J. N., Heady, W. N., Okamoto, D. K., Sivitilli, D. M., . . . Whippo, R. (2023). Sunflower Sea Star Predation on Urchins Can Facilitate Kelp Forest Recovery. *Proceedings of the Royal Society B, 290*(1993), 20221897. https://doi.org/10.1098/rspb.2022.1897

The recent collapse of predatory sunflower sea stars (*Pycnopodia helianthoides*) owing to sea star wasting disease (SSWD) is hypothesized to have contributed to proliferation of sea urchin barrens and losses of kelp forests on the North American west coast. We used experiments and a model to test whether restored *Pycnopodia* populations may help recover kelp forests through their consumption of nutritionally poor purple sea urchins (*Strongylocentrotus purpuratus*) typical of barrens. *Pycnopodia* consumed 0.68 *S. purpuratus* d-1, and our model and sensitivity analysis shows that the magnitude of recent *Pycnopodia* declines is consistent with urchin proliferation after modest sea urchin recruitment,

and even small *Pycnopodia* recoveries could generally lead to lower densities of sea urchins that are consistent with kelp-urchin coexistence. *Pycnopodia* seem unable to chemically distinguish starved from fed urchins and indeed have higher predation rates on starved urchins owing to shorter handling times. These results highlight the importance of *Pycnopodia* in regulating purple sea urchin populations and maintaining healthy kelp forests through top-down control. The recovery of this important predator to densities commonly found prior to SSWD, whether through natural means or human-assisted reintroductions, may therefore be a key step in kelp forest restoration at ecologically significant scales.

Greer, D. L. (1961). *Feeding Behaviour and Morphology of the Digestive System of the Sea Star Pycnopodia helianthoides (Brandt) Stimpson.* (M.S.), University of Washington.

Abstract not available.

Iyengar, E. V., Sitvarin, M. I., & Cataldo, M. (2008). Function of the Flexible Periostracal Hairs in *Trichotropis cancellata* (Mollusca, Gastropoda). *INVERTEBRATE BIOLOGY, 127*(3), 299-313. https://doi.org/10.1111/j.1744-7410.2008.00141.x

The marine snail *Trichotropis cancellata* possesses hairy projections of periostracum (outer shell layer) whose function is unknown. Although rigid shell projections in molluscs have been studied extensively, the selective advantage of flexible extensions of periostracum is less clear. None of the functions proposed previously for periostracum (e.g., protection from erosion and boring) are promoted when it is drawn into hair-like projections. We investigated hypothetical functions that may be served by flexible periostracal hairs, including predator deterrence, alteration of flow vectors to promote feeding or affect turbulence dynamics during freefall, and providing a differential substratum for epibionts. Our laboratory results indicate that crabs, *Cancer oregonensis*, and sea stars, *Pycnopodia helianthoides*, consumed snails with the periostracum removed more often than snails with an intact hairy periostracum. However, in both predatory species, some individuals showed no significant preference, and another crab species (*Cancer productus*) did not strongly discriminate based on the shell periostracum. Field studies showed no difference in the rate of predation on hairy- versus smooth-shelled snails. The hairs did not alter flow around the shells consistently in laboratory flume experiments. Additionally, hairy- and smooth-shelled kleptoparasitic snails grew at rates that were statistically indistinguishable, while hairy, suspension-feeding snails grew more slowly. The hairs did not impact the orientation of a snail after a falling event or the time to righting after a fall. The presence of the hairs did deter settlement by barnacles. We conclude that the hairy periostracum acts as a slight deterrent to crab and sea star predators and as a stronger deterrent to the settlement of large calcareous epibionts, such as barnacles, that would increase the weight the snail must bear and potentially increase drag.

Mauzey, K. P., Birkeland, C., & Dayton, P. K. (1968). Feeding Behavior of Asteroids and Escape Responses of Their Prey in the Puget Sound Region. *ECOLOGY, 49*(4), 603-619. https://doi.org/10.2307/1935526

Observations were made with scuba on the diet and behavior of 18 species of undisturbed sea stars in their natural habitats along the shores of Washington state through all seasons. Some sea stars are specialists. *Hippasteria spinosa* feeds almost exclusively on a sea pen; *Solaster stimpsoni* eats holothurians; full—sized *Orthasterias koehleri* consume the venerid clam *Humilaria*; *Solaster dawsoni*

eats its congener *S. stimpsoni*. Others show remarkably variable diets. In different habitats, *Dermasterias imbricata* specializes on either anemones, holothurians or sea pens, but within these habitats its diet is consistent throughout the year. The diet of *Mediaster aequalis* varies with both habitat and season. *Pycnopodia helianthoides* feeds on sea urchins on rocky substrata but digs clams from sand and cobble. Many other sea stars, including *Luidia foliolata*, *Pteraster tesselatus*, *Pisater ochraceus*, *Evasterias troschelii* and *Leptasterias hexactis*, are quite generalized in their diet and, though often demonstrating preferences in laboratory studies, will feed on a variety of prey determined largely by relative abundance of prey species in the particular habitat. The areal and seasonal variation in the diet of sea stars coupled with the reluctance of some to eat any prey in the laboratory makes extension of laboratory observations to the field diet suspect. Laboratory observations can be used to provide a more detailed understanding of field observations. [Excerpt from abstract]

Moitoza, D. J., & Phillips, D. W. (1979). Prey Defense, Predator Preference, and Nonrandom Diet: The Interactions between *Pycnopodia helianthoides* and Two Species of Sea Urchins. *MARINE BIOLOGY, 53*(4), 299-304. https://doi.org/10.1007/bf00391611

Interactions between the predatory sea star *Pycnopodia helianthoides* (Brandt, 1835) and two of its natural prey, the sea urchins *Strongylocentrotus purpuratus* (Stimpson, 1857) and *S. franciscanus* (Agassiz, 1863), are examined with regard to predator preference, predator diet, and prey defenses. The sea star is able to detect both species of sea urchin upstream in a Y-trough, but does not consistently choose one over the other (i.e., no preference). However, when the sea star is presented with equal numbers of similar-sized specimens of the two species of sea urchin, its diet is markedly nonrandom, since *S. purpuratus* is eaten almost 98% of the time. The defensive responses of the two species of sea urchin differ in form and effectiveness. *S. franciscanus* employs its long spines as defensive weapons, pinching the rays of an attacking sea star. This defensive response is more effective than the pedicellarial response used by *S. purpuratus*. The nonrandom diet of the predator seems to result primarily from prey defensive responses that differ in effectiveness, rather than from an intrinsic, behavioral preference of the predator at an earlier stage in the predator/prey interaction.

Nance, J. M., & Braithwaite, L. F. (1979). The Function of Mucous Secretions in the Cushion Star *Pteraster tesselatu*s Ives. *JOURNAL OF EXPERIMENTAL MARINE BIOLOGY AND ECOLOGY, 40*(3), 259-266. https://doi.org/10.1016/0022-0981(79)90055-8

In all previous studies involving the behavior of the cushion star *Pteraster tesselatus* Ives, the possibility that this asteroid's copious secretions of mucus are defensive in nature has been suggested, but never studied to any degree. Our research shows that discharge of mucus from *Pteraster* was triggered not only by physical stimulation, but also from contact with the asteroid-consuming sea stars *Solaster dawsoni* Verrill and *Pycnopodia helianthoides* (Brandt). It was also found that mucus repelled these two asteroids so effectively that it provided *Pteraster tesselatus* with protection from predation for essentially 100% of the time. *Pteraster* specimens were easily and harmlessly rendered defenseless by removing their mucous-cell-containing supradorsal membranes by dissection. Without the mucous secretions available for discharge, it was shown that *P. tesselatus* was easily preyed upon by both *Solaster dawsoni* and *Pycnopodia helianthoides*.

Paul, A. J., & Feder, H. M. (1975). The Food of the Sea Star *Pycnopodia helianthoides* (Brandt) in Prince William Sound, Alaska. *OPHELIA, 14*(1-2), 15-22. Retrieved from https://www.proquest.com/scholarly-journals/food-sea-star-pycnopodia-helianthoides-brandt/docview/17979320/se-2?accountid=28258

P. helianthoides feeds on small organisms, primarily mollusks, in Prince William Sound, Alaska. *P. helianthoides* with prey in their stomachs ranged between 44-100% throughout the yr. During the winter and early spring, the number of prey items found in the stomachs was reduced.

Sloan, N. A. (1980). Aspects of the Feeding Biology of Asteroids. In *Oceanography and Marine Biology: An Annual Review.* H. B. Barnes & M. Barnes (Eds.), (Vol. 18, pp. 57-124): Aberdeen University Press.

Abstract not available.

Sloan, N. A., & Robinson, S. M. C. (1983). Winter Feeding by Asteroids on a Subtidal Sandbed in British Columbia. *OPHELIA, 22*(2), 125-140. https://doi.org/10.1080/00785326.1983.10426591

The winter feeding of the asteroids *Mediaster aequalis, Luidia foliolata, Pisaster brevispinus* and *Pycnopodia helianthoides* on a subtidal sandbed in British Columbia is reported. Bivalve predation and experiments with the latter three species examining size-related predation, sand as a prey refuge and prey escape behavior are reported using the cockle *Clinocardium nuttallii*. *M. aequalis* is a small species with a very broad diet and mainly a microphagous feeder which may graze recently settled bivalve larvae. *L. foliolata* is a burrowing species which specializes in swallowing small infaunal bivalves whose size usually cannot exceed its disc (mouth) diameter of 40 mm. *P. brevispinus* is large and grazes barnacles on hard substrates, and on sand specializes in excavation of larger bivalves such as the geoduck clam *Panope abrupta* and the jacknife clam *Solen sicarius*. *P. helianthoides* is a large, highly opportunistic predator which grazes epifauna on hard substrates, excavates larger bivalves from sand, and, after encounter, pursues exposed prey such as large cockles. Thus, the different asteroid feeding modes vary in effect on different sizes and species of bivalves. All bivalves to 40 cm depth in the sand are potentially available prey for one or more of the asteroid species.

Smith, J. G. Z. (2021). *Patch Dynamics, Behavioral Responses, and Kelp Forest Stability across a Mosaic of Ecosystem States.* (Ph.D.), University of California, Santa Cruz. Retrieved from https://escholarship.org/uc/item/0q16g293

Empirical evaluations of the ecological processes that enhance or dampen the likelihood of shifts between top-down (i.e., predator-driven) and bottom-up (i.e., resource-driven) forcing are essential to understanding the potential for cascading effects that can underpin community functioning, productivity, and stability. This suite of research used an extraordinary herbivore-outbreak in kelp forests along the central coast of California as a natural field setting to disentangle: (1) how alternations in the foraging behavior of a primary consumer drives patch state transition dynamics, (2) whether predation or resource abundance are the predominant drivers of community regulation, and (3) community-wide consequences to the formation of alternative ecosystem states. This dissertation was motivated by a rapid and dramatic decline in the abundance of a sea star predator (*Pycnopodia helianthoides*) of sea

urchins, and a decline of a primary producer (*Macrocystis pyrifera*, 'kelp') that initiated a fundamental change in purple sea urchin (*Strongylocentrotus purpuratus*) foraging behavior and condition, resulting in a spatial mosaic of remnant kelp forests interspersed with patches of sea urchin barrens... Collectively, the results of this dissertation highlight how patch dynamics, behavioral responses, and biotic and environmental perturbations underpin the structure and stability of ecosystems. [Excerpt from abstract]

Strathmann, R. (1968, 1968). *Feeding of Echinoderm Larvae.* Paper presented at the American Society of Zoologists Sixity-Fifth Annual Meeting, Dallas, Texas. Retrieved from https://www.jstor.org/stable/3881377

Planktotrophic echinoderm larvae of different classes show striking morphological similarities which are probably the result of convergent evolution. The degree to which morphological similarities reflect functional similarities was examined in the following species: *Strongylocentrotus droebachiensis, Dendraster excentricus* (Echinoidea); *Parastichopus californicus* (Holothuroidea); *Ophipholis aculeata* (Ophiuroidea); *Pisaster ochraeceus, Pycnopodia helianthoides, Luidia foliolata* (Asteroidea).
Cilia in most parts of the ciliary band beat away from the circumoral field. Algae coming close to the circumoral field are transported to the mouth; algae contacting the larva elsewhere are not. The feeding currents of the ophiopluteus are similar to those of the echinopluteus, and those of the auricularia are similar to those of the bipinnaria. However, the latter two reject particles and turn by quite different means.

The auricularia, echinopluteus, and ophiopluteus reverse ciliary beat in order to back away and turn when encountering an object, and to reject particles entering the stomodaeum. The ophipluteus and echinopluteus can raise the preoral transverse band of cilia, thereby opening the mouth wider to aid in rejection by ciliary reversal. The bipinnaria and brachiolaria have not been observed to reverse ciliary beat, but turn and reject particles by contraction of dorsal muscles. All the larvae can contract the muscles of the esophagus to eject particles rather than swallow them. The feeding mechanisms of larvae of all four classes are more similar to each other than they are to that described by Garstand for the tornaria larva of hemichordates. (Supported by an NSF graduate fellowship, NSF grant GB 6518 X, and the Friday Harbor Laboratories).

Strathmann, R. R. (1971). The Feeding Behavior of Planktotrophic Echinoderm Larvae: Mechanisms, Regulation, and Rates of Suspensionfeeding. *JOURNAL OF EXPERIMENTAL MARINE BIOLOGY AND ECOLOGY, 6*(2), 109-160. https://doi.org/10.1016/0022-0981(71)90054-2

Feeding mechanisms, rejection mechanisms, and feeding rates of planktotrophic echinoderm larvae of 15 species of four classes have been compared; larvae of 12 species were cultured from fertilization through metamorphosis. The currents created by the ciliated and adoral bands and the mechanisms of removing algae from suspension are similar in the larvae of all four classes. The major differences in feeding are related to the density of cilia in the circumoral field and the differences in overall configuration which distinguish the auricularia and the bipinnaria from the larvae of the pluteus type. In all the larvae the cilia of the ciliated band produce a water current away from the circumoral field. The posteriorly directed components of these currents result in forward swimming. During feeding, particles are retained at the inner side of the ciliated band but water is passed over the band. Particles are transported toward the mouth by water currents, by cilia of the circumoral field, and probably by cilia of the ciliated band. There is little exchange of water in the buccal cavity. Distribution of epidermal

secretory cells varies with species.The larvae can cease feeding by directing particles over the ciliated band. Particles can be ejected from the buccal cavity by ciliary reversal and from the esophagus by contraction of esophageal muscles. These types of rejection are often aided by contractions of other muscles in varying combinations. The sets of muscles aiding rejection differ among the classes. The echinoplutei and ophioplutei frequently reverse the ciliary beat along most of the ciliated band to aid such rejection. The auricularia (*Parastichopus*), ophiopluteus (*Ophiopholis*), and echinopluteus (*Brisaster, Dendraster, Allocentrotus, Strongylocentrotus*) can move backwards by reversing the beat of all or most of the ciliated band. The bipinnaria (*Luidia, Patiria, Evasterias, Pisaster, Pycnopodia*) were not observed to reverse beat but turn by muscular contractions. Particles are sorted in the gut. The rate of passage through the gut is determined largely by the rate of passage from upper to lower stomach. The larvae ingested Sephadex spheres of diameters slightly less than the diameter of the esophagus. The larvae ate rods (*Ditylum*) longer than 100 or 200µ depending on the stage and species of larva. In *Ophiopholis* and *Strongylocentrotus* the presence of *Ditylum* interfered with feeding on smaller cells. Most fully developed larvae cleared suspensions of *Amphidinium* at rates of 3 to 4 µl/min and probably clear *Cricosphaera* and some other particles at twice this rate. Fully developed *Luidia* larvae cleared *Amphidinium* at 9 µl/min. The clearance rate is roughly proportional to the length of the ciliated band. The clearance and ingestion rates vary with concentration of food as in other suspension feeders. Questions are raised concerning the larval nervous system, the evolution of clearance rates, and ways in which each larval type may be suited to the development of juveniles of its class.

Thornber, C. (2007). Associational Resistance Mediates Predator--Prey Interactions in a Marine Subtidal System. *Marine Ecology, 28*(4), 480-486. https://doi.org/10.1111/j.1439-0485.2007.00187.x

There is a growing awareness of the role that indirect interactions play in influencing food webs and ecosystem structure. In this study, the hypothesis that crustose algal epibionts provide gastropods associational resistance from predation was investigated through field surveys and laboratory feeding assays. In rocky low intertidal/shallow subtidal systems in the northeast Pacific, several species of crustose algae (the red alga *Peyssonnelia meridionalis* and crustose corallines) can colonize the shells of living *Tegula brunnea* snails. The growth patterns of these epibiontic crustose algae allow them to cover their host's surface completely, which may, in turn, protect their hosts from predation. A multi-site field survey of *T. brunnea* revealed that >60% of snails were at least 75% covered with one or more species of crustose algae, with 35% fully covered, indicating that this is common in the field. Laboratory feeding assays revealed that sea stars, a primary predator of *T. brunnea*, distinguished among snails with different shell coverings; *Pisaster* consumed nearly three times as many bare (i.e. no crustose algae) snails as those covered with *Peyssonnelia*, while *Pycnopodia* consumed four times as many bare snails as those covered with crustose corallines. These results suggest that epibiont crustose algae can benefit their hosts via associational resistance; this finding may have implications for the role of associational resistance in trophic interactions.

Ward, D. E. (1978). Unorthodox Dining Habits of Sea Stars. *Oceans, 11*(4), 14-17. Retrieved from https://www.proquest.com/scholarly-journals/unorthodox-dining-habits-sea-stars/docview/15113578/se-2?accountid=28258

Observations on the asteroid *Evasterias troscheli* form the basis of this general account of feeding on bivalves by sea stars. Surprising adaptations are exhibited by the sea stars which enable them to prise apart the valves and digest the preys, though some bivalves such as the clam *Humilaria* have evolved

protective features and strategies. Not all sea stars feed on bivalves in this fashion; the crown-of-thorns sea star *Acanthaster planci* attacks live corals, while the 20-armed sun star *Pycnopodia helianthoides* adopts a variety of feeding mechanisms.

Wobber, D. R. (1973). Aboral Extrusion of Squid Pens by the Sea Star *Pycnopodia helianthoides*. *Veliger, 16*(2), 203-206. Retrieved from https://biostor.org/reference/129066

The breaking of the aboral body wall of the sea star *Astropecten californicus* Fischer, 1906, which swallowed a large bivalve, *Donax vittatus* da Costa, 1789, is mentioned by Christensen (1970: 58). Christensen assumed the breakage was due to the sea star being washed ashore and left to dry in the sun during low tide. Since previous reports had been based on dead and, in most cases, dried specimens, Christensen was convinced that fissures in body walls of these sea stars were of post mortal origin. After spawning, dead and dying squid, *Loligo opalescens* Berry, 1911, are found in great numbers on the floor of Monterey Bay, California. Many of these spent animals become a temporary part of the diet of the sea star *Pycnopodia helianthoides* (Brandt, 1835).

After spawning, dead and dying squid, Loligo opalescens Berry, 1911, are found in great numbers on the floor of Monterey Bay, California. Many of these spent animals become a temporary part of the diet of the sea star *Pycnopodia helianthoides* (Brandt, 1835). In April, 1971, on the seaward side of the United States Coastguard Breakwater at the southwest end of Cannery Row, Monterey, California, a *Pycnopodia helianthoides* was found subtidally with the anterior end of the pen (or shell) of a *Loligo opalescens* protruding 3 cm out through its aboral surface. The pen was 8 cm distant from the madreporite, and it was not through the sea star's anus. Two of the sea star's rays were up over the disc, wrapped around the pen. When the pen was extracted, a white, fleshy substance, presumed to be partly digested squid material, came out of the slit.

An experimental feeding in the field of 20 to 30 fresh market *Loligo opalescens* to individual *Pycnopodia helianthoides* resulted in the observation of only one sea star with a squid pen protruding 5 cm through its aboral surface. Since the fed sea stars were unmarked, some may have moved out of sight beneath the rocks. A *P. helianthoides* fed a squid in the laboratory did not put the whole animal into its stomach as did sea stars in the field. An experiment was devised to determine whether *P. helianthoides* typically eliminates squid pens in the field by forcing them through its aboral surface. [Introduction]

Section III: Defense Responses of Prey

Ajeska, R. A., & Nybakken, J. (1976). Contributions to the Biology of *Melibe leonina* (Gould, 1852) Mollusca: Opisthobranchia. *VELIGER, 19*(1), 19-26. Retrieved from https://www.proquest.com/scholarly-journals/contributions-biology-melibe-leonina-gould-1852/docview/17987272/se-2?accountid=28258

The nudibranch *M. leonina* inhabits shallow-water Zostera beds in Puget Sound, but occurs in Monterey Bay associated with the kelp *Macrocystis integrifolia. M. leonina* is mobile within a population and changes its position within the group occasionally movement is usually at night. Fluctuations in the

number of *M. leonina* per plant are greatest at the outskirts of a population and decrease as the centre of the population is approached. Adult *M. leonina* exhibit 2 characteristic positions: feeding and mating/resting. The feeding position is characterized by an erection of the cerata and a 'casting' of the oral hood in an attempt to capture planktonic prey. During feeding the body remains in a fixed position while the oral hood performs the feeding movements. In the mating and resting position the nudibranch's cerata are pressed close against the body, the oral hood is held down against the substratum with the cirri folded inwards, and the animal remains stationary. Metabolic demands differ between young and adult *M. leonina.* The immature animals, due to a more active feeding behaviour, have a metabolic rate which is higher than that of adults. The young feed during daylight and evening hours, whereas the adults seemingly feed only during the evening. The diet of the young consists mainly of *Macrocystis integrifolia*-associated organisms, while the adults depend upon planktonic organisms for the greater part of their diet. Predation upon *M. leonina* appears restricted to the kelp crab, *Pugettia producta*. No incident involving predation by vertebrates, such as fishes, was observed. *Pycnopodia helianthoides*, a potential predator of *M. leonina*, exhibits an escape response which is triggered by physical contact with the nudibranch. This is probably caused by a secretion of the odoriferous glands which cover the epidermis. A commensal relationship between the polynoid polychaete worm *Halosydna brevisetosa* and *M. leonina* exists in which the worm feeds on the fecal matter of the nudibranch.

Bryan, P. J., McClintock, J. B., & Hamann, M. (1997). Behavioral and Chemical Defenses of Marine Prosobranch Gastropod *Calliostoma canaliculatum* in Response to Sympatric Seastars. *JOURNAL OF CHEMICAL ECOLOGY, 23*(3), 645-658. https://doi.org/10.1023/B:JOEC.0000006401.97339.b9

The gastropod *Calliostoma canaliculatum* displays a series of aggressive escape behaviors upon contact with tube feet of the predatory seastars *Pycnopodia helianthoides* and *Pisaster giganteus*. Escape behaviors are predator specific. *Calliostoma canaliculatum* moves away from contact with *P. giganteus* more frequently than *P. helianthoides*, clamping down with the foot or retracting the head and foot into the shell when exposed to *P. helianthoides*. If escape from the grasp of either seastar fails, *C. canaliculatum* releases a yellow-colored exudate from the hypobranchial gland and subsequently retracts both the head and foot fully into the shell. This exudate contains noxious compound(s) as evidenced by retraction of tube feet and arms away from the exudate in both seastars. Tube-foot retraction responses to dilutions of the exudate indicates that both species of seastars are able to detect the exudate at a concentration of 3.2 × 10^sup -3^ mg exudate/ml seawater. *Pisaster giganteus* is more responsive to the exudate than *Pycnopodia helianthoides*, moving away from the source as well as retracting the tube feet and arm. Snails spread the exudate over their shells with their foot, perhaps to ensure defense from predators for some time period after exudate release. The exudate was collected and extracted in chloroform-ethyl acetate (1:1), then fractionated using flash chromatography. The most bioactive fraction, as evidenced by tube-foot retraction, was soluble in ethyl acetate and appeared to contain two major compounds.

Bullock, T. H. (1953). Predator Recognition and Escape Responses of Some Intertidal Gastropods in Presence of Starfish. *Behaviour, 5*(2), 130-140. Retrieved from http://www.jstor.org/stable/4532772

A series of common species of limpets, snails and abalone are shown to have a specific pattern of reaction to any of a series of common carnivorous asteroid species. The pattern of reaction may be

regarded as an escape response and is significant as an example of a little studied aspect of invertebrate behavior, specific predator recognition by prey species. 2. The reaction is markedly different from any elicited by other forms of stimuli, including other common animals, plants, inanimate objects, echinoids, holothuroids and even certain other species of starfish which are chiefly herbivorous. 3. Certain species of gastropods do not react although of the same genus as others which do. The significant common denominator of the former appears to be that they are characteristic of ecologic situations where starfish predation must be rare. 4. The tube feet are the only very effective parts of the starfish. A single tube foot torn from a starfish is an adequate stimulus. 5. Although actual contact, as of tube feet to mantle edge, is usually necessary to ensure a response, many instances of the reaction beginning before contact have been observed. Distances of a few mm. up to some cm. are involved. The evidence suggests a chemical signal specific to predatory starfish and effective only on certain-adaptively susceptible-gastropods. 6. The groups concerned are abundant and motile, the number of contacts between them must be great. They are characteristically not found close together even in the situations where both are common. These facts are judged to be a measure of the general ecologic importance of the described specific behavior pattern.

Cameron, J. L., & Fankboner, P. V. (1989). Reproductive Biology of the Commercial Sea Cucumber *Parastichopus californicus* (Stimpson) (Echinodermata:Holothuroidea). II. Observations on the Ecology of Development, Recruitment, and the Juvenile Life Stage. *JOURNAL OF EXPERIMENTAL MARINE BIOLOGY AND ECOLOGY, 127*(1), 43-67. https://doi.org/10.1016/0022-0981(89)90208-6

Evidence from in vitro culture of embryos and larvae of *Parastichopus californicus* (Stimpson) suggests that asynchronization of development through metamorphosis and settlement results in a variable pelagic period for larvae within a particular cohort. Additionally, considerable variation in size of 0 + yr recruits observed in situ may indicate that settlement had occurred continuously for some months within the population studied. Recruitment of at least seven species of echinoderms (including P. californicus) was observed at distinct sites that were notably free of the predatory sea stars *Solaster dawsoni* (Verrill), *S. stimpsoni* (Verrill), and *S. endeca* (L.). The swimming response characteristic of adult *P. californicus* when touched by the sunflower star *Pycnopodia helianthoides* (Brandt) did not occur with the same regularity or intensity in juveniles. *S. dawsoni* preyed upon small (≤ 2 yr of age) *P. californicus* in aquaria; sea cucumbers >2 yr avoided predation by swimming. Periodic collections of *P. californicus* recruits revealed a pattern of somatic weight loss in the fall and winter that is coincident with a similar pattern reported for the adults of this species. Visceral atrophy was observed in juvenile animals collected in the late fall. The polynoid worm *Arctonoe pulchra* (Johnson) and the endoparasitic gastropod *Comenteroxenous parastichopoli* Tikasingh, common symbionts of adult *P. californicus*, were also noted on or within juvenile animals.

Cameron, J. L. Z. (1985). *Reproduction, Development, Processes of Feeding and Notes on the Early Life History of the Commercial Sea Cucumber Parastichopus californicus (Stimpson).* (Ph.D.), Simon Fraser University.

The commercial sea cucumber *Parastichopus californicus* (Stimpson) exhibits an annual reproductive cycle with spawning occurring in the late spring through summer. The sexes are separate, and occur at an approximately 1:1 ratio. Spawning is partially synchronous, and may be mediated by an increase in the duration of insolation. [Excerpt from abstract]

Donovan, D. A., Danko, J. P., & Carefoot, T. H. (1999). Functional Significance of Shell Sculpture in Gastropod Molluscs: Test of a Predator-Deterrent Hypothesis in *Ceratostoma Foliatum* (Gmelin). *JOURNAL OF EXPERIMENTAL MARINE BIOLOGY AND ECOLOGY, 236*(2), 235-251. https://doi.org/10.1016/S0022-0981(98)00200-7

A predator-deterrence function for the varices of the muricid gastropod *Ceratostoma foliatum* was tested. In the first set of experiments, snails of five treatment groups were presented over a 10-week period to one of three predators: sunflower stars (*Pycnopodia helianthoides* Brandt), red rock crabs (*Cancer productus* Randall), and kelp-greenling fish (*Hexagrammus decagrammus* Pallas). The five treatment groups were: snails with all varices removed, snails with one only of the right, middle, or left varix removed, and snails with all varices intact. The kelp-greenling fish ate no snails and were discarded from subsequent experiments. Seastars consumed significantly more snails with all varices removed than any of the other treatment groups. Crabs ate significantly more snails with all varices- and right varix-removed compared with the other three groups. Thus, snails with all varices intact were less likely to be eaten by either crab or seastar predators. Scoring the shells of *Ceratostoma*, but leaving the varices intact had no effect on consumption rates by either seastars or crabs. In a second set of experiments, the smooth-shelled *Nucella lamellosa* (Gmelin) was presented as a food item along with *Ceratostoma* with all varices removed and *Ceratostoma* with all varices intact for an 8-week period.

Farren, H. M., & Donovan, D. A. (2007). Effects of Sponge and Barnacle Encrustation on Survival of the Scallop *Chlamys hastata*. *HYDROBIOLOGIA, 592*(1), 225-234. https://doi.org/10.1007/s10750-007-0743-1

The scallop *Chlamys hastata* frequently carries epibionts such as sponges and barnacles on its shells. Although the scallop-sponge relationship has been characterized as a mutualism, little is known about the scallop-barnacle relationship. This study investigated the effects of sponge and barnacle encrustation on the ability of *C. hastata* to avoid predation by the sea star *Pycnopodia helianthoides*. In feeding trials, *P. helianthoides* caught and consumed significantly more barnacle-encrusted scallops (7.7 ± 0.8 out of 20 scallops) than scallops encrusted by either of the sponges *Myxilla incrustans* (4.1 ± 0.9) or *Mycale adhaerens* (3.0 ± 0.5). Epibiont-free scallops (5.7 ± 0.5) formed an intermediate treatment between barnacle-encrusted and sponge-encrusted scallops. Possible mechanisms by which the sponges protected the scallops were investigated in two ways: two feeding trials were videotaped to allow qualitative analysis of sea star and scallop behavior and sea star feeding responses to scallop and sponge homogenates were determined to investigate if sea stars accept scallops and sponges as prey. Sea stars displayed positive feeding responses to scallop puree 97.5% ± 1.6 of the time while only displaying positive responses to *Mycale adhaerens* homogenate 4.4% ± 2.0 of the time and to *Myxilla incrustans* homogenate 4.4% ± 2.9 of the time. The videotaped feeding trials indicated that interference with tube feet adhesion by the sponge deterred predation. Observations of both sea stars that were videotaped showed that neither avoided trying to capture sponge-encrusted scallops, and at no time was a captured scallop willingly released by the sea stars. Thus, it appears that sponges provide tactile-mechanical protection and possibly chemical or tactile camouflage in this predator/prey relationship. Finally, the effects of sponge encrustation on barnacle settlement were determined. Field experiments showed that barnacle larvae settled more frequently on epibiont-free scallops than on those with either of the two sponges, potentially protecting the scallops from an epibiont that increases the scallop's susceptibility to predation.

Feder, H. M. (1963). Gastropod Defensive Responses and Their Effectiveness in Reducing Predation by Starfishes. *ECOLOGY, 44*(3), 505-512. https://doi.org/10.2307/1932529

The majority of the animals taken in large numbers by the ochre starfish, *Pisaster ochraceus* (Brandt), for food appear to be protected by structure against starfish attack; for example, this would seem to be true for the California mussel, *Mytilus californianus*, and the barnacles *Balanus glandula, B. nubilis, B. tintinnabulum, Tetraclita squamosa rubescens,* and *Mitella polymerus*. Field and laboratory studies show that these apparent defenses form no real barrier to *Pisaster* predation (Feder 1955, 1956, 1959). Instead, the mussels and barnacles are fed upon more or less in direct proportion to their abundance and availability to *Pisaster*... Observations on predatory activities by the ochre starfish and several other species of sea stars on gastropods and the responsive behavior of the various gastropods have been made in the laboratory and in the field at the Hopkins Marine Station, Monterey Bay; the Kerckhoff Marine Laboratory, Newport Bay; the Scripps Institution of Oceanography, La Jolla; and Hartnell College, Salinas (laboratory observations only). [Excerpt from introduction]

Feder, H. M., & Lasker, R. (1964). Partial Purification of a Substance from Starfish Tube Feet Which Elicits Escape Responses in Gastropod Molluscs. *Life Sciences, 3*(9), 1047-1051. https://doi.org/10.1016/0024-3205(64)90118-3

Many species of gastropod molluscs along the California coast demonstrate escape responses when in the presence of, or contacted by, certain predatory starfish. The effectiveness of these responses in reducing predation by the ochre starfish. *Pisasterochraceus*, and the sunflower starfish, *Pycnopodia helianthoides*, was considered by Feder (1963). Earlier work on gastropod responses to starfish was reported by Bullock (1953). Feder (1956) described preliminary efforts to characterize a substance responsible for gastropod escape reactions. However, the exact source and nature of this substance or substances remains to be resolved. This paper reports a series of observations and experiments on the isolation and characterization of the active substance in *Pisaster ochraceus*.

Field, L. H., & Macmillan, D. L. (1973). An Electrophysiological and Behavioural Study of Sensory Responses in *Tritonia* (Gastropoda, Nudibranchia). *MARINE BEHAVIOUR AND PHYSIOLOGY, 2*(1-4), 171-185. https://doi.org/10.1080/10236247309386923

Recent investigations of the nudibranch *Tritonia* have concentrated on central interactions and the generation of motor output. This is the first description of some of the sensory input to the system and of some roles it may play in behaviour. 2) Recordings were made en passant and from the cut peripheral end of the posterior branch of cerebral nerve II (Willows, 1967) which innervates the oral veil tentacles. 3) *Pycnopodia (*Echinodermata, Asteroidea) tube feet and tube feet homogenates produced afferent activity which lasted for the duration of the stimulus and efferent activity of much longer duration. The total afferent response varied with homogenate concentration. 4) Mechanical deformation produced phasic afferent activity and efferent activity of longer duration. Water jets produced longer and repeated bursts of afferent activity. 5) *Tritonia* detects and orients into water currents above a minimum threshold velocity. 6) Interference with rhinophores, oral veil or cerata reduces but does not abolish rheotaxis. 7) The rhinophores appear to be the most critical of the sensory structures for rheotaxis.

Freeman, A. S. (2001). Grazing Behavior of Sea Urchins in Response to Waterborne Cues from Predators. *AMERICAN ZOOLOGIST, 41*(6), 1642-1643. Retrieved from https://www.jstor.org/stable/3884512

Modification of prey behavior due to predation threats can have cascading impacts on other community members. This study explored how a threat of predation altered the grazing behavior of two sea urchins (*Strongylocentrotus droebachiensis* and *S. franciscanus*). [Excerpt from abstract]

Frost, W. N., Brandon, C. L., & Mongeluzi, D. L. (1998). Sensitization of the *Tritonia* Escape Swim. *NEUROBIOLOGY OF LEARNING AND MEMORY, 69*(2), 126-135. https://doi.org/10.1006/nlme.1997.3816

When repeatedly elicited, the oscillatory escape swim of the marine mollusc *Tritonia diomedea* undergoes habituation of the number of cycles per swim. Previous work has shown that this habituation is accompanied by sensitization of another feature of the behavior: latency to swim onset. Here we focused on the behavioral features of sensitization itself. Test swims elicited 5 min after a strong sensitizing head stimulus differed in several ways from control swims: sensitized animals had shorter latencies for gill and rhinophore withdrawal, a shorter latency for swim onset, a lower threshold for swim initiation, and an increased number of cycles per swim. Sensitized animals did not, however, swim any faster (no change in cycle period). A separate experiment found that swim onset latency also sensitized when *Tritonia* came into contact with one of their natural predators, the seastar *Pycnopodia helianthoides*, demonstrating the ecological relevance of this form of nonassociative learning. These results define the set of behavioral changes to be explained by cellular studies of sensitization in *Tritonia*.

Getting, P. A. (1976). Afferent Neurons Mediating Escape Swimming of Marine Mollusk, *Tritonia*. *JOURNAL OF COMPARATIVE PHYSIOLOGY, 110*(3), 271-286. https://doi.org/10.1007/BF00659144

Intracellular recordings were made from afferent neurons with central cell bodies (S-cells) mediating reflexive withdrawals and escape swimming of the mollusc, *Tritonia diomedia*. Approximately 100 S-cells are located just under the somata of the trigger group neurons (TGN) in each pleural ganglion. S-cells are normally silent but respond phasically to tactile stimuli and tonically to noxious stimuli (NaC1 solution or contact with the tube feet of *Pycnopodia*). Directly driven S-cell activity results in reflexive withdrawals and escape swimming; the initiation of swimming requires both a higher frequency and number of S-cells. Further evidence is provided that the group of cells known as the trigger group neurons (TGN) may be neither necessary nor sufficient for the initiation of escape swimming, but that S-cell activity is the first causal step in the trigger process.

Harley, C. D., Anderson, K. M., Lebreton, C. A.-M., Mackay, A., Ayala-díaz, M., Chong, S. L., . . . Wong, D. C. (2013). The Introduction of *Littorina littorea* to British Columbia, Canada: Potential Impacts and the Importance of Biotic Resistance by Native Predators. *MARINE BIOLOGY, 160*(7), 1529-1541. https://doi.org/10.1007/s00227-013-2206-8

Although the establishment and spread of non-indigenous species depends upon survival in the face of novel environmental conditions and novel biological interactions, relatively little attention has been focused on the specific role of native predators in limiting invasion success. The European common periwinkle, *Littorina littorea*, was recently introduced to the Pacific coast of Canada and provides a case

study of an introduction into an area with an important predator guild (sea stars) that is functionally minor in the invader's native habitat. Here, we assess the likelihood of establishment, spread, and negative ecological impact of this introduced gastropod, with an emphasis on the role of native sea stars as agents of biotic resistance. Size frequency distributions and local market availability suggest that *L. littorea* was most likely introduced via the live seafood trade. Non-native hitchhikers (e.g., the trematode *Cryptocotyle lingua*) were found on/in both market and field specimens. Laboratory studies and field observations confirmed that *L. littorea* can survive seasonal low salinity in Vancouver, British Columbia. Periwinkles also readily consumed native *Ulva*, suggesting that periwinkles could impact native communities via herbivory or resource competition. Unlike native gastropods, however, *L. littorea* lacked behavioural avoidance responses to Northeast Pacific predatory sea stars (*Pisaster ochraceus* and *Pycnopodia helianthoides*), and sea star predation rates on *L. littorea* were much higher than predation rates on native turban snails (*Chlorostoma funebralis*) in common garden experiments. We therefore expect periwinkle establishment in British Columbia to be limited to areas with low predator density, as is seen in its field distribution to date. We caution that this conclusion may understate the importance of the *L. littorea* introduction if it also serves as a vector for additional non-indigenous species such as *C. lingua*.

Herrlinger, T. J. (1983). *The Diet and Predator-Prey Relationships of the Sea Star Pycnopodia helianthoides (Brandt) from a Central California Kelp Forest.* (M.A.), Moss Landing Marine Laboratories. Retrieved from https://scholarworks.calstate.edu/downloads/9306t446x

The diet of *Pycnopodia helianthoides* from a kelp forest in central California is dominated by gastropods (79%). *Calliostoma ligatum* and *Tegula pulligo* are the most important prey species. There is a 3 to 1 ratio of *C. ligatum* to *T. pulligo* in *Pycnopodia* stomachs, whereas a 2 to 1 ratio exists for their field abundances. This apparent preference occurs despite *T. pulligo* containing more than four times as many calories as an individual *C. ligatum*. *Pycnopodia* digests *C. ligatum* in half the time required to digest *T. pulligo*. *Pycnopodia* selects all sizes of *C. ligatum* but ignores small *T. pulligo*. Both the opportunistic *Pycnopodia* and its prey appear to utilize a chemotactile exchange of information rather than distance chemoreception in their predator- prey relationships. *Calliostoma ligatum* displays a violent somersaulting escape response when contacted by *Pycnopodia*, whereas *T. pulligo* does not move. Neither species is able to adhere to the substratum strongly to prevent predation. Although *T. pulligo* contains more calories than *C. ligatum, C. ligatum* appears to be preferred by *Pycnopodia*. The results of this diet study from the northern end of the California range of the sea otter are very similar to the diet of *Pycnopodia*. The results of this diet study from the northern end of the California range of the sea otter are very similar to the diet of *Pycnopodia* from the southern end of the otter's range (Dayton et al., 1980). Otters probably influence the diet of *Pycnopodia*, since the sea star consumes sea urchins and bivalves outside the range of *Enhydra lutris*. *Balanophyllia elegans* provides protection to *C. ligatum* from *Pycnopodia* predation by stinging advancing sea stars with its nematocysts. When *C. ligatum* was tethered in an area with *B. elegans* and an area without the coral, *Pycnopodia* produced significantly greater *C. ligatum* mortalities in the coral- free area. *Calliostoma ligatum* benefits in a second manner while on non- horizontal surfaces by releasing itself from the substratum and dropping to safety below. *Calliostoma ligatum* are not significantly more abundant around *B. elegans* but large snails are more common on steep sloping rocks. These two refugia (coral patches and vertical walls) may allow the gastropod to maintain its density despite heavy predation pressure by *Pycnopodia*.

Herstoff, E. M., & Iyengar, E. V. (2011). Individuals of *Crepidula adunca* (Mollusca, Gastropoda) Avoid Shared Doom through Host Specificity. *JOURNAL OF EXPERIMENTAL MARINE BIOLOGY AND ECOLOGY, 406*(1-2), 79-86. https://doi.org/10.1016/j.jembe.2011.06.007

Individuals of the epibiotic gastropod *Crepidula adunca* predominantly utilize the gastropod *Calliostoma ligatum* as their hosts in the San Juan Islands, Washington, rather than exploiting other potential host species. Snails of *Margarites pupillus* would appear to be particularly good alternate hosts, given their similarities in microhabitat choice, shell shape, and taxonomic closeness with *Calliostoma ligatum*. However, *M. pupillus* are almost never utilized as a host by *Crepidula adunca*. We examined the reasons for host fidelity by *Crepidula adunca* in the San Juan Islands. The small but voracious sea star *Leptasterias hexactis* was common across all our intertidal survey sites and consumed significantly more *M. pupillus* than *Calliostoma ligatum* in laboratory experiments. Individuals of *Calliostoma ligatum* stimulated by tube feet from *Leptasterias hexactis* moved significantly more quickly than non-stimulated individuals, but snails of this species stimulated by *Pycnopodia helianthoides* did not move at a significantly different rate than non-stimulated snails. There was a significant positive correlation between gastropod size and the rate of movement for *Calliostoma ligatum* stimulated by *Leptasterias hexactis*, but this correlation was not significant for non-stimulated individuals. Neither stimulation by asteroids nor gastropod size (whether for stimulated or non-stimulated snails) had a significant effect on the rate of movement for *M. pupillus.* Thus *Calliostoma ligatum*, and especially large individuals of this species, react more than *M. pupillus* to the presence of a common predator (*Leptasterias hexactis*) in such a way that likely elevates the snails' chance of escape. Finally, we found that *Calliostoma ligatum* used both chemical and physical defenses to effectively repel attacks by *Leptasterias hexactis*, while defenses by *M. pupillus* were less successful. We suggest that epibiotic *Crepidula adunca* specialize on *Calliostoma ligatum* in the San Juan Islands because this particular host species is more likely to protect the epibiont from shared doom due to its effective defenses against potential predators.

Hoffman, D. L. (1979). *Predator Induced Responses of Prosobranch Gastropods from the U. S. Pacific Coast.* Paper presented at the Annual Meeting of the American Society of Zoologists, Society of Systematic Zoology and the American Microscopial Society, Tampa, Florida.

Five species of intertidal to subtidal snails were tested under laboratory conditions to their responsiveness to certain predatory seastars and snails. The following observations were made using artificial tide pools and a Y-maze. *Homalopoma carpenteri* generally showed no response to the scent or contact with the tested predators. *Margarites pupillus*, *M. salmoneus*, and *M. rhodia* responded moderately (tentacular movement, increased gait) to the scent and very strongly (shell twisting, somersaulting) to contact with such seastars as *Leptasterias hexactis* and *Pisaster ochraceus*, and the whelk, *Searlesia dira*. Moderate responses to scent were elicited in *Calliostoma ligatum* by *Lepasterias, Pisaster* and *Pycnopodia helianthoides*. Contact with these species gave a very strong response similar to *Margarites* but including movement up vertical surfaces and the evacuation of water. Neither the scent nor touch of *Searlesia* had any effect on *Calliostoma*. *Nucella lamellosa* appeared not to have any effect on the species tested. Food preference experiments and field observations appear to corroborate the laboratory data.

Hoffman, D. L. (1980). Defensive Responses of Marine Gastropods (Prosobranchia, Trochidae) to Certain Predatory Seastars and the Dire Whelk, *Searlesia dira* (Reeve). *PACIFIC SCIENCE, 34*(3), 233-243. Retrieved from http://hdl.handle.net/10125/1622

Qualitative comparisons of the predator-induced defensive behaviors of four species of trochid gastropod, *Margarites pupillus*, *M. salmoneus*, *M. rhodia*, and *Calliostoma ligatum*, under controlled laboratory conditions indicate that the degree and strength of the response varies according to the sensory information received from a predator and according to the species of predatory seastar or gastropod inducing the response. Generally, all four species of gastropod demonstrate a weak to moderate avoidance response to the scent of such predatory seastars as *Leptasterias hexactis* and *Pisaster ochraceus*; whereas direct contact with their soft parts elicits strong and often violent defensive behaviors characterized by shell twisting, propodial rearing which often leads to a loss of contact with the substrate, and somersaulting by metapodial thrusting. It is hypothesized that the inversion of the shell induced by direct contact with a predator sets up the metapodial thrusting behavior and also part of the righting repertoire, which facilitates more rapid flight from the predator. *Margarites* spp. respond to the scent and contact with the dire whelk, *Searlesia dira*; whereas *Calliostoma* is unresponsive to the snail, but more responsive to the scent and contact of the sunstar *Pycnopodia helianthoides* than are the other species of gastropods studied.

Kunz, C., & Connor, V. M. (1986). Roles of the Home Scar of *Collisella scabra* (Gould). *VELIGER, 29*(1), 25-30. Retrieved from https://biostor.org/reference/131986

Most individuals of the prosobranch limpet species *Collisella scabra* (Gould, 1846) form a permanent home depression or home scar from which they forage. Laboratory experiments indicate that while on a scar, limpets are significantly less vulnerable to predation by *Pycnopodia helianthoides* (Asteroidea), *Pachygrapsus crassipes* (Crustacea), *Clinocottus* spp. (Pisces), *Octopus dofleini* (Cephalopoda), and *Freemania litoricola* (Turbellaria). A home scar effectively reduces predation by *Cancer antennarius* (Crustacea) only when limpets without home scars are more abundant than limpets on home scars. A home scar does not significantly reduce predation by *Pisaster ochraceus* (Asteroidea). Field work suggests that other roles of the home scar include a reduction in desiccation-induced mortality, as well as improved survival following sand burial. Limpets on home scars adhere to the rock more tightly than limpets off home scars.

Lawrence, K. A., & Watson, W. H. (2002). Swimming Behavior of the Nudibranch *Melibe leonina*. *The Biological Bulletin, 203*(2), 144-151. https://doi.org/10.2307/1543383

Swimming in the nudibranch *Melibe leonina* consists of five types of movements that occur in the following sequence: (1) withdrawal, (2) lateral flattening, (3) a series of lateral flexions, (4) unrolling and swinging, and (5) termination. *Melibe* swims spontaneously, as well as in response to different types of aversive stimuli. In this study, swimming was elicited by contact with the tube feet of the predatory sea star *Pycnopodia helianthoides*, pinching with forceps, or application of a 1 M KCl solution. During an episode of swimming, the duration of swim cycles (2.7 +/- 0.2 s [mean +/- SEM], n = 29) and the amplitude of lateral flexions remained relatively constant. However, the latency between the application of a stimulus and initiation of swimming was more variable, as was the duration of an episode of swimming. For example, when touched with a single tube foot from a sea star (n = 32), the latency to swim was 7.0 +/- 2.4 s, and swimming continued for 53.7 +/- 9.4 s, whereas application of KCl resulted in a longer latency to swim (22.3 +/- 4.5 s) and more prolonged swimming episodes (174.9 +/- 32.1 s). Swimming individuals tended to move in a direction perpendicular to the long axis of the foot, which propelled them laterally when they were oriented with the oral hood toward the surface of the water.

The results of this study indicate that swimming in *Melibe*, like that in several other molluscs, is a stereotyped fixed action pattern that can be reliably elicited in the laboratory. These characteristics, along with the large identifiable neurons typical of many molluscs, make swimming in this nudibranch amenable to neuroethological analyses.

Lawrence, K. A. Z. (1997). *Neuroethology of the Swimming Behavior in the Pacific Nudibranch, Melibe leonina.* (Ph.D.), University of New Hampshire, Durham. Retrieved from https://scholars.unh.edu/dissertation/1970

Melibe leonina is a subtidal nudibranch which is found in association with eelgrass and kelp. Melibe swims when disturbed, or knocked off of its substrate, by slow lateral undulations. Swimming is stereotyped in its form and execution, and can be reliably reproduced in the laboratory. Swimming consists of phases: (1) withdrawal, (2) flattening, (3) lateral flexions, (4) unfolding and swinging and (5) termination. Swimming can be reliably elicited using 1M KCl or contact with the tube feet of the predatory seastar *Pycnopodia helianthoides*. The duration of a single swim cycle and the amplitude of swimming flexions remain relatively constant, however, both the latency to swim, and the swimming duration, are more variable. Swimming moves the animal upward and anteriorly and the direction of travel is fairly predictable from one flexion to the next. *Melibe* swimming is a stereotyped fixed action pattern that is probably used, in part, to escape from predators.

The brain in *Melibe* is composed of four bilateral pairs of fused ganglia which surround the esophagus. The neural components for swimming make up a central pattern generator within the brain of *Melibe*. The nerves which innervate swimming structures arise from the pedal ganglion, and the motorneurons which drive swimming are also located within the pedal ganglion. Intracellular recordings of swimming can be reliably obtained in semi-intact and isolated brain preparations, however only if the pedal commisure is left intact and the ambient lighting is turned down. *Melibe* swimming is amenable for further neurophysiological studies to more rigorously look at the neural basis of swimming.

Light has a profound effect on the likelihood of swimming in *Melibe*. The initiation or termination of light cannot start or stop swimming, however, animals locomote and swim significantly more in the dark. This effect was also seen in isolated brain preparations, where fictive swimming was disrupted by, even low level, light. This effect could be reversed, however, if the eyes were removed. Thus *Melibe* is a model swimming system, that of a lateral bend swimmer, whose behavior is reliably modulated by natural inputs which can be methodically tested in the laboratory.

Margolin, A. S. (1976). Swimming of the Sea Cucumber *Parastichopus californicus* (Stimpson) in Response to Sea Stars. *OPHELIA, 15*(2), 105-114. https://doi.org/10.1080/00785326.1976.10425452

P. californicus displays a degree of activity which is in strong contrast to its usual lethargic habits, when it is contacted by certain spp of sea stars. This active response begins with local contraction and crawling, accompanied by bending of the body, and culminates with active swimming, in which the animal moves freely and vigorously through the water in an undulating manner. All of 16 spp of sea stars tested produced at least some response, but only *Pycnopodia helianthoides*, 3 spp of the gen *Solaster, Luidia foliolata*, and *Dermasterias imbricata* produced a swimming reaction in an appreciable percentage of the trials; *Pycnopodia* always caused a swimming response. Actual contact appeared to be necessary to

evoke the response. Repeated stimulation of the same individual gave no evidence of adaption on the part of the cucumber. Continuous stimulation produced swimming and crawling for 37 to 40 minutes, with final exhaustion accompanied by a temporary increase in the size of the holothurian. No satisfactory evidence is available for a predator prey relationship between *P. Californicus* and any of the sea stars tested, raising the question as to whether there is justification for terming this a true 'escape response'.

McNeill, M. (2011). *Predation Avoidance Response Behaviors, Oviposition and Distribution of the Intertidal Gastropod Lirularia succincta.* (M.S.), University of Oregon. Retrieved from http://hdl.handle.net/1794/11491

The small trochid gastropod *Lirularia succincta* occurs in rocky intertidal habitats along the Pacific coast of North America. Strong escape responses of adult *L. succincta* were elicited by the predatory seastars *Leptasterias hexactis* and *Pycnopodia helianthoides* but not by the nonpredatory seastar *Henricia* sp. Escape responses to juvenile *L. hexactis* were not observed in newly-hatched *L. succincta*. The snails exhibited weak avoidance responses to water-borne chemical stimuli from *L. hexactis*. The vertical distribution of a population of *L. succincta* was described, and changes in the size-frequency distribution of the population in the spring and summer were documented. Finally, factors that may affect oviposition in *L. succincta* were investigated in the laboratory. The snails deposit egg masses year round with a peak in reproductive output in the summer. In the laboratory and in the field, egg masses are preferentially deposited in crevices.

Miller, J. A., & Byrne, M. (2000). Ceratal Autotomy and Regeneration in the Aeolid Nudibranch *Phidiana crassicornis* and the Role of Predators. *INVERTEBRATE BIOLOGY, 119*(2), 167-176. https://doi.org/10.1111/j.1744-7410.2000.tb00005.x

Ceratal autotomy by the aeolid nudibranch *Phidiana crassicornis* is common in the field and was induced in the laboratory by mechanical and predatory stimuli. The ceras detaches from the body wall along an autotomy plane located at its basal constriction. Cerata released copious amounts of mucus during autotomy and exhibited a prolonged writhing response that continued for several hours after detachment. Regeneration of cerata autotomized in the field and in the laboratory was documented. Four days after autotomy, regenerating cerata appeared as small protuberances. By day 24 the regenerates acquired their mature structural organisation and vivid colour. The cerata subsequently increased in length and diameter and were indistinguishable from surrounding cerata by 41 to 43 days after autotomy. Regeneration rates of cerata induced to autotomize in the laboratory and regeneration of cerata autotomized in the field were similar, averaging 0.08 and 0.067 mm/day, respectively. The sequence of morphological events involved with regeneration following experimental and natural induction of autotomy was identical. The kelp crab *Pugettia producta* induced autotomy by holding cerata with its chelae. This crab also fed on autotomized cerata and consumed locomotory and ceratal mucus. Ceratal autotomy may be an important mechanism of escape from this predatory crustacean. Other potential predators including hermit crabs and tidepool sculpins did not elicit defensive behaviour in *P. crassicornis*. Nematocysts were present in the cnidosacs and their role in defense was investigated. Fired nematocysts were observed in podia of the asteroid *Crossaster papposus* following ceratal contact but were not seen in the podia of *Pycnopodia helianthoides* in a similar trial. For *P. crassicornis*, the cnidosacs may function primarily as a storage device for safe sequestering of nematocysts that could

pose a threat to the digestive system. They did not play a major defensive role against the predators tested, but may be important in the field against other predators.

Montgomery, D. H. (1967). Responses of Two Haliolid Gastropods (Mollusca) *Haliotis assimilis* and *Haliotis rufescens* to the Forcipulate Asteroids (Echinodermata), *Pycnopodia helianthoides* and *Pisaster ochraceus*. *VELIGER, 9*, 359-368. Retrieved from https://www.biodiversitylibrary.org/item/134958#page/1/mode/1up

Introduction: Since 1949 the study of responses of gastropods stimulated by asteroids has received much attention. The stimulating substance is liberated from the tube foot epidermis (Bullock, 1953; Fange, 1963; Feder 1963, Feder & Lasker, 1964; Kohn, 1961 ; Margolin, 1964 a, b; Yarnall, 1964). Some evidence (Feder, 1959, 1963; Margolin, 1964 a, b) indicates that the response is part of a predator-prey escape pattern. Other animals tested exhibit similar responses but information is lacking as to their exact relationships with the asteroids. Responses to asteroids are not limited to gastropods. Experiments with pelecypods (Ray, 1959), actinozoans (Robson, 1961, 1963; Yentsch & Pierce, 1955) and other echinoderms (MacGinitie & MacGinitie, 1949) also showed responses.

Cox (1962) lists a zone from the intertidal to 540 feet as the depth range for *Haliotis rufescens*, with the majority of animals found at 20 to 50 feet. The range of *Haliotis assimilis* is given as 10 to 120 feet with major concentrations between 70 and 100 feet. These abalones overlap in their habitats, but *H. assimilis* is found in much smaller numbers. Light (1954) lists *Pisaster ochraceus* and *Pycnopodia helianthoides* as intertidal animals but *Pisaster ochraceus* usually does not extend much beyond the intertidal, while *Pycnopodia helianthoides* is a permanent resident of subtidal waters. Dredging in Puget Sound, Washington, rarely produced a specimen of *Pisaster ochraceus* from the deeper waters, yet large numbers of *Pycnopodia helianthoides* were easily obtained from like depths. The earlier work of Bennett (1927) and later experiments by Bullock (1953) and Feder (1963) indicate that haliotid gastropods respond to stimulation by asteroids.

For this study only the common forcipulate sea stars in the intertidal (*Pisaster ochraceus*) and the subtidal (*Pycnopodia helianthoides*) were used to initiate responses in the intertidal abalone (*Haliotis rufescens*) and a subtidal abalone (*H. assimilis*).

Nishizaki, M. T. (2002). *Factors Influencing Juvenile Sheltering in Sea Urchins (Strongylocentrotus franciscanus and S. droebachiensis).* (M.S.), University of Northern British Columbia. Retrieved from https://core.ac.uk/download/84872652.pdf

Juvenile red sea urchins (*Strongylocentrotus franciscanus*) are often found under the spines of adults, but those of the green urchin (*S. droebachiensis*) do not shelter to the same extent. As broadcast-spawners with free-swimming larvae, two questions arise: (1) why and; (2) how does sheltering occur? Juvenile *S. franciscanus* increased sheltering in response to increased predation risk and hydrodynamic factors, whereas juvenile *S. droebachiensis* did not. Sheltering afforded protection from a predatory starfish (i.e. *Pycnopodia helianthoides*) in *S. franciscanus* but not *S. droebachiensis*. Water velocities were reduced by 90% within 5 cm of adults where juveniles sheltered. Field surveys confirmed that juvenile abundance is positively correlated with increased water motion. However, results indicate that juveniles compete with adults for kelp, displaying lower growth rates when exposed to adults. Juvenile *S. franciscanus* displayed consistent movement towards a secondary chemical signal

released by adults exposed to *P. helianthoides*, whereas adults did not respond in the same manner. These results highlight the importance of post-settlement processes and call for the inclusion of juvenile stages in predictions of recruitment and population dynamics.

Nishizaki, M. T., & Ackerman, J. D. (2001). Gimme Shelter: Factors Influencing Juvenile Sheltering in the Red Sea Urchin *Strongylocentrotus franciscanus*. In *Echinoderms 2000: Proceedings of the 10th International Conference, Dunedin, 31 January-4 February 2000.* M. Barker (Ed.), (pp. 515-520). Lisse: A.A. Balkema.

Many benthic marine invertebrates disperse during an obligate, planktonic larval phase and subsequent recruitment into the adult population is often unpredictable in both time and space. Thus, the common occurrence of juvenile sea urchins "sheltering" under adults is peculiar given that they possess a pelagic larval stage. An explanation for this pattern cannot be provided by models based on larval transport or larval settlement and it is most probable that post-settlement processes (i.e. behaviour and/or mortality of juveniles) influence this sheltering phenomenon. Laboratory experiments were conducted to determine the relationship between juvenile sheltering in the red sea urchin *Strongylocentrotus franciscanus* and three factors, water motion, risk of predation, and nutrition. Juvenile sea urchins (6.50+/-0.11 mm TD; test diameter) in a laboratory aquarium exhibited a significant increase ($p < 0.001$) in the percentage of sheltering juveniles under high energy water conditions (speed, U = 3.22 cm/s) compared to low energy conditions (U = 1.71 cm/s). Likewise, the proportion of juveniles sheltering was significantly increased ($p = 0.003$) using water passed over a starved predator (*Pycnopodia helianthoides*). A nutritional benefit for sheltering was also evident in recently settled urchins (1.41+/-0.02 mm TD), which had significant growth ($p = 0.013$) when provided with kelp (*Macrocystis integrifolia*) blades, whereas growth was not significantly different from controls when urchins were fed ground kelp or kelp processed by adults. These results indicate that juvenile movements related to post-settlement processes is a possible mechanism to explain the association between juvenile and adult sea urchins.

Nishizaki, M. T., & Ackerman, J. D. (2005). A Secondary Chemical Cue Facilitates Juvenile-Adult Postsettlement Associations in Red Sea Urchins. *LIMNOLOGY AND OCEANOGRAPHY, 50*(1), 354-362. https://doi.org/10.4319/lo.2005.50.1.0354

Responses to predator odors or chemical alarm cues or both from conspecifics in aquatic systems generally involve a single chemical cue. We report a secondary chemical cue, released by adult red sea urchins after they detect primary chemical cues from a predatory sea star. This secondary cue, which is detected by juvenile urchins, leads to the aggregation of juveniles underneath adults for protection. In choice experiments, juvenile *Strongylocentrotus franciscanus* moved toward adults in response to a chemical cue produced by adults held downstream of a predatory sea star (*Pycnopodia helianthoides*), but showed no such response to predators presented in the absence of adults or when adults were held upstream of predators. Furthermore, this response was size dependent and not symmetrical, since larger urchins did not respond to the secondary cue. This secondary chemical cue system may confer a selective advantage for juveniles, allowing them to balance risk of predation versus competition with adults. This result underscores the significance of postsettlement processes in the recruitment of mobile benthic invertebrates, which in the case of red sea urchins involves a unique behavioral strategy.

Nishizaki, M. T., & Ackerman, J. D. (2007). Juvenile-Adult Associations in Sea Urchins (*Strongylocentrotus franciscanus* and *S. droebachiensis*): Protection from Predation and Hydrodynamics in *S. franciscanus*. *MARINE BIOLOGY, 151*(1), 135-145. https://doi.org/10.1007/s00227-006-0462-6

Juvenile red sea urchins, *Strongylocentrotus franciscanus*, aggregate under adult conspecifics, whereas sympatric juvenile green sea urchins, *Strongylocentrotus droebachiensis*, are typically more solitary and dispersed. Neither the potential advantage of juvenile sheltering nor the differences in post-settlement behavior between the two species has been demonstrated experimentally, but may be related to protection from predators and/or hydrodynamics. In predation experiments, juvenile vulnerability differed in the two species as the seastar *Pycnopodia helianthoides* consistently chose juvenile *S. franciscanus* over *S. droebachiensis* (100% vs. 0%). When associated with adults, juvenile mortality decreased dramatically in *S. franciscanus* (90% alone vs. 5% with adults), but very little in *S. droebachiensis* (85% vs. 75%). Not surprisingly, juvenile behavioral responses in the two species reflect this difference in vulnerability. Juvenile *S. franciscanus* sheltered under adults when predation risk was high, but not when risk was low (44% vs. 13%), whereas sheltering in *S. droebachiensis* was infrequent and not related to predation risk (7% for high risk versus 5% for low risk). From a hydrodynamic perspective, the presence of an adult led to the creation of a hydrodynamic refuge for juveniles, where average water velocities were reduced by > 60% around the adult urchin. Again, striking differences in sheltering rate were apparent in *S. franciscanus* (52% vs. 13% for high flow and low flow, respectively), but not *S. droebachiensis* (5% for high flow versus 4% for low flow). Sheltering behavior was also species-specific as juveniles did not shelter at high rates under adults of the opposite species (16% or less). A field survey confirmed these finding in that juvenile *S. franciscanus* abundance was associated with both adults and water motion ($R^2 = 0.80$, $P = 0.008$, best-subsets regression). These results suggest that sheltering confers juvenile *S. franciscanus* with a degree of protection from predators and water motion, and that species-specific differences in this post-settlement behavior may be related to the differences in the protection afforded by adults.

Palmer, A. R., Szymanska, J., & Thomas, L. (1982). Prolonged Withdrawal: A Possible Predator Evasion Behavior in *Balanus glandula* (Crustacea: Cirripedia). *MARINE BIOLOGY, 67*(1), 51-55. https://doi.org/10.1007/bf00397094

The duration of cirral withdrawal in *Balanus glandula* (Darwin) varies by a factor of three depending on the type of stimulus applied. Contact with potential predators including thaidid gastropods (*Thais emarginata, T. lamellosa*), and forcipulate asteroids (*Leptasterias hexactis*, *Pycnopodia helianthoides*) elicits significantly longer withdrawal durations than contact with an herbivorous gastropod (*Tegula pulligo*), a grazing, spinulosid asteroid (*Henricia leviuscula*) or a neutral, brown algal stimulus (*Fucus distichus*). By substantially attenuating the release of metabolites, prolonged withdrawal probably increases the likelihood of being bypassed by nonvisual predators relying on chemical cues to verify that barnacles are alive. The reduced response to the non-predatory species indicates that this is not a generalized response to gastropods or asteroids, but rather that it appears to be specific to potential predatory species.

Phillips, D. W. (1976). The Effect of a Species-Specific Avoidance Response to Predatory Starfish on the Intertidal Distribution of Two Gastropods. *OECOLOGIA, 23*(2), 83-94. https://doi.org/10.1007/bf00557847

The gastropods *Acmaea (Collisella) limatula* and *Acmaea (Notoacmea) scutum* respond to water flowing over certain predatory starfish (i.e. to the scent of the starfish) by moving rapidly up a submerged, vertical surface. These limpets respond with upward movement to the scent of *Pisaster ochraceus, Pisaster giganteus, Pycnopodia helianthoides*, and *Leptasterias aequalis*. All of these starfish are predators on molluscs and at least occasionally inhabit the intertidal. In contrast, the limpets respond weakly or not at all to the scent of *Patiria miniata* and *Pisaster brevispinus*. *Patiria* is an omnivorous scavenger, and *P. brevispinus* is predaceous but strictly subtidal when it occurs on rocky shores. For the starfish tested, then, the limpets only give avoidance responses to starfish species naturally encountered as predators.The avoidance response of *A. limatula* and *A. scutum* to predatory stafish can also be demonstrated in the field. When one *Pisaster ochraceus* is placed beneath a population of limpets in the intertidal and confined so that contacts between the starfish and limpets are impossible, the limpet population is displaced significantly upward after one tidal cycle. In addition, the closer the limpets are to the starfish, the greater is their upward displacement.

Phillips, D. W. (1977). Avoidance and Escape Responses of the Gastropod Mollusc *Olivella biplicata* (Sowerby) to Predatory Asteroids. *JOURNAL OF EXPERIMENTAL MARINE BIOLOGY AND ECOLOGY, 28*(1), 77-86. https://doi.org/10.1016/0022-0981(77)90064-8

The sand-dwelling gastropod *Olivella biplicata* (Sowerby) gives two chemically-mediated defensive responses to predatory asteroids — an avoidance and an escape response. An avoidance response is triggered by water-borne chemicals diffusing from distant starfish. When snails on the surface of the sand sense a distant predatory starfish, they avoid the predator by burying themselves in the sand. Strong avoidance responses are given to the predatory asteroids *Pisaster brevispinus* (Stimpson), *P. ochraceus* (Brandt), and *Pycnopodia helianthoides* (Brandt). Little or no response is given to the omnivorous asteroid *Patiria miniata* (Brandt) or to the predatory gastropod *Polinices lewisii* (Gould). An escape response is given when a snail on the surface is contacted by the starfish *Pisaster brevispinus*. Upon contact, the snail immediately retracts the propodium, sometimes throwing the metapodium forward at the same time; the snail then turns sharply away from the point of contact, and buries itself. Both avoidance and escape responses can be observed in the field and laboratory.

Phillips, D. W. (1978). Chemical Mediation of Invertebrate Defensive Behaviors and the Ability to Distinguish between Foraging and Inactive Predators. *MARINE BIOLOGY, 49*(3), 237-243. https://doi.org/10.1007/bf00391136

When the predatory sea star *Pycnopodia helianthoides* was placed upstream, the sea urchin *Strongylocentrotus purpuratus* responded defensively by extending and opening its globiferous pedicellariae. No pedicellaria response was given in control seawater or when the sea star was downstream. The snail *Tegula funebralis* responded by moving up vertical surfaces when *Pycnopodia helianthoides* or when *Pisaster ochraceus* were placed upstream. When these sea stars were introduced downstream, the snail's response was not significantly different from that in control seawater. Water collected from an aquarium containing a single sea star was sufficient to trigger the response of *S. purpuratus* and *T. funebralis*; the physical presence of the sea star was not essential. This indicated that a chemical stimulus was involved, and the lack of responses when sea stars were downstream argued strongly against the possible additional involvement of visual or vibrational stimuli. *S. purpuratus* gave stronger pedicellaria responses to water flowing over an active *Pycnopodia helianthoides* than to water flowing over the same sea star when it was inactive. The significance of the ability to distinguish

between actively foraging and inactive predators is discussed, and a mechanism is proposed to explain differences in the amount of stimulatory chemicals released by active and inactive sea stars.

Watanabe, J. M. (1983). Anti-Predator Defenses of Three Kelp Forest Gastropods: Contrasting Adaptations of Closely-Related Prey Species. *JOURNAL OF EXPERIMENTAL MARINE BIOLOGY AND ECOLOGY, 71*(3), 257-270. https://doi.org/10.1016/0022-0981(83)90119-3

The defensive adaptations of three species of *Tegula* that inhabit kelp forests along the central California coast were investigated. Their principal predators are the starfishes *Pisaster giganteus* (Stimpson) and *Pycnopodia helanthoides* (Brandt). *Tegula brunnea* (Philippi) relies on avoidance and flight to escape from both species of starfish. *Tegula pulligo* (Gmelin) flees from contact with *Pisaster*, but not *Pycnopodia*. When attacked by the latter species, *Tegula pulligo* clamps its shell down against the substratum. *T. montereyi* (Kiener) possesses the most effective defenses of the three turban snail species. It flees from *Pisaster*. When captured, it withdraws quickly and deeply into its shell, which is larger (relative to body dry weight) than those of the other two species. This withdrawal caused *Tegula montereyi* to be rejected by *Pisaster* more often than the other two species, possibly through erroneous decisions by the starfish that the shell was empty. *Tegula montereyi* does not withdraw into its shell when captured by *Pycnopodia*; observations indicate that *Tegula montereyi* may be distasteful to *Pycnopodia*. Despite the close taxonomic relationship of the three *Tegula* species and their similar ecological requirements, defensive responses to their principal predators differ. In addition, two of the three species appear to distinguish between the two starfish species and respond in a different manner to each.

Watson, W. H., Lawrence, K. A., & Newcomb, J. M. (2001). Neuroethology of *Melibe leonina* Swimming Behavior. *AMERICAN ZOOLOGIST, 41*(4), 1026-1035. https://doi.org/10.1668/0003-1569(2001)041[1026:nomlsb]2.0.co;2

The nudibranch *Melibe leonina* swims by rhythmically flexing its body from side to side at a frequency of 1 cycle every 25 sec. *Melibe* swim spontaneously, when they are dislodged from the substrate, or when they come in contact with predatory seastars, such as *Pycnopodia helianthoides*. Intracellular recordings obtained from semi-intact swimming *Melibe* reveal a population of 15 swim motoneurons (SMNs) in each pedal ganglion. In general, SMNs in one pedal ganglion fire out-of-phase with SMNs in the opposite pedal ganglion, resulting in rhythmic side-to-side bending movements. In isolated brains, recordings from SMNs yield similar results, indicating the existence of a swim central pattern generator (CPG). There is no evidence for synaptic interactions between SMNs and either inhibiting or exciting SMNs has no impact on the swim pattern. The SMNs are driven by a CPG consisting of 4 interneurons; 2 in the cerebropleural ganglia and 1 in each pedal ganglion. Appropriate bursting activity in the swim interneurons is necessary for swimming to occur. Either hyperpolarization or depolarization of any of the 4 CPG interneurons disrupts the normal swim pattern. Swimming behavior, and the fictive swim motor program expressed by the isolated brain, are inhibited by light and nitric oxide donors. NADPH-diaphorase staining and nitric oxide synthase (NOS) immunocytochemistry of *Melibe* brains suggests the source of nitric oxide might be a pair of bilaterally symmetrical cells located in the cerebropleural ganglia.

Weightman, J. O., & Arsenault, D. J. (2002). Predator Classification by the Sea Pen *Ptilosarcus gurneyi* (Cnidaria): Role of Waterborne Chemical Cues and Physical Contact with Predatory Sea Stars. *CANADIAN JOURNAL OF ZOOLOGY, 80*(1), 185-190. https://doi.org/10.1139/z01-211

Using laboratory and field experiments we examined the defensive behaviour of the sea pen *Ptilosarcus gurneyi* (Gray) towards three species of sea stars representing three levels of predatory threat. In the laboratory we first quantified the behaviour of *P. gurneyi* following physical contact with the sea stars *Dermasterias imbricata* (specialist predator), *Pycnopodia helianthoides* (generalist predator), and *Pisaster ochraceus* (nonpredator). Whereas the majority (73%) of the sea pens rapidly burrowed into the sediment following contact with *D. imbricata*, their response to *P. helianthoides* was highly variable and only 23% exhibited burrowing. In contrast, the response of *P. gurneyi* to *P. ochraceus* was weak and similar to that elicited by contact with a glass rod (control). Also, whereas the majority of sea pens displayed colony-wide bioluminescent flashes towards *D. imbricata* and *P. helianthoides*, their responses to *P. ochraceus* and the control were weaker and more localized. We subsequently examined whether waterborne predator chemical cues alone could trigger the defensive responses of *P. gurneyi* to *D. imbricata* and *P. helianthoides*, using laboratory bioassays of varying stimulus intensity. Interestingly, although exposure to chemical cues from predatory sea stars did not elicit any defensive response in *P. gurneyi*, subsequent physical contact with these predators triggered complete burrowing. Field bioassays using SCUBA yielded similar results, as *P. gurneyi* did not respond to the proximity of predators but rather delayed its response until physical contact occurred. Our study thus provides the first experimental evidence of predator-classification abilities in cnidarians and suggests that physical contact with predatory sea stars is required to trigger defensive behaviours in *P. gurneyi*.

Section IV: Ecology

Anderson, R. C., & Shimek, R. L. (2010). Arm Deflation in the Rare Thorny Sea Star, *Poraniopsis inflatus* (Asteroidea: Poraniidae), a Defensive Response to Other Sea Stars? *The Canadian Field-Naturalist, 124*(3), 199-203. https://doi.org/10.22621/cfn.v124i3.1073

The Thorny Sea Star, *Poraniopsis inflatus*, is rare in the Northeastern Pacific. It lacks pedicellariae or other overt defenses for protection against other predatory sea stars. During an earlier study, a *P. inflatus* confronted by an asteroid-eating sea star was observed to exhibit a possible defensive reaction: "arm deflation." It was 15 years before another *P. inflatus* specimen could be obtained and that hypothesis confirmed by testing with individuals of 18 other sea-star species. Contact with individuals of four predatory sea-stars, *Asterina miniata*, *Crossaster papposus*, *Solaster dawsoni*, and *Pycnopodia helianthoides*, elicited the reaction in the *P. inflatus*. The specimen collapsed ("deflated") an arm closest to the predatory star, possibly by expelling coelomic fluid, exposing more of its embedded thorns (hence its common name) which may discourage other sea stars from attempting to eat it.

Bolwerk, A. (2021). *The Rocky Shores of Prince of Wales, Alaska: Intertidal Ecology, Abalone, and Community Sustainability.* (M.S.), University of Alaska Fairbanks. Retrieved from http://hdl.handle.net/11122/12539

Rocky, nearshore ecosystems are diverse and dynamic environments that function as the link between land and sea and provide important resources for people. In this two-part thesis, I first examined rocky intertidal ecological communities to better understand biotic and abiotic drivers in this system, and then I investigated the abundance of pinto abalone (*Haliotis kamtschatkana*), a key subsistence resource that local community members identified as the most important because of limited harvest and drastic declines. Pinto abalone are tied to Haida subsistence, culture, and spiritual identity and have been a traditional harvest species for the Haida people for millennia. Pinto abalone were harvested by non-Native fishermen through heavy commercial (1970-1996) and personal use harvest, causing a crash of the population. In the rocky intertidal I surveyed the upper and lower extents of major biobands, frequency of occurrence of sessile organisms, and abundance of mobile invertebrates across a vertical gradient at 18 sites near the west coast of Prince of Wales Island. A multivariate approach was used to identify the major drivers of rocky intertidal community composition and structure. Sea otter (*Enhydra lutris*) occupation time, average fetch, beach aspect, rugosity, and rock texture were all identified as influential forces for at least one tidal zone and/or biological metrics. Sea otters were not found to restructure the ecosystem, as they do in deeper kelp forest habitats. To assess the current viability of pinto abalone harvest, concerns about sustainability, and their ecological relationships, I partnered with local harvesters within the community of Hydaburg on Prince of Wales Island to combine Indigenous Knowledge about pinto abalone harvest with SCUBA surveys at historically productive traditional harvest sites. Only four (out of 17) of our shallow transects (2 x 20 m), which are within the depth range for traditional harvest methods, had legal-sized pinto abalone (max = 1 abalone). The traditional pinto abalone harvest fishery failed three out of four fishery recovery criteria that were examined. Fourteen out of eighteen sites did not have large (≥ 100 mm) pinto abalone, and pinto large abalone densities were below 0.1 abalone/m2 at all sites. All intermediate size classes of pinto abalone were represented within the fishery, but only 20% of large size classes were observed. Low pinto abalone abundance leads to concerns about traditional harvest viability and spawning failure and thus recruitment failure, for this density-dependent spawning species. In our generalized linear models, pinto abalone presence, density, and biomass were affected by sea urchin biomass. This baseline study of the current state of pinto abalone at traditional harvest sites bestows critical information to a community that depends on pinto abalone as a resource. The Hydaburg Cooperative Association, as a federally recognized Tribe, can use this information to make local management decisions, which include adjustments to harvest guidelines, implementation of sea otter management zones, and/or the establishment of pinto abalone restoration projects. Working with the Tribe and community members throughout the research process led to better science, applicable data, and took a step toward equity and reciprocity in the research processes.

Bonaviri, C., Graham, M., Gianguzza, P., & Shears, N. T. (2017). Warmer Temperatures Reduce the Influence of an Important Keystone Predator. *JOURNAL OF ANIMAL ECOLOGY, 86*(3), 490-500. https://doi.org/10.1111/1365-2656.12634

Predator-prey interactions may be strongly influenced by temperature variations in marine ecosystems. Consequently, climate change may alter the importance of predators with repercussions for ecosystem functioning and structure. In North-eastern Pacific kelp forests, the starfish *Pycnopodia helianthoides* is known to be an important predator of the purple sea urchin *Strongylocentrotus purpuratus*. Here we investigated the influence of water temperature on this predator-prey interaction by: (i) assessing the spatial distribution and temporal dynamics of both species across a temperature gradient in the northern Channel Islands, California, and (ii) investigating how the feeding rate of *P. helianthoides* on *S. purpuratus* is affected by temperature in laboratory tests. On average, at sites where mean annual temperatures were <14 °C, *P. helianthoides* were common, *S. purpuratus* was rare and kelp was

persistent, whereas where mean annual temperatures exceeded 14 °C, *P. helianthoides* and kelp were rare and *S. purpuratus* abundant. Temperature was found to be the primary environmental factor influencing *P. helianthoides* abundance, and in turn *P. helianthoides* was the primary determinant of *S. purpuratus* abundance. In the laboratory, temperatures >16 °C (equivalent to summer temperatures at sites where *P. helianthoides* were rare) reduced predation rates regardless of predator and prey sizes, although larger sea urchins were consumed only by large starfishes. These results clearly demonstrate that the effect of *P. helianthoides* on *S. purpuratus* is strongly mediated by temperature, and that the local abundance and predation rate of *P. helianthoides* on sea urchins will likely decrease with future warming. A reduction in top-down control on sea urchins, combined with other expected impacts of climate change on kelp, poses significant risks for the persistence of kelp forests in the future.

Burt, J. M. (2019). *Navigating Coexistence: Ecological Drivers and Social Implications of Predator-Induced Regime Shifts in the Northeast Pacific.* (Ph.D.), Simon Fraser University. Retrieved from https://summit.sfu.ca/item/18813

Societies are greatly challenged by regime shifts, when ecosystems undergo fundamental changes that are rapid, unexpected, and difficult to reverse. In order to better navigate these transitions, we need information on the drivers, species interactions, and feedbacks that influence ecosystem dynamics, and an understanding of how human communities are adapting to the profound shifts in ecosystem resources. My thesis applies this social-ecological system lens to an iconic regime shift – the recovery of sea otters (*Enhydra lutris*) in the Northeast Pacific that is triggering a trophic cascade which causes sea urchin and shellfish-dominated rocky reefs to become productive macroalgae-dominated forests. To examine how predation and herbivory interactions affect the structure, function, and resilience of reef communities on the central coast of British Columbia (BC), I conducted four years of subtidal surveys and experiments. These data confirm the critical role of sea otter predation in suppressing urchin populations, but also demonstrate for the first time, that complementary predation by mesopredators (i.e. sunflower sea star *Pycnopodia helianthoides*) further enhance the resilience of kelp forests by consuming smaller-sized urchins that are otherwise unconsumed by otters. I also experimentally quantified how numerical and behavioural factors collectively influence herbivory rates that maintain alternative reef states. Kelp consumption rates showed a positive but non-linear relationship with urchin biomass, whereas food subsidies and predator-avoidance behaviour reduced urchin grazing rates. Next, to understand how sea otter recovery influences coastal Indigenous communities, I worked in a collaborative Indigenous partnership to host workshops and conduct survey interviews in a comparative case study. We identified 22 social-ecological conditions that can influence Indigenous peoples' ability to adapt to otters, and revealed how perceptions and adaptive capacity differed between a BC First Nations community and an Alaska Sugpiaq Tribe. These quantitative and qualitative data suggest that coexistence with sea otters could be improved through strengthening Indigenous agency and authority and enabling collaborative adaptive otter management grounded in traditional knowledge and western science. As a whole, this thesis highlights the complexities, surprises, and contextual nuances that characterize sea otter recovery in tightly coupled social-ecological systems, and provides the foundations for a road map to improve future human-otter coexistence.

Burt, J. M., Tinker, M. T., Okamoto, D. K., Demes, K. W., Holmes, K., & Salomon, A. K. (2018). Sudden Collapse of a Mesopredator Reveals Its Complementary Role in Mediating Rocky Reef Regime Shifts. *Proceedings of the Royal Society B, 285*(1883), 20180553. https://doi.org/10.1098/rspb.2018.0553

While changes in the abundance of keystone predators can have cascading effects resulting in regime shifts, the role of mesopredators in these processes remains underexplored. We conducted annual surveys of rocky reef communities that varied in the recovery of a keystone predator (sea otter, *Enhydra lutris*) and the mass mortality of a mesopredator (sunflower sea star, *Pycnopodia helianthoides*) due to an infectious wasting disease. By fitting a population model to empirical data, we show that sea otters had the greatest impact on the mortality of large sea urchins, but that *Pycnopodia* decline corresponded to a 311% increase in medium urchins and a 30% decline in kelp densities. Our results reveal that predator complementarity in size-selective prey consumption strengthens top-down control on urchins, affecting the resilience of alternative reef states by reinforcing the resilience of kelp forests and eroding the resilience of urchin barrens. We reveal previously underappreciated species interactions within a 'classic' trophic cascade and regime shift, highlighting the critical role of middle-level predators in mediating rocky reef state transitions.

Dayton, P. K. (1975). Experimental Evaluation of Ecological Dominance in a Rocky Intertidal Algal Community. *ECOLOGICAL MONOGRAPHS, 45*(2), 137-159. https://doi.org/10.2307/1942404

The mechanisms by which various species exert influence disproportionate to their abundance or mass on the structure of a lower intertidal algal community were evaluated experimentally. These functional roles were evaluated experimentally. These functional roles were evaluated by various controlled manipulations at seven stations along the Washington coastline ranked according to an exposure/desiccation gradient. The algae were divided into three categories: canopy species, which grow above the other species and apparently succeed in competitively dominating the light resources as demonstrated by algal blooms following their removal; obligate understory species, which die after the canopy species are removed; and fugitive species, which are quick to colonize new space. Ecological dominance was exerted in areas of moderate wave exposure by *Hedophyllum* sessile, which competitively displaces a large number of fugitive algal species and which furnishes a protected habitat for many obligate understory algae that die or defoliate after the removal of *Hedophyllum*. *Hedophyllum* loses this dominance in the most exposed areas, although such sites apparently represent its physiologically optimal habitat, because in these areas it is out—competed by *Laminaria setchellii* and *Lessoniopsis littoralis*. In these wave exposed habitats *Lessoniopsis* was demonstrated to exert a strong competitive dominance over all the other species in the association. The molluscan herbivores were not observed to express any measurable effects on the recruitment or survival of the algae. However, the echinoid *Strongylocentrotus purpuratus* often overexploits its prey and has a pronounced influence on most of the algal species. In this respect *S. purpuratus* enjoys an important community role singular among the many herbivores. Similarly, *Pycnopodia helianthoides* and *Anthopleura xanthogrammica* are disproportionately important carnivores, because their predation on *Strongylocentrotus*, clearing large areas of urchins, results in patches in which algal succession follows. The rate of algal succession following removal of the dominant algal species or of *Strongylocentrotus* is proportional to the degree of wave exposure. The *Hedophyllum* canopy recovery at the Eagle Point area of San Juan Island, a site exposed to relatively little wave action and thus high levels of desiccation, was relatively slow, with only 10%—26% cover reestablished after 3 yr. In contrast, *Hedophyllum* canopy developed up to 66% cover in only 1 yr in the exposed area of Waadah Island; it then quickly lost its dominance to *Laminaria* and *Lessoniopsis*. Algal succession in deeper Portage Head tidepools was found to be relatively slow with no clear dominance expressed after 5 yr.

Duggins, D. O. Z. (1980). *Kelp Dominated Communities: Experimental Studies on the Relationships between Sea Urchins, Their Predators and Their Algal Resources.* (Ph.D.), University of Washington, Seattle, Washington.

Abstract not available.

Eisaguirre, J. H., Eisaguirre, J. M., Davis, K., Carlson, P. M., Gaines, S. D., & Caselle, J. E. (2020). Trophic Redundancy and Predator Size Class Structure Drive Differences in Kelp Forest Ecosystem Dynamics. *ECOLOGY, 101*(5), 1-11. https://doi.org/10.1002/ecy.2993

Ecosystems are changing at alarming rates because of climate change and a wide variety of other anthropogenic stressors. These stressors have the potential to cause phase shifts to less productive ecosystems. A major challenge for ecologists is to identify ecosystem attributes that enhance resilience and can buffer systems from shifts to less desirable alternative states. In this study, we used the Northern Channel Islands, California, as a model kelp forest ecosystem that had been perturbed from the loss of an important sea star predator due to a sea star wasting disease. To determine the mechanisms that prevent phase shifts from productive kelp forests to less productive urchin barrens, we compared pre- and postdisease predator assemblages as predictors of purple urchin densities. We found that prior to the onset of the disease outbreak, the sunflower sea star exerted strong predation pressures and was able to suppress purple urchin populations effectively. After the disease outbreak, which functionally extirpated the sunflower star, we found that the ecosystem response—urchin and algal abundances—depended on the abundance and/or size of remaining predator species. Inside Marine Protected Areas (MPAs), the large numbers and sizes of other urchin predators suppressed purple urchin populations resulting in kelp and understory algal growth. Outside of the MPAs, where these alternative urchin predators are fished, less abundant, and smaller, urchin populations grew dramatically in the absence of sunflower stars resulting in less kelp at these locations. Our results demonstrate that protected trophic redundancy inside MPAs creates a net of stability that could limit kelp forest ecosystem phase shifts to less desirable, alternative states when perturbed. This highlights the importance of harboring diversity and managing predator guilds.

Elliott Smith, E. A., Harrod, C., & Newsome, S. D. (2018). The Importance of Kelp to an Intertidal Ecosystem Varies by Trophic Level: Insights from Amino Acid Δ 13 C Analysis. *ECOSPHERE, 9*(11), 1-14. https://doi.org/10.1002/ecs2.2516

A fundamental question in ecology is understanding how energy and nutrients move through and between food webs, and which sources of production support consumers. In marine ecosystems, these basic questions have been challenging to answer given the limitation of observational methods. Stable isotope analysis of essential amino acids (EAA δ13C) has great potential as a tool to quantify energy and nutrient flow through marine food webs; however, it has been primarily utilized at large spatial scales. Here, we used EAA δ13C analysis to test for connectivity between adjacent subtidal and intertidal components of a nearshore ecosystem in south central Alaska. We measured δ13C of six EAA from four marine producer groups: subtidal kelp (*Laminaria* sp.), offshore particulate organic matter (POM), and intertidal red (*Neorhodomela* sp.) and green (*Ulva* sp.) algae. In addition, we sampled four intertidal invertebrate consumer species spanning a range of trophic/functional groups: *Mytilus* sp., *Strongylocentrotus droebachiensis*, *Nucella* sp., and *Pycnopodia helianthoides*. Using canonical analysis of principal coordinates (CAP) and isotope mixing models (MixSIAR), we tested for differences among

producer EAA δ13C fingerprints and quantified the contribution of producer EAA to consumers. We compared these results to previously published EAA δ13C data on marine producers to examine the generality of this technique. We found the EAA δ13C fingerprints of subtidal kelps (*Laminaria*), *Ulva*, and *Neorhodomela* were highly distinct from one another. Further, our measured EAA δ13C patterns for kelp and red algae matched those previously reported from other localities, suggesting unique and universal EAA δ13C signatures for these groups. However, CAP could not distinguish between microalgae (POM) and *Ulva*, possibly due to similar biochemical pathways for the synthesis of EAA. Using these producer fingerprints, we found upper trophic-level invertebrate consumers, *Nucella* and *Pycnopodia*, derived more than 60% of their essential amino acids from subtidal kelps. In contrast, the sampled primary consumers in the system, *Mytilus* and *Strongylocentrotus*, relied more heavily on *Ulva* and/or offshore POM. Our results provide evidence for connectivity between two adjacent nearshore ecosystems and exemplify EAA δ13C as a powerful new tool in tracing energy and nutrient flow within and among marine food webs.

Elsmore, K. Z. (2021). *Consequences of Kelp Loss: Using Restoration as a Tool to Inform Ecology.* (Ph.D.), University of California Davis. Retrieved from https://escholarship.org/uc/item/51f7192k

In recent years, northern California's *N. luetkeana* forests were hit with what scientists have called the "perfect storm" of conditions, resulting in catastrophic loss of this canopy-forming species (Rogers-Bennet and Catton 2019). While not completely understood, the suite of conditions that aligned to facilitate a loss of 90% of California's bull kelp forests are three-fold: 1) elevated seawater temperatures, which weaken bull kelp individuals 2) sea star wasting disease, which led to the decimation of the sunflower sea star (*Pycnopodia helianthoides*), an important predator in the kelp forest system, and 3) most relevant here, an explosion of purple urchins (*Strongylocentrotus purpuratus*), which notoriously overgraze kelp forests when in high numbers (Rogers-Bennett and Catton 2019). What was once extensive bull kelp forests has now become desolate seascapes of bare rock, caked with purple urchins and red urchins (*Mesocentrotus franciscanus*). Deforestation is a challenge faced by nearshore kelp communities around the globe, and though each system has a unique suite of triggering conditions, the consequences are the same – profound loss of biogenic habitat and dramatically altered community structure and functioning. Restoration has emerged as a mechanism by which to facilitate kelp recovery around the world (Eger et al. 2020; Ray et al. in review). In California, recent kelp restoration efforts have focused on reducing the urchin grazing pressure exerted on the remaining kelp adults and new recruits. In partnership with local commercial urchin divers, nongovernmental organizations The Bay Foundation and Reef Check are working to reduce purple urchin densities along the Palos Verdes Peninsula and Mendocino coastline, respectively. Subsequent recovery of kelp, in response to urchin culling (Williams et al. 2021; Reef Check unpublished data), provides a unique experimental framework by which to explore physical and biological consequences of kelp loss, recovery, and the role kelp forests play in modulating their physical environment. Loss and regrowth of kelp forests can each have profound impacts on their surrounding environment. Here I explore the consequences of *Macrocystis pyrifera* forests' disappearance and regrowth on the local surface gravity waves and alongshore current velocities as well as the consequences of *Nereocystis luetkeana* forest disappearance on jaw-test allometry of two important species of sea urchin (*Strongylocentrotus purpuratus* and *Mesocentrotus franciscanus*). [Excerpt from abstract]

Hartwick, E. B., & Thorarinsson, G. (1978). Den Associates of Giant Pacific Octopus, *Octopus dofleini* (Wulker). *OPHELIA, 17*(1), 163-166. https://doi.org/10.1080/00785326.1978.10425480

During a population study of *Octopus dofleini*, the dens of octopus were checked for other organisms. A variety of organisms were consistently associated with the dens or with debris accumulating at the den arising from the feeding behaviour of the octopus. These co-inhabitants included fishes, sea stars and crabs. For some organisms the association involved scavenging, but in other cases the relationship was not clear.

Hewson, I., Bistolas, K. S. I., Quijano Cardé, E. M., Button, J. B., Foster, P. J., Flanzenbaum, J. M., . . . Lewis, C. K. (2018). Investigating the Complex Association between Viral Ecology, Environment, and Northeast Pacific Sea Star Wasting. *FRONTIERS IN MARINE SCIENCE*. https://doi.org/10.3389/fmars.2018.00077

Sea Star Wasting Disease (SSWD) describes a suite of disease signs that affected > 20 species of asteroid since 2013 along a broad geographic range from the Alaska Peninsula to Baja California. Previous work identified the Sea Star associated Densovirus (SSaDV) as the best candidate pathogen for SSWD in 3 species of common asteroid (*Pycnopodia helianthoides, Pisaster ochraceus* and *Evasterias troscheli*), and virus-sized material (<0.22 µm) elicited SSWD signs in *P. helianthoides*. However, the ability of virus-sized material to elicit SSWD in other species of asteroids was not known. Discordance between detection of SSaDV by qPCR and by viral metagenomics inspired the redesign of qPCR primers to encompass SSaDV and two densoviral genotypes detected in wasting asteroids. Analysis of asteroid samples collected during SSWD emergence in 2013-2014 showed an association between wasting asteroid-associated densoviruses (WAaDs) and SSWD in only one species (*P. helianthoides*). WAaDs were found in association with asymptomatic asteroids in contemporary (2016 and later) populations, suggesting that they form subclinical infections at the times they were sampled. WAaDs were found in SSWD-affected *P. helianthoides* after being absent in asymptomatic individuals a year earlier at one location (Kodiak). Direct challenge of *P. ochraceus, Pisaster brevispinus* and *E. troscheli* with virus-sized material from SSWD-affected individuals did not elicit SSWD in any trial. RNA viral genomes discovered in viral metagenomes and host transcriptomes had viral loads and metagenome fragment recruitment patterns that were inconsistent with SSWD. Analysis of water temperature and precipitation patterns on a regional scale suggests that SSWD occurred following dry conditions at several locations, but mostly was inconsistently associated with either parameter. Semi-continuous monitoring of SSWD subtidally at two sites in the Salish Sea from 2013-2017 indicated that SSWD in *E. troscheli* and *P. ochraceus* was associated with elevated water temperatures, but wasting in *P. helianthoides* occurred irrespective of environmental conditions. Our data therefore do not support that widespread SSWD in species other than *P. helianthoides* is associated with potential viral pathogens. Rather, we speculate that SSWD may represent a syndrome of heterogeneous etiologies between geographic locations, between species, or even within a species between locations.

Karpov, K. A., Geibel, J. J., & Law, P. M. (1997). *Relative Abundance and Size Composition of Subtidal Abalone, Haliotis Spp., Sea Urchin, Strongylocentrotus Spp., and Abundance of Sea Stars Off Fitzgerald Marine Reserve, September 1993.* California Department of Fish and Game, Marine Resources Division. Retrieved from http://hdl.handle.net/1834/18071

Data were collected at twenty-six dive stations at seven discrete latitudes along Fitzgerald Marine Reserve (FMR). Dive stations were targeted at three stratified depth zones: shallow (6.1 m), medium (10.7 m), and deep (16.8 m) in six of the seven locations. Two types of line transects, emergent and

invasive, were completed by separate dive teams at each dive station. The area surveyed totalled 1,510 m2 for emergent and 560 m2 for invasive transects. Reef habitat dominated all depth zones, with moveable boulder and cobble increasing at medium and shallow depths. Encrusting coraline and surface algae dominated (49%), followed by turf (37%), sub-canopy (11.2%), and rare canopy (0.2%). Canopy was found only at shallow depths. Turf and sub-canopy decreased with depth. Only two species of abalone, red, *Haliotis rufescens,* and flat, *H. walallensis*, were found. Flat abalone were extremely rare with only two found on invasive transects (0.004 abalone m-2). Red abalone densities were low at both emergent (0.02 abalone m-2, s.e.=O.Ol) and invasive (0.07 abalone m-2, s.e.=0.03) transects. Red abalone concentrations differed significantly by depth and location. No abalone were found at deep depths and only one sport-legal (178 mm shell length) abalone was found at medium depth. One commercial legal (198 mm shell length) abalone was found on the entire survey. Most sport-legal abalone were located in cryptic habitat in shallow invasive transects (38%), compared to 7% on emergent transects. The only evidence of recruitment was found on invasive transects where three young-of-the-year (<=31 mm shell length) red abalone were found. Evidence from our survey and other sources suggests that sport and commercial fisheries are not sustainable off the San Mateo coast. Red urchin, *Strongylocentrotus franciscanus*, were more abundant than purple urchin, *S. purpuratus*, or red abalone. Red urchin densities were lower in emergent (1.08 urchin m-2,s.e.=0.04) than invasive (1.52, s.e.=0.06 m-2) transects. Densities of red urchin at deep stations in areas of lower algal abundance and potentially greater commercial fishing pressure were about one-half the densities at medium and shallow depths. ANOVA showed significant differences by depth and location. Mean Test Diameter (MTD) increased from deep to medium to shallow depths, while juvenile (<=50 mm) MTD showed an inverse relationship with depth. Shallow-depth invasive transects revealed a missing mode of 83 mm red urchin. This size mode was not found in emergent transects, probably due to cryptic habitat. Purple urchin were found at low densities at all three depth strata. Purple urchin densities were comparable in emergent (0.11 urchin m-2, s.e.=0.02) and invasive (0.09 urchin m-2,s.e.=0.03) transects. ANOVA showed densities varied significantly by location but not depth. 'Juvenile' purple urchin abundance showed an inverse relation to juvenile red urchin, increasing from deep to shallow depths. Purple urchin MTD of 84 mm (s.d.=23) was larger than reported for intertidal areas off FMR. Sea stars were found in high abundance off FMR. Bat stars, *Asterina minata*, had the highest densities (0.79 sea stars m-2, s.e.=0.03) followed by *Pisaster* sp. (0.47 sea stars m-2,s.e.=0.03), and sunflower stars, *Pycnopodia helianthoides*, (0.11 sea stars m-2, s.e.=0.04). *Pisaster* sp. was the only group of sea stars where differences in density were significant by depth or location. (30pp.)

Kvitek, R. G., Oliver, J. S., DeGange, A. R., & Anderson, B. S. (1992). Changes in Alaskan Soft-Bottom Prey Communities Along a Gradient in Sea Otter Predation. *ECOLOGY, 73*(2), 413-428. https://doi.org/10.2307/1940749

Sea Otter (*Enhydra lutris*), well documented as "keystone" predators in rocky marine communities, were found to exert a strong influence on infaunal prey communities in soft—sediment habitats. Direct and indirect effects of sea otter predation on subtidal soft—bottom prey communities were evaluated along a temporal gradient of sea otter occupancy around the Kodiak Archipelago. The results indicate that Kodiak otters forage primarily on bivalve prey and dramatically reduce infaunal bivalve and green sea urchin (*Strongylocentrotus droebachiensis*) prey populations. Bivalve prey abundance, biomass, and size were inversely related to duration of sea otter occupancy. The relative conditions of shells discarded by otters in shallow (<10 m) vs. deep (> 20 m) water at the same sites indicate that otters first exploited Saxidomus in shallow—water feeding areas, and later switched to Macoma spp. in deeper water. Otter—cracked shells of the deep—burrowing clam *Tresus capax* were rarely found, even at otter

foraging sites where the clam accounted for the majority of available prey biomass, suggesting that it has a partial depth refuge from otter predation. The indirect effects of otter predation included substratum disturbance and the facilitation of sea star predation on infaunal prey. Sea stars, *Pycnopodia helianthoides*, were attracted to experimentally dug excavations as well as natural sea otter foraging pits, where the sea stars foraged on smaller size classes of infaunal bivalves than those eaten by otters. Otters also discard clam shells on the sediment surface and expose old, buried shells during excavation. Surface shells were found to provide attachment sites for large anemones and kelp. Our study shows that sea otters can affect soft—sediment communities, not only through predation, as in rocky habitats, but also through disturbance, and thus retain a high degree of influence in two very different habitat types.

Lawrence, J. M. (1991). A Chemical Alarm Response in *Pycnopodia helianthoides* (Echinodermata: Asteroidea). *MARINE BEHAVIOUR AND PHYSIOLOGY, 19*(1), 39-44. https://doi.org/10.1080/10236249109378793

Adult *Pycnopodia helianthoides* exhibit a classic alarm response, moving away from fragments and tissue fluid of the tube feet, pyloric caeca, and body wall of conspecific individuals.

Lee, L. C., Watson, J. C., Trebilco, R., & Salomon, A. K. (2016). Indirect Effects and Prey Behavior Mediate Interactions between an Endangered Prey and Recovering Predator. *ECOSPHERE, 7*(12). https://doi.org/10.1002/ecs2.1604

Managing for simultaneous recovery of interacting species, particularly top predators and their prey, is a longstanding challenge in applied ecology and conservation. The effects of sea otters (*Enhydra lutris kenyoni*) on abalone (*Haliotis* spp.) is a salient example along North America's west coast where sea otters are recovering from 18th- and 19th-century fur trade while efforts are being made to recover abalone from more recent overfishing. To understand the direct and indirect effects of sea otters on northern abalone (*H. kamtschatkana*) and the relative influence of biotic and abiotic conditions, we surveyed subtidal rocky reef sites varying in otter occupation time in three regions of British Columbia, Canada. Sites occupied by sea otters for over 30 years had 16 times lower densities of exposed abalone than sites where otters have yet to recover (0.46 ± 0.08/20 m2 vs. 7.56 ± 0.98/20 m2), but they also had higher densities of cryptic abalone (2.17 ± 1.31/20 m2 vs. 1.31 ± 0.20/20 m2). Abalone densities were greater in deeper vs. shallower habitats at sites with sea otters compared to sites without otters. Sea otter effects on exposed abalone density were three times greater in magnitude than those of any other factor, whereas substrate and wave exposure effects on cryptic abalone were six times greater than those of sea otters. While higher substrate complexity may benefit abalone by providing refugia from sea otter predation, laboratory experiments revealed that it may also lead to higher capture efficiency by sunflower stars (*Pycnopodia helianthoides*), a ubiquitous mesopredator, compared to habitat with lower complexity. Sea otter recovery indirectly benefitted abalone by decreasing biomass of predatory sunflower stars and competitive grazing sea urchins, while increasing stipe density and depth of kelp that provides food and protective habitat. Importantly, abalone persisted in the face of sea otter recovery, albeit at lower densities of smaller and more cryptic individuals. We provide empirical evidence of how complex ecological interactions influence the effects of recovering predators on their recovering prey. This ecosystem-based understanding can inform conservation trade-offs when balancing multifaceted ecological, cultural, and socio-economic objectives for species at risk.

Masuda, M. M., & Stone, R. P. (2003). Biological and Spatial Characteristics of the Weathervane Scallop *Patinopecten caurinus* at Chiniak Gully in the Central Gulf of Alaska. *Alaska Fishery Research Bulletin, 10*(2), 104-118. Retrieved from https://www.proquest.com/scholarly-journals/biological-spatial-characteristics-weathervane/docview/17767429/se-2?accountid=28258

A manned submersible was used to collect biological and behavioral information on a deepwater population of weathervane scallops Patinopecten caurinus near Kodiak Island in the central Gulf of Alaska. Counts and positions of weathervane scallops and 3 additional species groups (anemones [*Cribrinopsis fernaldi* and *Metridium senile*], sunflower sea stars *Pycnopodia helianthoides*, and sea whips [*Protoptilum* sp. and *Halipteris willemoesi*]) along 20 fixed transects were compiled from video footage of the seafloor. The study site encompassed areas open to bottom trawling and scallop dredging and areas closed for 11 and 12 years. Statistical methods of circular tests, neighbor K analysis for one-dimensional data, analysis of variance, and Spearman rank correlation coefficient were used to assess weathervane scallop orientation, spatial characteristics, differences in abundance and size distributions between open and closed areas, and faunal associations. Orientation of weathervane scallops was directed with most oriented towards the strongest, prevailing bottom currents or the reciprocal, weaker currents. Adult weathervane scallops were aggregated in patch lengths ranging from less than 10 m to over 700 m. In 1999 only, the open area had higher prerecruit abundance relative to recruit abundance than the closed area. Weathervane scallop density (number of scallops m super(-2)) was not significantly lower in the open than in the closed area. There was some evidence of positive spatial associations between adult weathervane scallops and both large sea whips and anemones, and negative spatial association between adult weathervane scallops and sunflower sea stars. Juvenile weathervane scallops exhibited positive spatial association with anemones. Weathervane scallop density tended to be high in areas of high sea whip density and low in areas of high sunflower sea star density.

McPherson, M. L., Finger, D. J. I., Houskeeper, H. F., Bell, T. W., Carr, M. H., Rogers-Bennett, L., & Kudela, R. M. (2021). Large-Scale Shift in the Structure of a Kelp Forest Ecosystem Co-Occurs with an Epizootic and Marine Heatwave. *Communications Biology, 4*(1), 1-9. https://doi.org/10.1038/s42003-021-01827-6

Climate change is responsible for increased frequency, intensity, and duration of extreme events, such as marine heatwaves (MHWs). Within eastern boundary current systems, MHWs have profound impacts on temperature-nutrient dynamics that drive primary productivity. Bull kelp (*Nereocystis luetkeana*) forests, a vital nearshore habitat, experienced unprecedented losses along 350 km of coastline in northern California beginning in 2014 and continuing through 2019. These losses have had devastating consequences to northern California communities, economies, and fisheries. Using a suite of in situ and satellite-derived data, we demonstrate that the abrupt ecosystem shift initiated by a multi-year MHW was preceded by declines in keystone predator population densities. We show strong evidence that northern California kelp forests, while temporally dynamic, were historically resilient to fluctuating environmental conditions, even in the absence of key top predators, but that a series of coupled environmental and biological shifts between 2014 and 2016 resulted in the formation of a persistent, altered ecosystem state with low primary productivity. Based on our findings, we recommend the implementation of ecosystem-based and adaptive management strategies, such as (1) monitoring the status of key ecosystem attributes: kelp distribution and abundance, and densities of sea urchins and their predators, (2) developing management responses to threshold levels of these attributes, and (3) creating quantitative restoration suitability indices for informing kelp restoration efforts.

Mladenov, P. V. (1983). Rate of Arm Regeneration and Potential Causes of Arm Loss in the Feather Star *Florometra serratissima* (Echinodermata: Crinoidea). *CANADIAN JOURNAL OF ZOOLOGY, 61*(12), 2873-2879. https://doi.org/10.1139/z83-375

Rate of arm regeneration was measured in caged specimens of the stalkless crinoid *Florometra serratissima* (A. H. Clark) with one, two, three, and five amputated arms. A single arm amputated at the base regenerates to a fully functional condition in under 9 months. Contrary to earlier speculation, the rate of regeneration per arm decreases slightly as the number of regenerating arms on an individual increases. However, the total rate of regeneration of new arm tissue on an individual increases with increasing number of regenerating arms. An arm amputated midway regenerates at a rate similar to that of an arm amputated near the base. In the population of *F. serratissima* under study, just under 80% of the individuals had at least one regenerating arm. The potential causes of arm loss are considered and some observations are presented which suggest that the sea star *Pycnopodia helianthoides* and the crab *Oregonia gracilis* will attack this feather star and cause it to autotomize arms.

Phillips, D. W. (1980, 1980). *Steroid Saponins Concentrated from Water Surrounding Living Specimens of the Sea-Stars Pycnopodia helianthoides and Patiria miniata.* Paper presented at the Annual Meeting of the American Society of Zoologists, American Microscopical Society, American Society of Limnology and Oceanography, Animal Behavior Society, Canadian Society of Zoologists, Ecological Society of America, Society of Systematic Zoology and the Western Society of Naturalists, Seattle, Washington.

Steroid saponins have been proposed as the chemicals eliciting defensive responses by seastar prey. Non-ionic exchange resin was used to concentrate low levels of saponin directly from seawater surrounding living specimens of the seastars *Pycnopodia helianthoides* and *Patiria miniata*. The total amount of saponin released into the water by *Pycnopodia*, a predatory seastar known to elicit defensive responses by many of its prey, and *Patiria*, a seastar rarely eliciting such responses, was similar. Thinlayer chromatography revealed differences between the steroids of the two seastars. The general approach of isolating proposed chemical signals directly from water surrounding living animals has advantages over the traditional use of whole-body extracts. The two principal benefits are that it provides direct access to the set of biologically relevant signals, namely the chemicals actually released into the water, and it provides a means of estimating what concentration of stimulatory chemical is physiologically appropriate.

Pirtle, J. L. (2010). *Habitat Function in Alaska Nearshore Marine Ecosystems.* (Ph.D.), University of Alaska Fairbanks, Fairbanks, AK. Retrieved from http://hdl.handle.net/11122/9064

This research demonstrates how habitat structures subtidal communities and supports individual species in Alaska nearshore marine ecosystems. This was accomplished through a case study of southeast Alaska coastal regions, and an in-depth investigation of red king crab *Paralithodes camtschaticus* early life stage ecology and nursery habitat. How subtidal communities reflect variation in the marine environment of southeast Alaska is poorly understood. The purpose of the first part of this body of research was to identify and compare patterns of community structure for macroalgae, invertebrate, and fish communities at shallow subtidal depths between inner coast and outer coast regions, and link patterns

of community structure to environmental variability in southeast Alaska. The major hydrographic gradient of decreasing salinity and increasing temperature from the outer coast to the inner coast affected regional community structure, with greater species diversity at the outer coast. Species distribution for invertebrate communities was linked to variation in benthic habitat at local scales among sites within regions. This study improves understanding of processes that structure marine communities to better predict how environmental change will affect Alaska marine ecosystems. Many Alaska red king crab populations have collapsed and continue to experience little recovery, even for areas without a commercial fishery. Several aspects of red king crab early life stage ecology were investigated because reasons for the lack of recovery may be related to the early life history of this species. Field experiments were conducted in southeast Alaska. Settlement timing was consistent between study years (2008--09) and with historical data for this region. Local oceanographic processes that influence larval transport may be responsible for spatial variation in larval supply. In laboratory and field experiments, early juvenile crabs (age 0 and 1) demonstrated refuge response behavior to a predator threat that changed with crab ontogeny. When predators were absent, juvenile crabs preferred highly structured biogenic habitats due to foraging opportunities, and associated with any structural habitat to improve survival when predators were present. This research shows how availability of high quality nursery habitat affects red king crab early life stage success and potential for population recovery.

Rogers-Bennett, L., & Catton, C. A. (2019). Marine Heat Wave and Multiple Stressors Tip Bull Kelp Forest to Sea Urchin Barrens. *Scientific Reports, 9*(1), 15050. https://doi.org/10.1038/s41598-019-51114-y

Extreme climatic events have recently impacted marine ecosystems around the world, including foundation species such as corals and kelps. Here, we describe the rapid climate-driven catastrophic shift in 2014 from a previously robust kelp forest to unproductive large scale urchin barrens in northern California. Bull kelp canopy was reduced by >90% along more than 350 km of coastline. Twenty years of kelp ecosystem surveys reveal the timing and magnitude of events, including mass mortalities of sea stars (2013-), intense ocean warming (2014-2017), and sea urchin barrens (2015-). Multiple stressors led to the unprecedented and long-lasting decline of the kelp forest. Kelp deforestation triggered mass (80%) abalone mortality (2017) resulting in the closure in 2018 of the recreational abalone fishery worth an estimated $44 M and the collapse of the north coast commercial red sea urchin fishery (2015-) worth $3 M. Key questions remain such as the relative roles of ocean warming and sea star disease in the massive purple sea urchin population increase. Science and policy will need to partner to better understand drivers, build climate-resilient fisheries and kelp forest recovery strategies in order to restore essential kelp forest ecosystem services.

Rogers-Bennett, L., & Okamoto, D. (2020). Chapter 32 - *Mesocentrotus franciscanus* and *Strongylocentrotus purpuratus*. In *Sea Urchins: Biology and Ecology.* J. M. Lawrence (Ed.), (Vol. 43, pp. 593-608) https://doi.org/10.1016/b978-0-12-819570-3.00032-9

In the northeast Pacific, the sea urchins *Mesocentrotus franciscanus* and *Strongylocentrotus purpuratus* are ecologically important species that play a dominant role in intertidal and subtidal rocky ecosystems. *M. franciscanus* are the basis for important commercial fisheries and serve as an indigenous traditional food resource as well as model species in developmental research. Both species are important ecosystem structuring species (ecosystem engineers) that control the flow of resources within marine communities. Recent work continues to reveal factors that shape their population dynamics, role in the

ecosystem, and how climate change may alter both of these. Over the past decade, the coast-wide collapse of the predatory sea star *Pycnopodia helianthoides* and a massive, long-lasting marine heat wave corresponded with historically stable, kelp forests transitioning to species-poor barrens dominated by *M. franciscanus* and *S. purpuratus*. In contrast, some sea urchin populations have experienced declines due to disease in southern California, toxins in northern California, expanding populations of the sea otter *Enhydra lutris* in Alaska and British Columbia or the recovery of sea urchin predators in California's marine protected areas. Such radical changes in population dynamics have direct and indirect consequences for the productivity and diversity of kelp forests. In northern California, the recent destruction of the kelp forest by sea urchins has had cascading impacts resulting in the collapse of both the commercial *M. franciscanus* and recreational red abalone, *Haliotis rufescens*, fisheries. Currently, there are efforts to ameliorate the proliferation of barrens or poor quality of sea urchin roe include kelp restoration through culling, sea urchin ranching, and plans for rebuilding populations of sea urchin predators. A looming question for both sea urchins and kelp forests is how climate change will affect reproduction and recruitment via larval production, development, ocean transport, budding, survival and settlement, and how these processes vary across space and time. Research continues to reveal both physiological sensitivity and resilience to effects of climate change of sea urchins, such as warming, food deficiencies, hypoxia, salinity, low pH, and ocean circulation. How both climatic effects and the ecological factors that impact the dynamics of sea urchin populations, and the ecosystems they control, remains a critical area of research for these ecologically, culturally, and commercially important species.

Roopnarine, P. D., Banker, R. M. W., & Sampson, S. D. (2022). Impact of the Extinct Megaherbivore Steller's Sea Cow (*Hydrodamalis gigas*) on Kelp Forest Resilience. *FRONTIERS IN ECOLOGY AND EVOLUTION, 10*, 983558. https://doi.org/10.3389/fevo.2022.983558

Giant kelp forests off the west coast of North America are maintained primarily by sea otter (*Enhydra lutris*) and sunflower sea star (*Pycnopodia helianthoides*) predation of sea urchins. Human hunting of sea otters in historical times, together with a marine heat wave and sea star wasting disease epidemic in the past decade, devastated these predators, leading to widespread occurrences of urchin barrens. Since the late Neogene, species of the megaherbivorous sirenian Hydrodamalis ranged throughout North Pacific giant kelp forests. The last species, *H. gigas*, was driven to extinction by human hunting in the mid-eighteen century. *H. gigas* was an obligate kelp canopy browser, and its body size implies that it would have had a significant impact on the system. Here, we hypothesize that sea cow browsing may have enhanced forest resilience. We tested this hypothesis with a mathematical model, comparing historical and modern community responses to marine heat waves and sea star wasting disease. Results indicate that forest communities were highly resistant to marine heat waves, yet susceptible to sea star wasting disease, and to disease in combination with warming. Resistance was greatest among systems with both sea cows and sea otters present. The model additionally predicts that historical communities may have exhibited delayed transitions after perturbation and faster recovery times. Sea cow browsing may therefore have enhanced resilience against modern perturbations. We propose that operationalizing these findings by mimicking sea cow herbivory could enhance kelp forest resilience.

Rubin, S. P., Foley, M. M., Miller, I. M., Stevens, A. W., Warrick, J. A., Berry, H. D., . . . Gelfenbaum, G. (2023). Nearshore Subtidal Community Response During and after Sediment Disturbance Associated with Dam Removal. *FRONTIERS IN ECOLOGY AND EVOLUTION, 11*, 1233895. https://doi.org/10.3389/fevo.2023.1233895

Dam removal is used increasingly to restore aquatic ecosystems and remove unnecessary or high-risk infrastructure. As the number of removals increases, there is a growing understanding about the hydrologic, geomorphic, and ecological responses to these removals. Most dam removal studies, however, focus on river and watershed responses to dam removal. The removal of two dams on the Elwha River provided a unique opportunity to characterize the response of nearshore (coastal) ecosystems. We conducted SCUBA surveys between 2011 and 2022 to quantify trajectories of change in a nearshore ecosystem during and after dam removal. We focused on the degree to which the abundances of kelp, benthic invertebrates, and fish changed in response to patterns of sediment fluxes during and after dam removal. Our findings point to two pathways of response depending on the disturbance mechanism and species type. Sites with persistent sediment deposition were characterized by wholesale community changes that did not recover to a before dam removal condition. Instead, the sites were colonized by new species that were largely absent prior to dam removal. Sites that experienced high turbidity but lacked persistent seafloor deposition were primarily characterized by a reduction in the abundance of kelp and other algae during dam removal and a rapid recovery after sediment flux to the nearshore declined. Dam removal influences on invertebrates and fish at these sites were more variable, benefiting some species and disadvantaging others. In addition to dam removal, sea star wasting syndrome and a marine heatwave exerted distinct controls on subtidal communities during the same period. The loss of the predatory sea star *Pycnopodia helianthoides* was associated with gains in some of its prey species, and kelp community changes reflected regional trends in ocean temperature and kelp abundance. The results presented here have important implications for understanding the response of marine ecosystems to future dam removals and similar sediment perturbation events.

Sandoval, E. J. (2005). *Topographic Complexity and Benthic Community Variability within a Kelp Forest in Monterey Bay, Ca.* (M.S.), California State University, Monterey Bay. Retrieved from https://digitalcommons.csumb.edu/caps_thes/88

By understanding species and habitat associations, predictions of species composition can be made about a benthic community based on available habitat. In a kelp forest, topographic complexity can affect an organism, by modifying flow, altering food availability, altering light availability, and provide refuges and barriers that fragment the habitat. There are many qualitative ways to evaluate topographic complexity. Rugosity is a quantitative measure and is defined as the ratio of surface area to planar area. Using habitat maps developed in GIS from multibeam bathymetry data, regions of varying rugosity were mapped in southern Monterey Bay, CA. Associated benthic communities were examined to elucidate spatial patterns and similarities in community composition. In addition, transect rugosity, significant wave height (Hs), depth, the number of edges, the number of walls and the number of crevices were used to compare environmental spatial patterns with biological spatial patterns. Results from non-metric multidimensional scaling (MDS) plots and Analysis of Similarity (ANOSIM) indicated no differences among high, medium or low rugosity classes, but did indicate significant sample site differences. Results from a Biological-Environmental (BIO-ENV) analysis procedure suggest that Hs, transect rugosity and depth correlate best with community composition variation, but only explain up to 0.35 of the variation. These results suggest that variables that were previously thought to be important in predicting benthic community composition and spatial structure may in fact work in combination with other unexamined variables. By examining species/habitat associations at multiple scales and showing strong species to habitat correlation, a more accurate and detailed assessment of benthic communities can be made and allow researchers to refine spatial predictions of these communities.

Schultz, J. A., Cloutier, R. N., & Côté, I. M. (2016). Evidence for a Trophic Cascade on Rocky Reefs Following Sea Star Mass Mortality in British Columbia. *PEERJ*. https://doi.org/10.7717/peerj.1980

Echinoderm population collapses, driven by disease outbreaks and climatic events, may be important drivers of population dynamics, ecological shifts and biodiversity. The northeast Pacific recently experienced a mass mortality of sea stars. In Howe Sound, British Columbia, the sunflower star *Pycnopodia helianthoides*—a previously abundant predator of bottom-dwelling invertebrates—began to show signs of a wasting syndrome in early September 2013, and dense aggregations disappeared from many sites in a matter of weeks. Here, we assess changes in subtidal community composition by comparing the abundance of fish, invertebrates and macroalgae at 20 sites in Howe Sound before and after the 2013 sea star mortality to evaluate evidence for a trophic cascade. We observed changes in the abundance of several species after the sea star mortality, most notably a four-fold increase in the number of green sea urchins, *Strongylocentrotus droebachiensis*, and a significant decline in kelp cover, which are together consistent with a trophic cascade. Qualitative data on the abundance of sunflower stars and green urchins from a citizen science database show that the patterns of echinoderm abundance detected at our study sites reflected wider local trends. The trophic cascade evident at the scale of Howe Sound was observed at half of the study sites. It remains unclear whether the urchin response was triggered directly, via a reduction in urchin mortality, or indirectly, via a shift in urchin distribution into areas previously occupied by the predatory sea stars. Understanding the ecological implications of sudden and extreme population declines may further elucidate the role of echinoderms in temperate seas, and provide insight into the resilience of marine ecosystems to biological disturbances.

Smith, J. G., Tomoleoni, J., Staedler, M., Lyon, S., Fujii, J., & Tinker, M. T. (2021). Behavioral Responses across a Mosaic of Ecosystem States Restructure a Sea Otter–Urchin Trophic Cascade. *PROCEEDINGS OF THE NATIONAL ACADEMY OF SCIENCES OF THE UNITED STATES OF AMERICA, 118*(11), 1. https://doi.org/10.1073/pnas.2012493118

Consumer and predator foraging behavior can impart profound trait-mediated constraints on community regulation that scale up to influence the structure and stability of ecosystems. Here, we demonstrate how the behavioral response of an apex predator to changes in prey behavior and condition can dramatically alter the role and relative contribution of top-down forcing, depending on the spatial organization of ecosystem states. In 2014, a rapid and dramatic decline in the abundance of a mesopredator (*Pycnopodia helianthoides*) and primary producer (*Macrocystis pyrifera*) coincided with a fundamental change in purple sea urchin (*Strongylocentrotus purpuratus*) foraging behavior and condition, resulting in a spatial mosaic of kelp forests interspersed with patches of sea urchin barrens. We show that this mosaic of adjacent alternative ecosystem states led to an increase in the number of sea otters (*Enhydra lutris nereis*) specializing on urchin prey, a population-level increase in urchin consumption, and an increase in sea otter survivorship. We further show that the spatial distribution of sea otter foraging efforts for urchin prey was not directly linked to high prey density but rather was predicted by the distribution of energetically profitable prey. Therefore, we infer that spatially explicit sea otter foraging enhances the resistance of remnant forests to overgrazing but does not directly contribute to the resilience (recovery) of forests. These results highlight the role of consumer and predator trait-mediated responses to resource mosaics that are common throughout natural ecosystems and enhance understanding of reciprocal feedbacks between top-down and bottom-up forcing on the regional stability of ecosystems.

Tolimieri, N., Shelton, A. O., Samhouri, J. F., Harvey, C. J., Feist, B. E., Williams, G. D., . . . Waddell, J. (2023). Changes in Kelp Forest Communities Off Washington, USA, During and after the 2014-2016 Marine Heatwave and Sea Star Wasting Syndrome. *MARINE ECOLOGY PROGRESS SERIES, 703*, 47-66. https://doi.org/10.3354/meps14220

Canopy-forming kelps are foundation species in many coastal ecosystems, but kelp-forest communities are subject to abrupt state changes caused by environmental drivers and trophic dynamics. We examined changes in kelp communities at 5 sites along the Olympic Coast of Washington State, USA, during and following the recent perturbations of anomalous warm-water events and sea star wasting syndrome (SSWS). Anomalously warm water in 2013 and 2014 corresponded with a loss of approximately 50% of *Macrocystis pyrifera* and *Nereocystis luetkeana* canopy. However, the canopy quickly recovered, and stipe density increased after 2015. Purple sea urchins *Strongylocentrotus purpuratus* increased in density 164-fold, largely at one site, but this increase was first observed in 2017 and peaked in 2019, after the warm period. Sea stars did not show recovery from SSWS, with several species including *Pycnopodia helianthoides* continuing to decline. The majority of variation in assemblage structure occurred at the site level for kelps, macroinvertebrates, and fishes, while year explained most of the variability for juvenile rockfishes *Sebastes* spp. We did not see strong top-down effects of urchins on kelp, suggesting that top-down impacts were not dominant regionally during this period. In contrast, we found evidence for a bottom-up influence of kelp habitat on juvenile rockfishes, as rockfish recruits occurred with higher probability where kelp stipe density was higher. Our analyses highlight the importance of spatial variation in structuring changes in kelp forest communities associated with disturbance and suggest that it is essential to ensure the protection of a diversity of kelp forests.

Traiger, S. B. (2017). *Otters, Sea Stars, and Glacial Melt: Top-Down and Bottom-up Factors That Influence Kelp Communities.* (Ph.D.), University of Alaska Fairbanks, Fairbanks, AK. Retrieved from http://hdl.handle.net/11122/7903

Kelp beds are important features of the Alaska coastline and provide habitat, protect coastlines, and support commercial and subsistence harvests. Kelp beds are affected by top-down and bottom-up factors, which are changing due to human and climate-related impacts. The influences of these top-down and bottom-up factors on kelp beds are investigated in three chapters. My first chapter investigated the influence of glacial discharge on recruitment and early community development in subtidal kelp communities by monitoring benthic sessile algae and invertebrates on cleared rocks across a glacial gradient along with various physical and biological parameters in the summers of 2013-2014. It has been predicted that Alaska's glaciers will lose 30-60% of their volume by 2100. The melt from glaciers increases sedimentation and lowers salinity, impacting important habitat-providing kelp. I found that sites upstream from glacial discharge had higher kelp recruitment than downstream sites, and that up to 72% of the variation in community development was related to mobile invertebrates and kelp in the surrounding community. Glacially-influenced environmental factors did not explain any variation that was not already explained by biological factors. My second chapter explored whether patterns in the recruitment of the dominant canopy kelp, *Nereocystis luetkeana* and the subcanopy kelp, *Saccharina latissima* were a result of dispersal limitation or failure to grow to macroscopic size. My goals were to determine 1) whether glacial melt conditions affect adult fecundity (spore production) of either species, 2) how sedimentation affects early gametophyte growth and survival in each species, and 3) whether competitive interaction between species at the gametophyte stage is altered by sediments. I found that

glacial melt conditions did not affect the fecundity of either species, but sedimentation affected survival and competition. *Saccharina latissima* was the superior competitor under high sediment conditions. Because glacially-influenced coastal areas often have little exposed hard substrate and predation by sea otters and sea stars on clams can provide hard substrate for kelp colonization, my third chapter examined methods for determining predation on clams by these predators without direct observation. I found that foraging pits of sea otters and sea stars could not be distinguished using quantitative measurements. In contrast, shell litter proved useful in quantifying relative foraging rates. Clam consumption by sea otters and sea stars was equal at all but one site. Collectively, my thesis chapters provide information on the effects of glacial discharge on microscopic and early kelp life stages in Alaska which can be incorporated into management practices.

Van Veldhuizen, H. D., & Oakes, V. J. (1981). Behavioral Responses of Seven Species of Asteroids to the Asteroid Predator, *Solaster dawsoni* (Responses of Asteroids to the Predator *Solaster dawsoni*). *OECOLOGIA, 48*(2), 214-220. https://doi.org/10.1007/bf00347967

Seven asteroid species common to the northern California coast were studied for their defensive responses to the predator *Solaster dawsoni*. The presence or absence of an escape response was used to predict whether or not these species were susceptible to predation from *Solaster*. Strong escape responses were displayed by *Patiria miniata*, *Henricia leviuscula*, *Leptasterias hexactis*, *Pycnopodia helianthoides*, and small *Pisaster ochraceus*. Subsequent capture and consumption of *Patiria, Henricia, Leptasterias* and small *P. ochraceus* were observed. *Solaster* attacked all *Pisaster* spp. tested, but *Pisaster brevispinus* and larger *P. ochraceus* protected themselves from predation by utilizing their pedicellariae against *Solaster* whenever contact occurred. *Dermasterias imbricata* appeared to be immune to predation by *Solaster*. Contact between these two asteroids failed to elicit a defensive response in the former or an attack by the latter asteroid.

Vaughan, M. L. H. (2015). *Effects of Ocean Acidification on Predator-Prey Interactions in Echinoderms.* (M.S.), University of British Columbia. https://doi.org/10.14288/1.0166211

The need to understand future changes in marine ecosystems has become critically important as increasing atmospheric carbon dioxide (CO2) drives rapid ocean acidification (OA). OA may improve or reduce the performance of marine species, and the relative impacts on interacting species will largely determine changes at the community level. The goal of this thesis was to determine the effects of acidification on predator-prey interactions between red sea urchins (*Strongylocentrotus franciscanus*) and sunflower stars (*Pycnopodia helianthoides*), a key predator-prey pair in Northeast Pacific kelp forest ecosystems. I tested this question using laboratory mesocosm experiments. Sea urchins were acclimated to ambient (pCO2 ~ 500 µatm, pH ~ 8.0) or acidified (pCO2 ~ 1000 µatm, pH ~ 7.7) conditions, with or without a caged sea star, for 22 weeks in a recirculating seawater system. In Chapter 2, I investigated the effects of OA on the growth, calcification, and feeding rate of *P. helianthoides*. High CO2 had a significant positive effect on sea star growth, but no effect on calcified tissue mass. In addition, the consumption rate of turban snails (*Chlorostoma funebralis*) by sea stars was significantly higher in the high CO2 treatment. In Chapter 3, I examined the effects of OA on the responses of *S. franciscanus* to sea star cues. Predator presence and high CO2 negatively and additively affected sea urchin growth rates, but did not affect alarm responses to predator cues. Significantly higher grazing rates on kelp (*Macrocystis pyrifera*) were also observed in the presence of predators. Predators, but not CO2, had a significant negative effect on urchin calcified mass. Urchin spine length was also significantly reduced under

acidified conditions. Overall, these findings suggest *P. helianthoides* responds positively to ocean acidification, but *S. franciscanus* may suffer reduced fitness at seawater pCO2 levels predicted for the end of the century. Differential effects of ocean acidification on this predator-prey pair could increase the strength of the trophic interaction and lead to stronger top-down control in the future.

Wetmore, L. Z. (2022). *Predatory Regulation of Tegula Grazing Activity in Giant Kelp Forests.* (Ph.D.), San Diego State University; University of California, Davis. Retrieved from https://escholarship.org/uc/item/4mz705z2#main

Understanding the effects of predator-induced "top-down" grazing regulation is critical to effective management of subtidal rocky reefs along the California coast, where macroalgae such as the giant kelp, *Macrocystis pyrifera*, are essential to ecosystem function (Dayton 1985, Graham 2004, Falkenberg et al. 2012). Previous studies in California have documented significant correlations between fishery-reduced predator densities, increased herbivore (i.e., grazer) abundance, and subsequent decreases in macroalgal cover, suggesting that predator removal has the potential to drive kelp forest decline by disrupting grazing regulation of benthic herbivores (Lafferty et al. 2004, Hughes et al. 2013). Thus, as coastal predatory assemblages are increasingly altered by fishing pressure and other anthropogenic stressors, identifying and preserving the essential components of top-down regulation is becoming ever more urgent (Tegner and Dayton 2000. Steneck et al. 2002)…Through a series of natural field experiments and subsequent modeling approaches developed based on my empirical research results, I attempt here to address the following research questions: (1) do Tegula spp. alter their grazing behavior, dietary preferences, and/or algal utilization patterns in the presence of predatory sea stars?, (2) does long-term predator exposure history influence morphometric growth or energy allocation patterns (e.g., reproductive investment) in subtidal Tegula at a local population level, and are potential responses consistent across the three Tegula species commonly found in kelp forests throughout central California?, and (3) what are the potential ecosystem-level impacts of predatory sea star removal on Tegula population dynamics and productivity and stability of lower trophic levels in kelp forest food webs? [Excerpt from abstract]

Whippo, R. D. (2023). *Macroalgae and Their Associated Communities: Chemical, Conservation, and Trophic Ecology.* (Ph.D.), University of Oregon. Retrieved from https://www.proquest.com/dissertations-theses/macroalgae-their-associated-communities-chemical/docview/2844574626/se-2?accountid=28258

Marine macroalgae are ubiquitous across coastal oceans worldwide and provide critical habitat and services for diverse assemblages of organisms as well as services including fisheries production, carbon sequestration, and nutrient cycling. The effects of climate change are altering multiple aspects of macroalgal community ecology including food web structure, organismal diversity, and community resilience. In this dissertation, I approach macroalgal community ecology on multiple scales, across broad geographic space, and through various analytical lenses to capture key insights into the functioning of macroalgal forests. In Chapter II I identify the unique fatty acid profiles and stable isotope content of 31 Antarctic macroalgae. While the phylogenetic differentiation driven by fatty acids has a stronger influence on distinguishing Antarctic macroalgae, the added dimension of stable isotopes can likely make the combination of the two approaches particularly powerful in the application of food web studies. In Chapter III I provide a summary of the effects of conservation areas on algal assemblages. I find that all targeted kelp species are observed across the marine reserves but their presence varies

among sites and years. In Chapter IV I describe the feeding preferences of the sunflower seastar through meta-analysis and a cafeteria experiment. A total of 114 prey taxa are reported across all studies, with bivalves and urchins tending to be the primary observed prey items. This agrees with our cafeteria experiments that find *Pycnopodia* tended to prefer green and purple urchins, and mussels, although the quantity of each prey type consumed is highly variable. In Chapter V I provide evidence for non-consumptive effects of the sunflower seastar on grazing sea urchins. I find that the presence of a waterborne *Pycnopodia* cue reduces the grazing rate of fed urchins by 50% over short (~24 h) time scales. In contrast, starved urchins consume kelp and do not exhibit an escape response in the presence of a *Pycnopodia* cue. This chapter highlights a trait-mediated indirect interaction between *Pycnopodia, S. purpuratus* and kelp, and how the urchin response to a predator cue may differ based on urchin metabolic conditions. This dissertation includes previously published and unpublished co-authored material.

Section V: Distribution and Abundance

Alton, M. S. (1966). Bathymetric Distribution of Sea Stars (Asteroidea) Off the Northern Oregon Coast. *Journal of the Fisheries Research Board of Canada, 23*(11), 1673-1714. https://doi.org/10.1139/f66-158

During U.S. Bureau of Commercial Fisheries' Atomic Energy Commission trawling investigations in waters adjacent to the mouth of the Columbia River, a total of 54 species and one subspecies of sea stars was collected from bottom depths of 50-1050 fath. The sea stars in the area of study can be divided into four faunal assemblages by benthic zones: (1) an outer sublittoral fauna (50-108 fath) consisting of several shallow-water species, some of which have their apparent maximum depth of occurrence in this zone. The number of species and the availability of sea stars per hour of trawling is much lower in this zone compared to the other benthic zones in the study area; (2) an upper bathyal fauna (122-258 fath) consisting of several species having either a continuous or discontinuous circumboreal distribution; (3) a lower bathyal fauna (275-500 fath) characterized by a large number of species and a high availability of sea stars in terms of numbers and weight per hour of trawling. Several of the more frequently occurring and abundant species in this zone belong to genera endemic to the northeastern Pacific; and (4) an abyssal fauna (900-1050 fath) consisting almost entirely of species belonging to cosmopolitan genera.The bathyal-abyssal zone (585-850 fath) is considered a zone of transition because of the intrusion into this zone of elements of the sea star fauna from both the lower bathyal and the abyssal.

Anthony, J. A. M. (1995). *Habitat Utilization by Sea Otters (Enhydra lutris) in Port Valdez, Prince William Sound, Alaska.* University of Alaska Fairbanks, Fairbanks, AK. Retrieved from http://hdl.handle.net/11122/8519

Environmental constraints and human activity influence sea otter habitat use in Port Valdez. Nonetheless, a small subpopulation consistently uses food and space resources there. Otter number, distribution, response to human activity, energetics, and behavior in the Alyeska Marine Terminal (an industrial area) were compared to Shoup Bay (an area with low human activity) from September 1989 to September 1991. Low numbers averaged 102 otters monthly and were predominantly juvenile males.

Shoup Bay densities were higher than the Terminal. Terminal boat traffic was more than twice Shoup Bay, resulting in more otter encounters with moving boats and more behavioral changes. Petroleum hydrocarbon levels were low or undetectable in mussels, the main otter prey in the port. Diets varied more in the Terminal than Shoup Bay. Despite lower mussel caloric content in Shoup Bay, otters spent significantly more time feeding at the Terminal. Time-activity budgets in Shoup Bay were more variable.

Brown, J. A., Burton, E., DeVogelaere, A., Hoover, B., Lonhart, S. I., Broughton, K., & Gittings, S. R. (2015). *Monterey Bay National Marine Sanctuary Condition Report Partial Update: A New Assessment of the State of Sanctuary Resources 2015*. Silver Spring, MD: U.S. Department of Commerce, National Oceanic and Atmospheric Administration (NOAA), Office of National Marine Sanctuaries (ONMS). Retrieved from https://sanctuaries.noaa.gov/science/condition/monterey-bay-2015/

This document provides a partial update to Monterey Bay National Marine Sanctuary's 2009 Condition Report. The 2009 report provided a summary of resources in the National Oceanic and Atmospheric Administration's Monterey Bay National Marine Sanctuary (MBNMS or sanctuary), pressures on those resources, current conditions and trends, and management responses to reduce or mitigate human pressures...This report has been peer reviewed and complies with the White House Office of Management and Budget's peer review standards, as outlined in the Final Information Quality Bulletin for Peer Review. This is the second effort to comprehensively describe the status and trends of resources at Monterey Bay National Marine Sanctuary. The report helps identify gaps in current monitoring efforts, as well as causal factors that may require monitoring and potential remediation in the years to come. The data discussed will not only enable resource managers and stakeholders to acknowledge prior changes in resource status, but will also provide guidance for future management challenges imposed by issues such as increasing coastal populations and climate change. This updated condition report also serves as a supporting document for the revision of the Monterey Bay National Marine Sanctuary Management Plan and will help inform constituents who wish to participate in that process. [Excerpt from introduction]

Byrnes, J., Stachowicz, J. J., Hultgren, K. M., Randall Hughes, A., Olyarnik, S. V., & Thornber, C. S. (2006). Predator Diversity Strengthens Trophic Cascades in Kelp Forests by Modifying Herbivore Behaviour. *Ecol Lett, 9*(1), 61-71. https://doi.org/10.1111/j.1461-0248.2005.00842.x

Although human-mediated extinctions disproportionately affect higher trophic levels, the ecosystem consequences of declining diversity are best known for plants and herbivores. We combined field surveys and experimental manipulations to examine the consequences of changing predator diversity for trophic cascades in kelp forests. In field surveys we found that predator diversity was negatively correlated with herbivore abundance and positively correlated with kelp abundance. To assess whether this relationship was causal, we manipulated predator richness in kelp mesocosms, and found that decreasing predator richness increased herbivore grazing, leading to a decrease in the biomass of the giant kelp *Macrocystis*. The presence of different predators caused different herbivores to alter their behaviour by reducing grazing, such that total grazing was lowest at highest predator diversity. Our results suggest that declining predator diversity can have cascading effects on community structure by reducing the abundance of key habitat-providing species.

Casendino, H. R., McElroy, K. N., Sorel, M. H., Quinn, T. P., & Wood, C. L. (2023). Two Decades of Change in Sea Star Abundance at a Subtidal Site in Puget Sound, Washington. *PLOS ONE, 18*(6), e0286384. https://doi.org/10.1371/journal.pone.0286384

Long-term datasets can reveal otherwise undetectable ecological trends, illuminating the historical context of contemporary ecosystem states. We used two decades (1997-2019) of scientific trawling data from a subtidal, benthic site in Puget Sound, Washington, USA to test for gradual trends and sudden shifts in total sea star abundance across 11 species. We specifically assessed whether this community responded to the sea star wasting disease (SSWD) epizootic, which began in 2013. We sampled at depths of 10, 25, 50 and 70 m near Port Madison, WA, and obtained long-term water temperature data. To account for species-level differences in SSWD susceptibility, we divided our sea star abundance data into two categories, depending on the extent to which the species is susceptible to SSWD, then conducted parallel analyses for high-susceptibility and moderate-susceptibility species. The abundance of high-susceptibility sea stars declined in 2014 across depths. In contrast, the abundance of moderate-susceptibility species trended downward throughout the years at the deepest depths- 50 and 70 m-and suddenly declined in 2006 across depths. Water temperature was positively correlated with the abundance of moderate-susceptibility species, and uncorrelated with high-susceptibility sea star abundance. The reported emergence of SSWD in Washington State in the summer of 2014 provides a plausible explanation for the subsequent decline in abundance of high-susceptibility species. However, no long-term stressors or mortality events affecting sea stars were reported in Washington State prior to these years, leaving the declines we observed in moderate-susceptibility species preceding the 2013-2015 SSWD epizootic unexplained. These results suggest that the subtidal sea star community in Port Madison is dynamic, and emphasizes the value of long-term datasets for evaluating patterns of change.

Dean, T. A., Jewett, S. C., Laur, D. R., & Smith, R. O. (1996). *Injury to Epibenthic Invertebrates Resulting from the Exxon Valdez Oil Spill.* Paper presented at the Exxon Valdez Oil Spill Symposium, Anchorage, Alaska. Retrieved from https://www.proquest.com/books/injury-epibenthic-invertebrates-resulting-exxon/docview/15792212/se-2?accountid=28258

Injuries to subtidal populations of epibenthic invertebrates in Prince William Sound were assessed by comparing densities of dominant species at oiled versus non-oiled (control) sites between 1990 and 1993. Dominant taxa included five species of sea stars and one species of crab. Population densities of leather star *Dermasterias imbricata*, and helmet crab *Telmessus cheiragonus* were smaller at oiled sites than at controls in 1990. The same general pattern was observed in most habitats and depths sampled. There was possible injury to slender arm stars *Evasterias troschelii*, although the evidence for this was less convincing. The sunflower sea star *Pycnopodia helianthoides* was found in greater abundance at control sites within eelgrass beds, but in greater abundance at oiled sites in other habitats. Densities of two other species of sea stars did not differ between sites and were apparently unaffected by oiling. In shallow portions of bays, populations of *Dermasterias* and *Telmessus* were fully recovered by 1993; however, recovery was less than complete within eelgrass beds. There were no significant differences in the density of either *Dermasterias* or *Telmessus* between oiled and control eelgrass sites in 1993, but average densities remained more than twice as high at the controls. Polycyclic aromatic hydrocarbon (PAH) concentrations were higher at oiled sites, confirming our classification of sites with respect to oiling. There was a general correspondence between level of injury to epifaunal invertebrates and PAH concentrations. Injury was greatest and PAH levels were highest in shallow waters in eelgrass beds and

bays. Levels of both injury and PAHs declined between 1990 and 1993. It was unclear whether the injuries were the result of acute toxicity of oil, sublethal effects of oiling, collateral injury from cleanup activities, or a combination of these factors.

Eckert, G. L., Engle, J. M., & Kushner, D. J. (1999). *Sea Star Disease and Population Declines at the Channel Islands.* Paper presented at the Proceedings of the Fifth California Islands symposium.

In the summer of 1997, we quantified the incidence of wasting disease among multiple species of sea stars throughout the Channel Islands and adjacent mainland areas. The disease has been observed since 1978 during warmer water periods. Following the 1982-1983 El Niño, the disease and severe sea star population declines were observed, however, quantitative surveys of disease were not conducted. In our 1997 surveys, *Asterina miniata* and *Pisaster giganteus* were the species most severely affected; however, the disease was also observed in *Astropecten armatus*, *Dermasterias imbricata, Henricia leviuscula, Mediaster aequalis, Orthasterias koehleri, Pisaster brevispinus, Pisaster ochraceus*, and *Pycnopodia helianthoides*. Three species were not observed with the disease (*Henricia* sp., *Astropecten verrilli*, and *Luidia foliolata*); however, these species were rare. Population declines that might have resulted from disease are apparent in monitoring data from the Channel Islands Research Program and the Channel Islands National Park. Surveys at Catalina Island indicate that population declines occurred in summer and were not the result of winter El Niño-associated events such as storms or increased rainfall. In 1997, wasting disease was observed in other echinoderms (Echinoids, Ophiuroids, and Holothuroids) as well.

Elder, N., Rubin, S., Miller, I., Foley, M. M., Beirne, M., McHenry, M., . . . Pedersen, R. (2016). *Long-Term Nearshore Subtidal Sea Star Observations Pre and Post Sea Star Wasting Disease (SSWD) in the Central Us Strait of Juan De Fuca.* Paper presented at the 2016 Salish Sea Ecosystem Conference, Vancouver, B.C. Retrieved from https://cedar.wwu.edu/ssec/2016ssec/fate_and_effects_of_pollutants/9/

In June of 2013 sea stars (asteroids) on the Northeast Pacific Coast began to experience an outbreak of sea star wasting disease (SSWD), which caused mass die-offs from Alaska to Baja. Scuba surveys to assess pre and post Elwha River dam removal effects on benthic macroalgae, macroinvertebrates, and fish, in the Elwha subtidal region were conducted in July and August from 2008 to 2015. Two control sites to the east and west of the Elwha were also surveyed. Surveys include a comprehensive data set of densities for 14 species of sea stars. [Excerpt from abstract]

Esgro, M., & Ray, J. (2021). *Interim Action Plan for Protecting and Restoring California's Kelp Forests.* California Ocean Protection Council. Retrieved from https://www.opc.ca.gov/webmaster/ftp/pdf/agenda_items/20210216/Item7_KelpActionPlan_ExhibitA_FINAL.pdf

In support of OPC's Strategic Plan to Protect California's Coast and Ocean 2020-2025, (Objective 3.2, Target 3.2.1), this Action Plan is intended to summarize current state-supported kelp research and restoration initiatives, as well as other relevant efforts in California; highlight key knowledge gaps; and outline priorities for action in kelp research and monitoring, policy development, restoration, and community engagement. Those priorities include: completing pilot efforts; developing science-based metrics for tracking kelp forest ecosystem health; implementing statewide kelp forest monitoring based

on those metrics; initiating the development of a kelp restoration and management plan, which will include a restoration "toolkit"; and engaging with California's coastal communities and Native American Tribes. OPC has developed this interim Action Plan in partnership with CDFW to serve as a starting point for discussion between resource managers, the academic community, California Native American Tribes, coastal stakeholders (including the diving and fishing communities), and members of the public. OPC will offer opportunities for engagement on this draft throughout 2021, and a final version of the Action Plan will be presented to the Council for consideration and possible adoption in Spring 2022. That version will incorporate results from research and restoration projects currently underway, as well as scientific, Tribal, and public input. [Excerpt from executive summary]

Flores Miller, R. E., Gotshall, D. W., Geibel, J. J., & Karpov, K. A. (2014). Descriptive Analyses and Extended Distribution Records of Macroinvertebrates Based on Remotely Operated Vehicle Surveys Offshore of the Northern Channel Islands. *California Fish and Game, 100*(2), 319-342. Retrieved from https://wildlife.ca.gov/Publications/Journal/Contents#559872756-2014

In 2003, marine protected areas (MPAs) were established offshore of the northern Channel Islands, California. The MPAs are surveyed by remotely operated vehicle (ROV) as part of a larger, ongoing effort to evaluate their effectiveness. To determine macroinvertebrate species distribution and richness, we analyzed the ROV video data collected at five paired sites during 2007–2009. Percent occurrence was used to estimate species richness. Macroinvertebrates observed included harvested species and species with structure-forming potential. Fifty-three invertebrate species were identified along with 20 higher taxonomic complex level classifications when identification to species level was not possible. Two of the five site-pairs formed clusters in two different cluster analyses. Site clustering suggested an island effect or clinal change in the biogeographic regions from the Oregonian Province through the Transition Zone to the Californian Province. The ROV surveys yielded new depth records for three invertebrate species. In addition, the cnidarian *Stylaster californicus* was found offshore of Santa Rosa Island, expanding its documented distribution within the northern Channel Islands.

Goddard, J. (1997). *A Biological Survey of Rocky Shores in Oregon: Data Entry and Preliminary Analysis.* Oregon Institute of Marine Biology, University of Oregon Charleston, OR. Retrieved from http://hdl.handle.net/1794/6050

In June of 1994 two teams from the Oregon Department of Fish and Wildlife (ODFW) and the Oregon Institute of Marine Biology (OIMB) conducted a quantitative survey of intertidal habitats and biota at 12 sites on the Oregon coast (Fox, 1994). This study was undertaken with a view toward developing intertidal community descriptions that can be applied over a wide range of spatial scales and be used as a basis for management decisions (Fox, 1994). It also provides important baseline data, allowing us to gauge the effects on Oregon's rocky shores of potential large-scale perturbations such as oil spills, tectonic shifts in elevation, increased human use, and global climate change. This report presents the results of a preliminary analysis of the data collected during the survey, focusing on: (1) variation in the abundance and distribution of abundant or ecologically important species, and (2) site-specific differences in species richness. It concludes with suggestions for further analyses and recommendations for improving and repeating the survey.

Haight, R. E., Reid, G. M., & Weemes, N. (2006). *Distribution and Habitats of Marine Fish and Invertebrates in Katlian Bay, Southeastern Alaska, 1967 and 1968*. U.S. Department of Commerce, National Oceanic and Atmospheric Administration (NOAA), National Marine Fisheries Service (NMFS), Alaska Fisheries Science Center (AFSC).

In 1967 and 1968, scientists from the National Marine Fisheries Service's Auke Bay Laboratory carried out four surveys of marine fauna in Katlian Bay, near Sitka, Alaska as part of an impact study associated with plans to build a wood pulp processing plant in the bay. Here we report the results of our surveys and also provide a broad literature review on several of the species that were captured in the bay...While the pulp mill was never constructed, the data gathered on the marine fauna of Katlian Bay, their habitat, and aspects of life history do address the essential fish habitat provisions of the Magnuson-Stevens Fishery Conservation and Management Act as amended in 1996 which mandates that information on fauna and habitats within marine estuaries and outer shorelines be provided to fulfill requirements of the Act. [Excerpt from abstract]

Hamilton, S. L., Saccomanno, V. R., Heady, W. N., Gehman, A. L., Lonhart, S. I., Beas-Luna, R., . . . Gravem, S. A. (2021). Disease-Driven Mass Mortality Event Leads to Widespread Extirpation and Variable Recovery Potential of a Marine Predator across the Eastern Pacific. *Proceedings of the Royal Society B, 288*(1957), 20211195. https://doi.org/10.1098/rspb.2021.1195

The prevalence of disease-driven mass mortality events is increasing, but our understanding of spatial variation in their magnitude, timing and triggers are often poorly resolved. Here, we use a novel range-wide dataset comprised 48 810 surveys to quantify how sea star wasting disease affected *Pycnopodia helianthoides*, the sunflower sea star, across its range from Baja California, Mexico to the Aleutian Islands, USA. We found that the outbreak occurred more rapidly, killed a greater percentage of the population and left fewer survivors in the southern half of the species's range. *Pycnopodia* now appears to be functionally extinct (greater than 99.2% declines) from Baja California, Mexico to Cape Flattery, Washington, USA and exhibited severe declines (greater than 87.8%) from the Salish Sea to the Gulf of Alaska. The importance of temperature in predicting *Pycnopodia* distribution rose more than fourfold after the outbreak, suggesting latitudinal variation in outbreak severity may stem from an interaction between disease severity and warmer waters. We found no evidence of population recovery in the years since the outbreak. Natural recovery in the southern half of the range is unlikely over the short term. Thus, assisted recovery will probably be required to restore the functional role of this predator on ecologically relevant time scales.

Hopkins, T. S., & Crozier, G. F. (1966). Observations on the Asteroid Echinoderm Fauna Occurring in the Shallow Water of Southern California (Intertidal to 60 Meters). *Bulletin of the Southern California Academy of Sciences, 65*(3), 129-145. https://doi.org/10.3160/0038-3872-65.3.129

The Pacific Coast Asteroidea were monographed by Verrill (1914) and Fisher (1911, 1928, 1930). The purpose of this paper is to provide the field collector with a keyed guide to species that may be encountered from Pt. Conception to San Diego, based on species collected from various habitats encountered in the San Diego locale. In this manner, we hope that it will serve to complement Light's Manual (Smith, et. al, 1961), which is particularly good for Central and Northern California. The observations contained herein were obtained with the use of SCUBA. This tool has allowed us to work to

depths of 60 meters in the La Jolla and Scripps submarine canyons, and to make observations and collections efficiently; often in underwater terrain so rugged that dredges and grabs could not be used.

Jacobs Engineering Group Inc. (2021). *Record of Decision: U.S. Coast Guard Base Ketchikan, Ketchikan Alaska: Final.* Retrieved from https://dec.alaska.gov/Applications/SPAR/PublicMVC/CSP/Download?documentID=50865&fileName=1184_2021.06.17%20Ketchikan%20ROD%20Final%20-%20Buss%20Signed.pdf

This report was prepared for the U.S. Army Corps of Engineers & U.S. Coast Guard, Civil Engineering Unit Juneau Environmental Remediation, Project No: 33-J3905. This report provides an overview of remedies for four areas of concern at U.S. Coast Guard (USCG) Base Ketchikan, located on Revillagigedo Island.

Jewett, S., Clark, R., Chenelot, H., Harper, S., & Hoberg, M. (2012). Seastars of the Nearshore Aleutian Archipelago. In *Diving for Science 2012: Proceedings of the American Academy of Underwater Sciences 31st Symposium.* D. L. Steller & L. Kerr-Lobel (Eds.). Dauphin Island, AL: American Academy of Underwater Sciences.

Sea stars are one of the most diverse groups of epifaunal organisms in the shallow (< 20 m), nearshore region of the Aleutians. For the first time in more than a century scientists probed the Aleutian waters yielding information on sea stars throughout this remote region. Sea stars were collected using open-circuit scuba between 2004 and 2011 during five research surveys that covered all five major islands groups spanning approximately 2500 km. Nineteen divers made 841 dives on more than 100 sites. Although sea stars were not the focus of the dive surveys, sea stars were photographed and collected where possible, yielding 6 families, 18 genera, and 53 species. This paper lists those species and highlights some of the unique species found, including several species indigenous to the Aleutian Archipelago.

Konar, B., Edwards, M. S., Bland, A., Metzger, J., Ravelo, A., Traiger, S., & Weitzman, B. (2017). A Swath across the Great Divide: Kelp Forests across the Samalga Pass Biogeographic Break. *CONTINENTAL SHELF RESEARCH, 143*, 78-88. https://doi.org/10.1016/j.csr.2017.06.007

Biogeographic breaks are often described as locations where a large number of species reach their geographic range limits. Samalga Pass, in the eastern Aleutian Archipelago, is a known biogeographic break for the spatial distribution of several species of offshore-pelagic communities, including numerous species of cold-water corals, zooplankton, fish, marine mammals, and seabirds. However, it remains unclear whether Samalga Pass also serves as a biogeographic break for nearshore benthic communities. The occurrence of biogeographic breaks across multiple habitats has not often been described. In this study, we examined if the biogeographic break for offshore-pelagic communities applies to nearshore kelp forests. To examine whether Samalga Pass serves as a biogeographic break for kelp forest communities, this study compared abundance, biomass and percent bottom cover of species associated with kelp forests on either side of the pass. We observed marked differences in kelp forest community structure, with some species reaching their geographic range limits on the opposing sides of the pass. In particular, the habitat-forming kelp *Nereocystis luetkeana*, and the predatory sea stars *Pycnopodia helianthoides* and *Orthasterias koehleri* all occurred on the eastern side of Samalga Pass but were not observed west of the pass. In contrast, the sea star *Leptasterias camtschatica dispar* was observed only

on the western side of the pass. We also observed differences in overall abundance and biomass of numerous associated fish, invertebrate and macroalgal species on opposing sides of the pass. We conclude that Samalga Pass is important biogeographic break for kelp forest communities in the Aleutian Archipelago and may demark the geographic range limits of several ecologically important species.

Department of Fisheries and Oceans Canada (DFO) (2023). *Recommendations on the Design of a Multispecies Benthic Marine Invertebrate Dive Survey Program for Stock Monitoring*. (2023/003). Department of Fisheries and Oceans Canada. Retrieved from https://waves-vagues.dfo-mpo.gc.ca/library-bibliotheque/41097397.pdf

Stock assessment dive surveys for commercially fished benthic marine invertebrates (Northern Abalone1, Green and Red Sea Urchins, Giant Red Sea Cucumbers and Geoducks) in British Columbia (BC) have historically been conducted as single-species dive surveys that estimate density and/or biomass in different portions of the BC coast in different years. The data collected through these surveys have been used to estimate biomass and/or harvest options for their respective commercial fisheries and are generally not suitable for coast wide stock status monitoring. The biomass estimates or harvest options are used by Fisheries Management for setting quotas... The species of interest for the survey at this time include Green Sea Urchin, Red Sea Urchin, Giant Red Sea Cucumber, Geoducks (i.e., the four species targeted by BC commercial dive fisheries), the Purple Sea Urchin (whose abundance and distribution has shown dramatic shifts in California in recent years; Rogers-Bennett and Catton 2019), the endangered Northern Abalone (which was also previously subject to historically important fisheries) and the Sunflower Star (an important mesopredator whose population on the BC coast nearly collapsed between 2014 and 2015 due to sea star wasting disease; Burt et al. 2018; Hewson et al. 2014) (Table 1). The survey also collects information on substrate types and algae observed on survey transects. [Excerpt from background]

Lundquist, C. J., Rochet, M.-J., & Botsford, L. W. (2011). Estimating Larval Production of a Broadcast Spawner: The Influence of Density, Aggregation, and the Fertilization Allee Effect. *Canadian Journal of Fisheries and Aquatic Sciences, 68*(1), 30-42. https://doi.org/10.1139/f10-125

The effect of fishing on reproduction is typically quantified by computing the effects of changes in the species abundance and age structure on egg production. For broadcast spawners, reproduction also depends on the local spatial distribution of individuals. Broadcast spawners exhibit an Allee effect at low density: a decline in the fertilization of eggs, owing to increased distance between spawners. We present a method for assessing the likely impact of a fishery on broadcast spawners, based on gamete dispersion dynamics and individual spatial distributions. We use an individual-based model to simulate larval production over a range of uncertainties in dispersion characteristics. We illustrate our method for the red sea urchin, *Strongylocentrotus franciscanus*, fishery in northern California, USA. The density of red sea urchins varied over space (0.1–1.6m–2), and indices of aggregation were highest at low densities. As gamete dispersion distances increased, larval production exhibited a more linear relationship with density. Average larval production in 1996–1998 was 33.8% of production near the inception of the fishery. After accounting for decreases in mean density, the fertilization Allee effect accounted for 21.7 ± 4.1% of the decrease in larval production, and 45.2 ± 21.7% if sea urchins were not aggregated.

Miller, B. A. (1995). *Larval Abundance and Early Juvenile Recruitment of Echinoids, Asteroids, and Holothuroids on the Oregon Coast.* (M.S.), University of Oregon. Retrieved from http://hdl.handle.net/1794/10056

Larval abundance and settlement of red sea urchins (*Strongylocentrotus franciscanus*) and the purple sea urchins (*s. purpuratus*) was found to be variable over a two year period on the southern Oregon coast. A method of estimating age of early juvenile sea urchins was developed, based on temperature-dependent developmental rates of specific juvenile traits. This method was used to correlate sea urchin settlement to several relaxation events during the summer upwelling season. Occurrence of larvae and peak settlement events were linked to relaxation events characterized by warm water, a mixed water column, and strong northward wind. Occurrence of planktonic larvae of asteroids and holothuroids coincided with settlement. Asteroid and holothuroid settlement occurred regularly during the upwelling season, suggesting these groups may recruit by different mechanisms than those for sea urchin larvae.

Montecino-Latorre, D., Eisenlord, M. E., Turner, M., Yoshioka, R., Harvell, C. D., Pattengill-Semmens, C. V., . . . Gaydos, J. K. (2016). Devastating Transboundary Impacts of Sea Star Wasting Disease on Subtidal Asteroids. *PLOS ONE, 11*(10). https://doi.org/10.1371/journal.pone.0163190

Sea star wasting disease devastated intertidal sea star populations from Mexico to Alaska between 2013–15, but little detail is known about its impacts to subtidal species. We assessed the impacts of sea star wasting disease in the Salish Sea, a Canadian / United States transboundary marine ecosystem, and world-wide hotspot for temperate asteroid species diversity with a high degree of endemism. We analyzed roving diver survey data for the three most common subtidal sea star species collected by trained volunteer scuba divers between 2006–15 in 5 basins and on the outer coast of Washington, as well as scientific strip transect data for 11 common subtidal asteroid taxa collected by scientific divers in the San Juan Islands during the spring/summer of 2014 and 2015. Our findings highlight differential susceptibility and impact of sea star wasting disease among asteroid species populations and lack of differences between basins or on Washington's outer coast. Specifically, severe depletion of sunflower sea stars (*Pycnopodia helianthoides*) in the Salish Sea support reports of major declines in this species from California to Alaska, raising concern for the conservation of this ecologically important subtidal predator.

Pearse, J., & Hines, A. H. (1987). Long-Term Population Dynamics of Sea Urchins in a Central California Kelp Forest: Rare Recruitment and Rapid Decline. *MARINE ECOLOGY PROGRESS SERIES, 39*, 275-283. https://doi.org/10.3354/meps039275

Long-term data on density, size structure and microhabitat of 2 species of sea urchins in the Hopkins Marine Life Refuge, Pacific Grove, California (USA), are presented for the period 1972-1981. Densities of *Strongylocentrotus franciscanus* remained very low (ca 1 urchin m-2) throughout the study period, whereas the population of *S. purpuratus* had one substantive recruitment event in 1975-76 when densities increased 25-fold from about 2 to about 50 urchins 10m^-2 New recruits initially were found throughout the algal-invertebrate turf, but soon they became concentrated in shallow cracks. As the urchins outgrew the cracks they invaded kelp holdfasts. They grew to 20 to 40 mm test diameter within 1 yr, and their biomass reached nearly 500 g 10m^-2 In winter 1976-1977, densities declined rapidly by more than 50%, probably as result of predation by the sea star *Pycnopodia helianthoides* and/or mortality from disease. Most of the remaining sea urchins were restricted to deep crevices, and their

densities continued to decrease slowly to about 6 urchins 10m^-2 in 1981. Sea urchins in the Hopkins Marine Life Refuge of central California appear to recruit at very low levels during most years. Moreover, the single episodic recruitment event observed during our decade-long study led to only a temporary increase in population density, and most of the recruits were killed 1 yr after they settled.

Pondella, D. J., Caselle, J. E., Claisse, J. T., Williams, J. P., Davis, K., Williams, C. M., & Zahn, L. A. (2015). *South Coast Baseline Program Final Report: Kelp and Shallow Rock Ecosystems.* California Sea Grant California Ocean Protection Council. Retrieved from https://data.ca.gov/dataset/shallow-rock-and-kelp-forest-ecosystems-california-south-coast-mpa-baseline-study-2011-to-2012

The Baseline Characterization of Kelp and Shallow Rock Ecosystems project is a collaboration between researchers at Vantuna Research Group at Occidental College and the Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO) at the University of California Santa Barbara. In this project, researchers characterized kelp and shallow rock ecosystems inside and outside MPAs in the South Coast region. The baseline surveys, together with historical and future data, are enabling scientists to measure changes in species and communities over both short and long time scales. From 2011-2013, SCUBA divers surveyed kelp forests and associated reference sites to estimate fish, kelp and benthic invertebrate densities, fish size distributions, and percent cover of invertebrates and algae to produce a quantitative baseline characterization of the structure of kelp and shallow rock ecosystems in the South Coast. Kelp and shallow rock ecosystems inside the MPAs were compared with associated reference areas outside MPAs. Surveys were conducted using methods developed by PISCO and the Cooperative Research and Assessment of Nearshore Ecosystems (CRANE) program, which allowed integration of historical, long-term datasets into this analysis. As part of this project, researchers also worked to develop easily interpretable ecosystem indicators for assessing the state of kelp forests and made recommendations for future monitoring. (From California Sea Grant)

Sanchez, M. (2022). *Before and after Sea Star Wasting Disease: Subtidal Sunflower Star (Pycnopodia helianthoides) Observations in the Central Us Strait of Juan De Fuca.* Paper presented at the Salish Sea Ecosystem Conference. Retrieved from https://cedar.wwu.edu/ssec/2022ssec/allsessions/257

From the rocky intertidal to subtidal plains, sea stars are important marine invertebrates that can profoundly affect the ecosystems they inhabit. Beginning in 2013, a sea star wasting disease (SSWD) epidemic led to the largest sea star die-off event seen on the Northeastern Pacific coast (1). Among the species of sea stars affected was the sunflower star (*Pycnopodia helianthoide*s). Before SSWD, sunflower stars were the most abundant subtidal sea star species. Since the epidemic, studies have reported massive declines in sunflower star populations and even local extinctions (2). Currently, the sunflower star is under review for listing under the ESA and was placed on the ICUN Red List of Threatened Species in December 2020. Assessing the effects of SSWD on sea star populations requires having data before and after the onset of SSWD, therefore long-term monitoring surveys are the best sources to analyze the historical context needed to track the status of sunflower stars. [Poster introduction]

Sewell, M. A., & Watson, J. C. (1993). A “Source” for Asteroid Larvae?: Recruitment of *Pisaster ochraceus*, *Pycnopodia helianthoides* and *Dermasterias imbricata* in Nootka Sound, British Columbia. *MARINE BIOLOGY, 117*(3), 387-398. https://doi.org/10.1007/bf00349314

A major recruitment of the forcipulate asteroid *Pisaster ochraceus* was observed in September 1987 in the channel leading into Boca del Infierno, a semi-enclosed bay on the southeastern shore of Nootka Island, on the west coast of Vancouver Island, British Columbia, Canada. Newly settled recruits were observed at high densities subtidally in the channel (mean maximal density=1.23x104m-2) and at nearby sites. Subsequent surveys in 1988 to 1991 and size-frequency distributions of adults indicated strong yearly recruitment of *P. ochraceus*. Recruits of *P. ochraceus* were found on all available substrata, including hard and soft bottoms and on benthic algae. The initial food of the recruits included newly settled mussels (*Mytilus* sp.), snails and barnacles. Recruitment of the forcipulate *Pycnopodia helianthoides* was observed in 1987 to 1989 and in 1991, while recruitment of the spinulosan *Dermasterias imbricata* occurred only in 1988. High densities of planktonic bipinnaria larvae were found in the bay of Boca del Infierno in late May. We hypothesise that the high density population of adult *P. ochraceus* found in the channel of Boca del Infierno spawns synchronously and most of the resulting embryos and larvae are retained within the bay. This area may act as a “source” of larvae that then disperse locally. Post-recruitment mortality was estimated by comparing the density of recruits of *P. ochraceus* in 1987 with the numbers of juveniles presumed to be 1 yr old in 1988. Post-recruitment mortality was in excess of 97% with few individuals surviving to 1 yr. Moreover, even after the first year, mortality or emigration of the juveniles resulted in the almost complete loss of the 1-yr cohort at North Saavedra between 1988 and 1989. This study provides evidence that the *P. ochraceus* population in this area of Nootka Island may not be open, but may be regularly supplied from a “source” of larvae in the bay of Boca del Infierno. Post-settlement processes may, however, have significant effects on the local population, resulting in a poor correlation between the rate of recruitment and the incorporation of yr-1 + individuals into the adult population.

Shivji, M., Parker, D., Hartwick, B., Smith, M. J., & Sloan, N. A. (1983). Feeding and Distribution Study of the Sunflower Sea Star *Pycnopodia helianthoides* (Brandt, 1835). *PACIFIC SCIENCE, 37*(2), 133-140. Retrieved from https://www.proquest.com/scholarly-journals/feeding-distribution-study-sunflower-sea-star/docview/13791447/se-2?accountid=28258

Observations are reported on the feeding biology of *P. helianthoides* in Barkley Sound, British Columbia, in areas of differing wave exposure. Three hundred asteroids were examined; 220 were feeding on prey representing 11 taxa, with heaviest predation on gastropods, bivalves, and crustaceans. *P. helianthoides* found on soft substrates were larger than those inhabiting hard substrates. Juvenile sea stars (<5 cm diameter) were found primarily at protected sites often on kelp substrate. Significant positive correlations were obtained between sea star size and prey size except in the case of the gastropod *Tegula pulligo*. The possible importance of sea star predation on this snail is discussed.

U.S. Department of the Interior, National Park Service (NPS) (1982-2015). *Channel Islands National Park Kelp Forest Monitoring Program: Annual Reports*. Fort Collins, Colorado: U.S. Department of the Interior, National Park Service (NPS). Retrieved from http://npshistory.com/publications/chis/index.htm

Channel Islands National Park (CHIS) has conducted long-term ecological monitoring of the kelp forests around San Miguel, Santa Rosa, Santa Cruz, Anacapa and Santa Barbara Islands since 1982, this being the 34th year of monitoring. The original permanent transects were established at 16 sites between 1981 and 1986 with the first sampling beginning in 1982. An additional site, Miracle Mile, was established at San Miguel Island in 2001 by a commercial fisherman with assistance from the park. Miracle Mile was partially monitored from 2002-2004, and then fully monitored (using all KFM protocols) since 2005. In 2005, 16 additional permanent sites were established to collect baseline data from inside and adjacent to four marine reserves that were established in 2003.

Note: This literature search returned multiple Channel Islands National Park Kelp Forest Monitoring Program Reports from 1990-2015. Reports were released under the names "Channel Islands National Park Kelp Forest Monitoring Program: Annual Report," "Kelp Forest Monitoring Annual Report, Channel Islands National Park," and "Kelp Forest Monitoring, Channel Islands National Park: Annual Report." All CHIS Kelp Forest Monitoring Program Reports from 1982-2015 can be found at: http://npshistory.com/publications/chis/index.htm

Wootton, J. T. (1997). Estimates and Tests of Per Capita Interaction Strength: Diet, Abundance, and Impact of Intertidally Foraging Birds. *ECOLOGICAL MONOGRAPHS, 67*(1), 45-64. https://doi.org/10.1890/0012-9615(1997)067[0045:EATOPC]2.0.CO;2

Predicting the dynamics of natural food webs requires estimates of the strength of interactions among species. The ability to estimate per capita interaction strength from observational data is desirable because of the logistical difficulty of using experimental manipulations to obtain such measures for all species within complex natural communities. In this paper, I derive observational measures of per capita interaction strength having units matching those of dynamic food web models (per capita consumption and assimilation rates). I also highlight the difference between per capita interaction strength (a parameter used in theoretical models) and species impact (empirical measures of total species effect). I then use behavioral observations and population censuses in a rocky intertidal community to estimate both per capita interaction strengths and species impacts on invertebrate prey of Glaucous-winged Gulls (*Larus glaucescens*), American Black Oystercatchers (*Haematopus bachmani*), and Northwestern Crows (*Corvus caurinus*). Estimated per capita interaction strengths exhibited a skewed distribution with many weak interactions and few strong interactions: mean +/- 1 SD of log(10)(interaction strength) = -1.95 +/- 1.40 (bird-day/m of shore)(-1). Per capita interaction strength correlated poorly (r(2) = 0.152-0.157) and nonlinearly with both consumption rates and percentage contribution of a prey species to the diet. Using my observational estimates of per capita interaction strengths, I predicted the species impact of bird predation on different prey taxa. Predictions included strong effects of birds on goose barnacles (*Pollicipes polymerus*), limpets (*Lottia* and *Tectura* spp.), sea urchins (*Strongylocentrotus* spp.), and large starfish (*Pycnopodia helianthoides* and *Solaster stimpsoni*), but little effect on mussels (*Mytilus californianus* and *M. trossulus*), dogwhelk snails (*Nucella* spp.), and acorn barnacles (*Semibalanus cariosus*). I compared nine of the predictions with 126 results of experimental manipulations of birds. The predictions agreed both qualitatively and quantitatively with the experimental results. These findings suggest that observational measures of interaction strength that have units matching those of dynamical food web models may be reasonable to use in estimating those found in natural communities.

Section VI: Threats and Conservation

Aquino, C. A., Besemer, R. M., DeRito, C. M., Kocian, J., Porter, I. R., Raimondi, P. T., . . . Hewson, I. (2020). Evidence That Microorganisms at the Animal-Water Interface Drive Sea Star Wasting Disease. *Frontiers in Microbiology, 11*, 610009. https://doi.org/10.3389/fmicb.2020.610009

Sea star wasting (SSW) disease describes a condition affecting asteroids that resulted in significant Northeastern Pacific population decline following a mass mortality event in 2013. The etiology of SSW is unresolved. We hypothesized that SSW is a sequela of microbial organic matter remineralization near respiratory surfaces, one consequence of which may be limited O(2) availability at the animal-water interface. Microbial assemblages inhabiting tissues and at the asteroid-water interface bore signatures of copiotroph proliferation before SSW onset, followed by the appearance of putatively facultative and strictly anaerobic taxa at the time of lesion genesis and as animals died. SSW lesions were induced in *Pisaster ochraceus* by enrichment with a variety of organic matter (OM) sources. These results together illustrate that depleted O(2) conditions at the animal-water interface may be established by heterotrophic microbial activity in response to organic matter loading. SSW was also induced by modestly (approximately 39%) depleted O(2) conditions in aquaria, suggesting that small perturbations in dissolved O(2) may exacerbate the condition. SSW susceptibility between species was significantly and positively correlated with surface rugosity, a key determinant of diffusive boundary layer thickness. Tissues of SSW-affected individuals collected in 2013-2014 bore delta(15)N signatures reflecting anaerobic processes, which suggests that this phenomenon may have affected asteroids during mass mortality at the time. The impacts of enhanced microbial activity and subsequent O(2) diffusion limitation may be more pronounced under higher temperatures due to lower O(2) solubility, in more rugose asteroid species due to restricted hydrodynamic flow, and in larger specimens due to their lower surface area to volume ratios which affects diffusive respiratory potential.

Dearden, A., & Miller, A. (2021). Marine Biodiversity Loss: Epidemic Wipes out Majority of Sunflower Sea Stars. In *Ocean Watch Spotlight* (pp. 9). Vancouver, Canada: Ocean Wise Conservation Association. Retrieved from https://oceanorg.blob.core.windows.net/oceanorg/2023/08/OceanWatch-Spotlight-Marine-Biodiversity-Loss-Epidemic-Wipes-Out-Majority-of-Sunflower-Sea-Stars.pdf

Introduction: In 2013, Sea Star Wasting Disease (SSWD) swept the coast of the Pacific Northwest, devastating sea star populations along the entire region from Alaska to Mexico. SSWD is the largest marine wildlife mortality event on record and it impacted over 20 sea star species.

These impacts have trickled down through the food web, affecting entire ecosystems, and influencing biodiversity along the coast. The sunflower sea star (*Pycnopodia helianthoides*) was one particularly hard hit species with huge losses of between 99-100% in some populations. As a result, through a huge international assessment effort, sunflower stars are now listed as Critically Endangered by the International Union for the Conservation of Nature (IUCN).

Although SSWD has been intensively studied in the past decade, there are many research gaps, and the disease continues to impact many sea star populations. Climate change and other threats also play a role

in the recovery of sea stars, making it difficult for them to rebound or even survive in some areas. For example, in some areas in their southern range, sunflower stars have completely disappeared and might not ever return.

This spotlight report will look at SSWD and its impacts on sunflower stars, including data contributed to IUCN by Ocean Wise researchers, links between climate change and sunflower star recovery, as well as current conservation efforts for the species. A list of things you can do to reduce your impact on the marine environment and encourage recovery of sunflower stars is located at the end of this report.

Center for Biological Diversity (2021). *Petition to List Sunflower Sea Star as Threatened or Endangered under the U.S. Endangered Species Act.* Center for Biological Diversity, Oakland, CA. Retrieved from https://media.fisheries.noaa.gov/2021-09/2021-08-18%20Petition%20sunflower%20sea%20star_508%20compliant.pdf

Introduction: The sunflower sea star (*Pycnopodia helianthoides*) is critically endangered. Since 2013 a severe disease outbreak has decimated more than 90 percent of the sunflower sea star population. From California to Alaska surveys showed 80 to 100 percent population declines between 2013 and 2017. The sea star has declined to near-zero densities along the outer coasts of the contiguous United States and Mexico. Between 2018–2019, only 20 of 3976 total surveys in all of the United States and Mexican contiguous outer coast recorded animals. No animals were recorded in California in 2019, and none have been recorded in Baja California since 2015. Sea star wasting disease is a gruesome killer that causes lesions; melting, twisting limbs; arm loss; and death. The disease outbreak has been called a “zombie apocalypse” of the sea.

The sea star wasting disease outbreak was particularly deadly for sunflower sea stars, whose populations have not recovered. The disease affected sea stars throughout their range from Alaska to southern California. Sea star wasting disease is tied to climate change. Warm waters resulted in more severe and deadly effects on sunflower sea stars. While disease is the primary driver of extinction risk for sunflower sea stars, they are so imperiled that they are also extremely vulnerable to other threats such as ocean acidification, pollution, and harvest.

Sunflower sea stars are one of the world’s largest sea stars with 16 to 24 arms that can extend more than three feet across. They are also a speedy sea star and can travel more than five feet per minute. Sunflower sea stars come in an array of colors—purple, red, orange, yellow, green, and brown.
The mass die-off of sunflower sea stars not only leaves them in danger of extinction, but it is also devastating for the entire kelp forest ecosystem in which they live. Sunflower sea stars are a keystone species and a top predator in the intertidal zone. In the absence of a healthy population of sea stars, sea urchins can proliferate and devour the kelp forests that provide habitat for a many fish and other wildlife. The decline of sunflower sea stars has caused a cascade of harmful changes in the ocean food web.

Favaro, B. (2013). *Can Fishing Gear Protect Non-Target Fish? Design and Evaluation of Bycatch Reduction Technology for Commercial Fisheries.* (Ph.D.), Simon Fraser University. Retrieved from https://summit.sfu.ca/item/13539

The impacts of commercial fishing extend far beyond direct effects on targeted species. As much as 40% of global marine catch is attributable to bycatch, or the capture of nontarget organisms which occurs during fishing. The amount of bycatch in a fishery is determined in part by the selectivity of the industry's fishing gear, and bycatch mitigation often focuses on improving the selectivity of these gears. This thesis explores bycatch mitigation through the design and evaluation of bycatch reduction devices (BRDs), or fishing gear modifications aimed specifically at reducing non-target catch while maintaining the catch of target species. I examine BRDs using a three-pronged assessment, which tests a modified gear's effects on non-target catch, on target catch, and on practicality for use in commercial fisheries (all relative to unmodified gear). I first perform a global-scale meta-analysis on technologies designed to protect elasmobranchs (sharks and rays) from longline fisheries. I show that most technologies are broadly ineffective at reducing elasmobranch bycatch, and that many studies fail to adequately assess novel BRDs across all three dimensions of gear performance. The remainder of my thesis focuses on the research and development of BRDs for a British Columbia fishery which employs trapping gear to capture spot prawns (*Pandalus platyceros*). Using data from fishery-independent surveys, I show that these traps catch rockfish (*Sebastes* spp.) as bycatch, a multi-species genus which is depleted due to overfishing and which suffers high discard mortality due to barotrauma incurred during the fishing process. I demonstrate that a novel underwater camera system can be used to study prawn traps in situ, and use insights from this analysis to inform the design of BRDs for prawn traps. I conclude my thesis with an assessment of BRDs of my own design, using both catch data and in situ observations conducted using my underwater camera apparatus. Overall, this thesis demonstrates the challenges in designing effective BRDs, and provides a framework for assessment that can be used as a template in future studies of fishing gear design.

Fuess, L. E., Eisenlord, M. E., Closek, C. J., Tracy, A. M., Mauntz, R., Gignoux-Wolfsohn, S., . . . Harvell, C. D. (2015). Up in Arms: Immune and Nervous System Response to Sea Star Wasting Disease. *PLOS ONE, 10*(7). https://doi.org/10.1371/journal.pone.0133053

Echinoderms, positioned taxonomically at the base of deuterostomes, provide an important system for the study of the evolution of the immune system. However, there is little known about the cellular components and genes associated with echinoderm immunity. The 2013-2014 sea star wasting disease outbreak is an emergent, rapidly spreading disease, which has led to large population declines of asteroids in the North American Pacific. While evidence suggests that the signs of this disease, twisting arms and lesions, may be attributed to a viral infection, the host response to infection is still poorly understood. In order to examine transcriptional responses of the sea star *Pycnopodia helianthoides* to sea star wasting disease, we injected a viral sized fraction (0.2 mu m) homogenate prepared from symptomatic *P. helianthoides* into apparently healthy stars. Nine days following injection, when all stars were displaying signs of the disease, specimens were sacrificed and coelomocytes were extracted for RNA-seq analyses. A number of immune genes, including those involved in Toll signaling pathways, complement cascade, melanization response, and arachidonic acid metabolism, were differentially expressed. Furthermore, genes involved in nervous system processes and tissue remodeling were also differentially expressed, pointing to transcriptional changes underlying the signs of sea star wasting disease. The genomic resources presented here not only increase understanding of host response to sea star wasting disease, but also provide greater insight into the mechanisms underlying immune function in echinoderms.

Gravem, S. A., Heady, W. N., Saccomanno, V. R., Alvstad, K. F., Gehman, A. L. M., Frierson, T. N., & Hamilton, S. L. (2021). *Pycnopodia helianthoides.* IUCN. https://doi.org/10.2305/IUCN.UK.2021-1.RLTS.T178290276A197818455.en

Sunflower Sea Star *Pycnopodia helianthoides* has most recently been assessed for The IUCN Red List of Threatened Species in 2020. *Pycnopodia helianthoides* is listed as Critically Endangered under criteria A2ace. Supplementary material can be found at: https://www.iucnredlist.org/species/178290276/197818455

Gravem, S. A., Heady, W. N., Saccomanno, V. R., Alvstad, K. F., Gehman, A. L. M., Frierson, T. N., & Hamilton, S. L. (2021). IUCN Red List Assessment: *Sunflower Sea Star (Pycnopodia helianthoides).* IUCN Red List of Threatened Species. Retrieved from: https://www.reefcheck.org/wp-content/uploads/2021/10/Final_IUCNAssessment.pdf

Pycnopodia helianthoides has experienced dramatic decreases in population size and range after enduring a global disease outbreak of sea star wasting syndrome (SSWS). From 2013-2017, *Pycnopodia* and other sea star species were devastated by SSWS, which affected a variety of sea star species across more than 5,000km of the western coast of North America (Hewson et al. 2014, 2019; Menge et al. 2016; Montecino-Latorre et al. 2016; Miner et al. 2018; Harvell et al. 2019; Konar et al. 2019). Prior to 2013, *Pycnopodia* was regularly found in a variety of shallow marine habitats from the Pacific Coast of Baja California, Mexico to the Aleutian Islands, Alaska, United States. It is a non-harvested, generalist species and had few major threats prior to the disease outbreak... *Pycnopodia* meets the qualification for Critically Endangered under Criterion A2ace on the basis of its 90.6% global decline. Additionally, it qualifies for Vulnerable under Criterion B2ab as its current area of occupancy is less than 2,000 km2, its number of locations could be as low as 1, and there is evidence for continuing population declines. Pycnopodia qualifies as Least Concern under Criteria C and D, and Data Deficient under Criterion E. For further details see the Supplementary Materials. [Excerpt from "Rationale"]

Gudenkauf, B. M., & Hewson, I. (2015). Metatranscriptomic Analysis of *Pycnopodia helianthoides* (Asteroidea) Affected by Sea Star Wasting Disease. *PLOS ONE, 10*(5). https://doi.org/10.1371/journal.pone.0128150

Sea star wasting disease (SSWD) describes a suite of symptoms reported in asteroids of the North American Pacific Coast. We performed a metatranscriptomic survey of asymptomatic and symptomatic sunflower star (*Pycnopodia helianthoides*) body wall tissues to understand holobiont gene expression in tissues affected by SSWD. Metatranscriptomes were highly variable between replicate libraries, and most differentially expressed genes represented either transcripts of associated microorganisms (particularly Pseudomonas and Vibrio relatives) or low-level echinoderm transcripts of unknown function. However, the pattern of annotated host functional genes reflects enhanced apoptotic and tissue degradation processes and decreased energy metabolism, while signalling of death-related proteins was greater in asymptomatic and symptomatic tissues. Our results suggest that the body wall tissues of SSWD-affected asteroids may undergo structural changes during disease progression, and that they are stimulated to undergo autocatalytic cell death processes.

Harvell, C. D., Montecino-Latorre, D., Caldwell, J. M., Burt, J. M., Bosley, K., Keller, A., . . . Gaydos, J. K. (2019). Disease Epidemic and a Marine Heat Wave Are Associated with the Continental-Scale Collapse of a Pivotal Predator (*Pycnopodia helianthoides*). *SCIENCE ADVANCES, 5*(1), eaau7042. https://doi.org/10.1126/sciadv.aau7042

Multihost infectious disease outbreaks have endangered wildlife, causing extinction of frogs and endemic birds, and widespread declines of bats, corals, and abalone. Since 2013, a sea star wasting disease has affected >20 sea star species from Mexico to Alaska. The common, predatory sunflower star (*Pycnopodia helianthoides*), shown to be highly susceptible to sea star wasting disease, has been extirpated across most of its range. Diver surveys conducted in shallow nearshore waters (n = 10,956; 2006-2017) from California to Alaska and deep offshore (55 to 1280 m) trawl surveys from California to Washington (n = 8968; 2004-2016) reveal 80 to 100% declines across a ~3000-km range. Furthermore, timing of peak declines in nearshore waters coincided with anomalously warm sea surface temperatures. The rapid, widespread decline of this pivotal subtidal predator threatens its persistence and may have large ecosystem-level consequences.

Heady, W. N., Beas-Luna, R., Dawson, M. N., Eddy, N., Elsmore, K., Francis, F. T., . . . Gravem, S. A. (2022). *Roadmap to Recovery for the Sunflower Sea Star (Pycnopodia helianthoides) Along the West Coast of North America.* The Nature Conservancy, Sacramento, CA. Retrieved from https://www.nature.org/content/dam/tnc/nature/en/documents/tnc_Roadmap_to_Recovery_for_the_Sunflower_Sea_Star_Nov2022.pdf

The sunflower sea star (*Pycnopodia helianthoides*) is among the largest sea stars in the world, ranging from Baja California, Mexico, to the Aleutian Islands of Alaska in the US. Adults are found in a wide range of depths and habitats. Even though they were once common and abundant, surprisingly little is known about the species' life history and ecology, including the role of sunflower sea stars in maintaining healthy kelp forest ecosystems through predation of grazers and how this varies geographically.

A sea star wasting disease (SSWD) event beginning in 2013 reduced the global population of sunflower sea stars by an estimated ninety-four percent, triggering the International Union for the Conservation of Nature (IUCN) to classify the species as Critically Endangered. Declines of ninety-nine to one hundred percent were estimated in the outer coast waters of Baja California, California, Oregon, and Washington. From the Salish Sea to the Gulf of Alaska, declines were greater than eighty-seven percent; however, there is uncertainty in estimates from Alaska due to limited sampling. A range-wide species distribution analysis showed that the importance of temperature in predicting sunflower sea star distribution rose over fourfold following the SSWD outbreak, suggesting latitudinal variation in outbreak severity may stem from an interaction between disease severity and warm waters. Given the widespread, rapid, and severe declines of sunflower sea stars, the continued mortality from persistent SSWD, and the potential for the disease to intensify in a warming future ocean, there is a need for a Roadmap to Recovery to guide scientists and conservationists as they aid the recovery of this Critically Endangered species.

The purpose of this document is to identify key questions and the sequencing of potential actions to prepare for, initiate, and accelerate the recovery of sunflower sea star populations throughout their range. This Roadmap was developed by leading experts to highlight these key questions, immediate and near-term actions, and any important sequencing among seven primary Objectives to streamline and coordinate collective action. Below we synthesize a set of prioritized actions among these seven primary Objectives. The degree of need and timeline of some recovery actions may vary by region. However,

given global declines, continued mortality from persistent SSWD, and likelihood of future declines, the need for each region to begin preparing for actions in each of the seven Objectives is clear. [Executive Summary]

Hewson, I., Button, J. B., Gudenkauf, B. M., Miner, B., Newton, A. L., Gaydos, J. K., . . . Harvell, C. D. (2014). Densovirus Associated with Sea-Star Wasting Disease and Mass Mortality. *PROCEEDINGS OF THE NATIONAL ACADEMY OF SCIENCES OF THE UNITED STATES OF AMERICA, 111*(48), 17278-17283. https://doi.org/10.1073/pnas.1416625111

Populations of at least 20 asteroid species on the Northeast Pacific Coast have recently experienced an extensive outbreak of sea-star (asteroid) wasting disease (SSWD). The disease leads to behavioral changes, lesions, loss of turgor, limb autotomy, and death characterized by rapid degradation ("melting"). Here, we present evidence from experimental challenge studies and field observations that link the mass mortalities to a densovirus (Parvoviridae). Virus-sized material (i.e., <0.2 mum) from symptomatic tissues that was inoculated into asymptomatic asteroids consistently resulted in SSWD signs whereas animals receiving heat-killed (i.e., control) virus-sized inoculum remained asymptomatic. Viral metagenomic investigations revealed the sea star-associated densovirus (SSaDV) as the most likely candidate virus associated with tissues from symptomatic asteroids. Quantification of SSaDV during transmission trials indicated that progression of SSWD paralleled increased SSaDV load. In field surveys, SSaDV loads were more abundant in symptomatic than in asymptomatic asteroids. SSaDV could be detected in plankton, sediments and in nonasteroid echinoderms, providing a possible mechanism for viral spread. SSaDV was detected in museum specimens of asteroids from 1942, suggesting that it has been present on the North American Pacific Coast for at least 72 y. SSaDV is therefore the most promising candidate disease agent responsible for asteroid mass mortality.

Hodin, J., Pearson-Lund, A., Anteau, F. P., Kitaeff, P., & Cefalu, S. (2021). Progress toward Complete Life-Cycle Culturing of the Endangered Sunflower Star, *Pycnopodia helianthoides*. *The Biological Bulletin, 241*(3), 243-258. https://doi.org/10.1086/716552

Until recently, the sunflower star, *Pycnopodia helianthoides*, was a dominant and common predator in a wide variety of benthic habitats in the northeast Pacific. Then, in 2013, its populations began to plummet across its entire range as a result of the spread of a phenomenon known as sea star wasting disease, or sea star wasting. Although dozens of sea star species were impacted by this wasting event, *P. helianthoides* seems to have suffered the greatest losses and is now listed by the International Union for the Conservation of Nature as the first critically endangered sea star. In order to learn more about the life history of this endangered predator and to explore the potential for its restoration, we have initiated a captive rearing program to attempt complete life-cycle (egg-to-egg) culture for *P. helianthoides*. We report our observations on holding and distinguishing individual adults, reproductive seasonality, larval development, inducers of settlement, and early juvenile growth and feeding. These efforts will promote and help guide conservation interventions to protect remaining populations of this species in the wild and facilitate its ultimate return.

Høj, L., Byrne, M., Kroon, F., & Westcott, D. (2020). *A Review of Biologically Based Control Technologies for Crown-of-Thorns Starfish: Options for Enhancing the Integrated Pest Management Approach.* National Environmental Science Program (NESP) Tropical Water Quality (TWQ) Hub. Reef and

Rainforest Research Centre. Retrieved from https://nesptropical.edu.au/wp-content/uploads/2021/01/NESP-TWQ-Project-3.1.1-Technical-Report-4.pdf

Executive Summary: Successful management of CoTS is increasingly important in light of cumulative pressures experienced by Great Barrier Reef coral, and the threat posed by CoTS to reef restoration efforts that involve coral deployments. Significant investment has been made in an ongoing CoTS control program, with current strategies based on manual culling using the single injection method and integrated pest management principles.

This report evaluates biologically based technologies that could be developed for CoTS as part of an integrated pest management strategy. While some of these methods have been considered and rejected after previous outbreaks, it is timely to revisit them now as technological development such as next generation sequencing, –omics approaches (genomics, transcriptomics, metabolomics), and ground breaking biotechnology developments (CRISPR/Cas9 gene editing, gene drives), are rapidly reconfiguring the pest management landscape. [Excerpt from executive summary]

Jackson, E. W., Wilhelm, R. C., Johnson, M. R., Lutz, H. L., Danforth, I., Gaydos, J. K., . . . Hewson, I. (2020). Diversity of Sea Star-Associated Densoviruses and Transcribed Endogenous Viral Elements of Densovirus Origin. *Journal of Virology, 95*(1). https://doi.org/10.1128/JVI.01594-20

A viral etiology of sea star wasting syndrome (SSWS) was originally explored with virus-sized material challenge experiments, field surveys, and metagenomics, leading to the conclusion that a densovirus is the predominant DNA virus associated with this syndrome and, thus, the most promising viral candidate pathogen. Single-stranded DNA viruses are, however, highly diverse and pervasive among eukaryotic organisms, which we hypothesize may confound the association between densoviruses and SSWS. To test this hypothesis and assess the association of densoviruses with SSWS, we compiled past metagenomic data with new metagenomic-derived viral genomes from sea stars collected from Antarctica, California, Washington, and Alaska. We used 179 publicly available sea star transcriptomes to complement our approaches for densovirus discovery. Lastly, we focus the study on sea star-associated densovirus (SSaDV), the first sea star densovirus discovered, by documenting its biogeography and putative tissue tropism. Transcriptomes contained only endogenized densovirus elements similar to the NS1 gene, while numerous extant densoviral genomes were recovered from viral metagenomes. SSaDV was associated with nearly all tested species from southern California to Alaska, and in contrast to previous work, we show that SSaDV is one genotype among a high diversity of densoviruses present in sea stars across the West Coast of the United States and globally that are commonly associated with grossly normal (i.e., healthy or asymptomatic) animals. The diversity and ubiquity of these viruses in sea stars confound the original hypothesis that one densovirus is the etiological agent of SSWS. IMPORTANCE The primary interest in sea star densoviruses, specifically SSaDV, has been their association with sea star wasting syndrome (SSWS), a disease that has decimated sea star populations across the West Coast of the United States since 2013. The association of SSaDV with SSWS was originally drawn from metagenomic analysis, which was further studied through field surveys using quantitative PCR (qPCR), with the conclusion that it was the most likely viral candidate in the metagenomic data based on its representation in symptomatic sea stars compared to asymptomatic sea stars. We reexamined the original metagenomic data with additional genomic data sets and found that SSaDV was 1 of 10 densoviruses present in the original data set and was no more represented in symptomatic sea stars than in asymptomatic sea stars. Instead, SSaDV appears to be a widespread, generalist virus that exists among a large diversity of densoviruses present in sea star populations.

Konar, B., Mitchell, T. J., Iken, K., Coletti, H., Dean, T., Esler, D., . . . Weitzman, B. (2019). Wasting Disease and Static Environmental Variables Drive Sea Star Assemblages in the Northern Gulf of Alaska. *JOURNAL OF EXPERIMENTAL MARINE BIOLOGY AND ECOLOGY, 520*. https://doi.org/10.1016/j.jembe.2019.151209

Sea stars are ecologically important in rocky intertidal habitats where they can play an apex predator role, completely restructuring communities. The recent sea star die-off throughout the eastern Pacific, known as Sea Star Wasting Disease, has prompted a need to understand spatial and temporal patterns of sea star assemblages and the environmental variables that structure these assemblages. We examined spatial and temporal patterns in sea star assemblages (composition and density) across regions in the northern Gulf of Alaska and assessed the role of seven static environmental variables (distance to freshwater inputs, tidewater glacial presence, exposure to wave action, fetch, beach slope, substrate composition, and tidal range) in influencing sea star assemblage structure before and after sea star declines. Environmental variables correlated with sea star distribution can serve as proxies to environmental stressors, such as desiccation, attachment, and wave action. Intertidal sea star surveys were conducted annually from 2005 to 2018 at five sites in each of four regions that were between 100 and 420 km apart across the northern Gulf of Alaska. In the pre-disease years, assemblages were different among regions, correlated mostly to tidewater glacier presence, fetch, and tidal range. The assemblages after wasting disease were different from those before the event with lower diversity and lower density. In addition to these declines, the disease manifested itself at different times across the northern Gulf of Alaska and did not impact all species uniformly across sites. Post sea star wasting, there was a shift in the environmental variables that correlated with sea star structure, resulting in sea star assemblages being highly correlated with slope, fetch, and tidal range. In essence, sea star wasting disease resulted in a shift in the sea star assemblage that is now correlating with a slightly different combination of environmental variables. Understanding the delicate interplay of environmental variables that influence sea star assemblages could expand knowledge of the habitat preferences and tolerance ranges of important and relatively unstudied species within the northern Gulf of Alaska.

Lahner, L., Haulena, M., Garner, M., Harvell, D., Hewson, I., Carpenter, T., & Christiansen, J. (2014). *Captive and Free-Ranging Sea Star Disease Findings from the Seattle, Washington, Waterfront During the 2013 Sea Star 'Wasting Disease' Unusual Mortality Event.* Paper presented at the Salish Sea Ecosystem Conference, Seattle, Washington. Retrieved from https://cedar.wwu.edu/ssec/2014ssec/Day3/75/

Sea star mortality in several genera including *Pycnopodia* and *Pisaster* was unusually high along the west coast of the United States, September-current (December) 2013. Captive and free-ranging animals were analyzed for signs of disease using a variety of diagnostics including cytology, microbiology, histopathology, and transmission electron microscopy. [Excerpt from abstract]

Lowry, D., Wright, S., Neuman, M., Stevenson, D., Hyde, J., Lindeberg, M., . . . Gustafson, R. (2022). *Endangered Species Act Status Review Report: Sunflower Sea Star (Pycnopodia helianthoides) [Draft]*. U.S. Department of Commerce, National Oceanic and Atmospheric Administration (NOAA), National Marine Fisheries Service (NMFS), Office of Protected Resources (OPR). Retrieved from

https://media.fisheries.noaa.gov/2023-03/pycnopodia-helianthoides-status-review-draft-2022.pdf

On August 18, 2021, the National Marine Fisheries Service (NMFS) received a petition from the Center for Biological Diversity to list the sunflower sea star (*Pycnopodia helianthoides*) as a threatened or endangered species throughout its range under the Endangered Species Act (ESA). After an initial evaluation using information provided in the petition and readily available in NMFS' records, we determined that the proposed action may be warranted (86 FR 73230) and a Status Review Team (SRT) was convened to initiate a full status review and evaluate overall extinction risk for the species. This team consisted of representatives from the NMFS West Coast and Alaska Regional Offices; NMFS Southwest, Northwest, and Alaska Fisheries Science Centers; United States Geological Survey; and Monterey Bay National Marine Sanctuary. This document is the status review and extinction risk assessment generated by the SRT and will be used to inform the listing decision for *P. helianthoides*, but does not in itself constitute a determination regarding protected status. [Excerpt from executive summary]

McCracken, A. R., Christensen, B. M., Munteanu, D., Case, B. K. M., Lloyd, M., Herbert, K. P., & Pespeni, M. H. (2023). Microbial Dysbiosis Precedes Signs of Sea Star Wasting Disease in Wild Populations of *Pycnopodia helianthoides*. *FRONTIERS IN MARINE SCIENCE, 10*, 1130912. https://doi.org/10.3389/fmars.2023.1130912

Sea star wasting (SSW) disease, a massive and ongoing epidemic with unknown cause(s), has led to the rapid death and decimation of sea star populations with cascading ecological consequences. Changes in microbial community structure have been previously associated with SSW, however, it remains unknown if SSW-associated dysbiosis is a mechanism or artifact of disease progression, particularly in wild populations. Here, we compare the microbiomes of the sunflower sea star, *Pycnopodia helianthoides*, before (Naïve) and during (Exposed and Wasting) the initial outbreak in Southeast Alaska to identify changes and interactions in the microbial communities associated with sea star health and disease exposure. We found an increase in microbial diversity (both alpha and beta diversity) preceding signs of disease and an increase in abundance of facultative and obligate anaerobes (most notably Vibrio) in both Exposed (apparently healthy) and Wasting animals. Complementing these changes in microbial composition was the initial gain of metabolic functions upon disease exposure, and loss of function with signs of wasting. Using Bayesian network clustering, we found evidence of dysbiosis in the form of co-colonization of taxa appearing in large numbers among Exposed and Wasting individuals, in addition to the loss of communities associated with Naïve sea stars. These changes in community structure suggest a shared set of colonizing microbes that may be important in the initial stages of SSW. Together, these results provide several complementary perspectives in support of an early dysbiotic event preceding visible signs of SSW.

Rudek, T., & Mochon Collura, E. (2023). *Sea Star Illness Treatment Protocol*. Protocol. Oregon Coast Aquarium. Retrieved from https://dx.doi.org/10.17504/protocols.io.q26g7yxjkgwz/v1

Sea Star Wasting Syndrome (SSWS) events of 2014 had a significant impact on the aquarium industry's health management and medical treatment protocols for sick/injured sea stars. The subsequent prescription involved 30ppm TMP-S baths (4- 6 hr/day) to manage secondary bacterial infections associated with the unidentified root cause for illness. In recent years, the use of TMP-S became

ineffective for several of Oregon Coast Aquarium's sea star medical cases. We observed several animals worsen during TMP-S treatment, sometimes dropping additional arms within one day.

An alternative approach was investigated and adopted. The Oregon Coast Aquarium's new methodology is outlined below and describes an experimental alternative to current industry practices, developed by Aquarist Staff and approved by OCAQ's Veterinary Staff. Successful response has been observed in several species of Pacific Northwest sea stars (10-13 degrees C) and early detection/intervention provided the best prognosis. The dosages and treatment duration are still in a trial phase and may change over time. Many of the steps are performed concurrently to manage variables such as water quality, spawning activity and body condition.

Schiebelhut, L. M., DeBiasse, M. B., Gabriel, L., Hoff, K. J., & Dawson, M. N. (2023). A Reference Genome for Ecological Restoration of the Sunflower Sea Star, *Pycnopodia helianthoides*. *The Journal of heredity*. https://doi.org/10.1093/jhered/esad054

Wildlife diseases, such as the sea star wasting (SSW) epizootic that outbroke in the mid-2010s, appear to be associated with acute and/or chronic abiotic environmental change; dissociating the effects of different drivers can be difficult. The sunflower sea star, *Pycnopodia helianthoides*, was the species most severely impacted during the SSW outbreak, which overlapped with periods of anomalous atmospheric and oceanographic conditions, and there is not yet a consensus on the cause(s). Genomic data may reveal underlying molecular signatures that implicate a subset of factors and, thus, clarify past events while also setting the scene for effective restoration efforts. To advance this goal, we used Pacific Biosciences HiFi long sequencing reads and Dovetail Omni-C proximity reads to generate a highly contiguous genome assembly that was then annotated using RNA-seq informed gene prediction. The genome assembly is 484Mb long, with contig N50 of 1.9Mb, scaffold N50 of 21.8Mb, BUSCO completeness score 96.1%, and 22 major scaffolds consistent with prior evidence that sea star genomes comprise 22 autosomes. These statistics generally fall between those of other recently assembled chromosome-scale assemblies for two species in the distantly related asteroid genus *Pisaster*. These novel genomic resources for *Pycnopodia helianthoides* will underwrite population genomic, comparative genomic, and phylogenomic analyses - as well as their integration across scales - of SSW and environmental stressors.

Schiebelhut, L. M., Giakoumis, M., Castilho, R., Garcia, V. E., Wares, J. P., Wessel, G. M., & Dawson, M. N. (2022). Is It in the Stars? Exploring the Relationships between Species' Traits and Sea Star Wasting Disease. *The Biological Bulletin, 243*(3), 315-327. https://doi.org/10.1086/722800

An explanation for variation in impacts of sea star wasting disease across asteroid species remains elusive. Although various traits have been suggested to play a potential role in sea star wasting susceptibility, currently we lack a thorough comparison that explores how life-history and natural history traits shape responses to mass mortality across diverse asteroid taxa. To explore how asteroid traits may relate to sea star wasting, using available data and recognizing the potential for biological correlations to be driven by phylogeny, we generated a supertree, tested traits for phylogenetic association, and evaluated associations between traits and sea star wasting impact. Our analyses show no evidence for a phylogenetic association with sea star wasting impact, but there does appear to be phylogenetic association for a subset of asteroid life-history traits, including diet, substrate, and reproductive season. We found no relationship between sea star wasting and developmental mode, diet, pelagic larval

duration, or substrate but did find a relationship with minimum depth, reproductive season, and rugosity (or surface complexity). Species with the greatest sea star wasting impacts tend to have shallower minimum depth distributions, they tend to have their median reproductive period 1.5 months earlier, and they tend to have higher rugosities relative to species less affected by sea star wasting. Fully understanding sea star wasting remains challenging, in part because dramatic gaps still exist in our understanding of the basic biology and phylogeny of asteroids. Future studies would benefit from a more robust phylogenetic understanding of sea stars, as well as leveraging intra- and interspecific comparative transcriptomics and genomics to elucidate the molecular pathways responding to sea star wasting.

Schiebelhut, L. M., Puritz, J. B., & Dawson, M. N. (2018). Decimation by Sea Star Wasting Disease and Rapid Genetic Change in a Keystone Species, *Pisaster ochraceus*. *PROCEEDINGS OF THE NATIONAL ACADEMY OF SCIENCES OF THE UNITED STATES OF AMERICA, 115*(27), 7069-7074. https://doi.org/10.1073/pnas.1800285115

Standing genetic variation enables or restricts a population's capacity to respond to changing conditions, including the extreme disturbances expected to increase in frequency and intensity with continuing anthropogenic climate change. However, we know little about how populations might respond to extreme events with rapid genetic shifts, or how population dynamics may influence and be influenced by population genomic change. We use a range-wide epizootic, sea star wasting disease, that onset in mid-2013 and caused mass mortality in *Pisaster ochraceus* to explore how a keystone marine species responded to an extreme perturbation. We integrated field surveys with restriction site-associated DNA sequencing data to (i) describe the population dynamics of mortality and recovery, and (ii) compare allele frequencies in mature *P. ochraceus* before the disease outbreak with allele frequencies in adults and new juveniles after the outbreak, to identify whether selection may have occurred. We found *P. ochraceus* suffered 81% mortality in the study region between 2012 and 2015, and experienced a concurrent 74-fold increase in recruitment beginning in late 2013. Comparison of pre- and postoutbreak adults revealed significant allele frequency changes at three loci, which showed consistent changes across the large majority of locations. Allele frequency shifts in juvenile *P. ochraceus* (spawned from premortality adults) were consistent with those seen in adult survivors. Such parallel shifts suggest detectable signals of selection and highlight the potential for persistence of this change in subsequent generations, which may influence the resilience of this keystone species to future outbreaks.

Schultz, J. A. (2016). *Mass Mortality Events of Echinoderms: Global Patterns and Local Consequences.* (M.S.), Simon Fraser University. Retrieved from https://summit.sfu.ca/item/16744

Wildlife mass mortality events can have profound ecological consequences and may be becoming more frequent or severe due to climate change, anthropogenic factors or other stressors. Mortality events involving echinoderms are of particular concern because of the important role echinoderms play in structuring marine ecosystems. In this thesis I explore the local consequences of a widespread sea star mortality event, and investigate the global trends in echinoderm mass mortality events. I found that the mass mortality of the sunflower sea star *Pycnopodia helianthoides*, which began in the summer of 2013 as a result of a wasting syndrome, resulted in a trophic cascade involving urchins and kelp at the local scale (i.e., Howe Sound, BC). A global review of reports of echinoderm die-offs revealed that these events have not become more frequent or extensive since 1897. However, disease and climate change may be playing an increasing role. This study provides some of the first evidence of subtidal community shifts following sea star wasting syndrome, and highlights the need for consistent and comprehensive

documentation of echinoderm population trends in the literature to increase our understanding of mass mortality events.

Stevens, B. G., Vining, I., Byersdorfer, S., & Donaldson, W. (2000). Ghost Fishing by Tanner Crab (*Chionoecetes bairdi*) Pots Off Kodiak, Alaska: Pot Density and Catch Per Trap as Determined from Sidescan Sonar and Pot Recovery Data. *FISHERY BULLETIN, 98*(2), 389-399. Retrieved from https://spo.nmfs.noaa.gov/content/ghost-fishing-tanner-crab-chionoecetes-bairdi-pots-kodiak-alaska-pot-density-and-catch-trap

Sidescan sonar was used to locate 189 putative lost crab pots in a 4.5 km super(2) area of Chiniak Bay, near Kodiak, Alaska. Subsequent observations of 15 such objects by submersible and ROV verified that they were indeed crab pots. In 1995 and 1996, 147 pots were recovered from the surveyed and adjacent nonsurveyed areas by grappling, and their condition and contents were examined. Tanner crabs, *Chionoecetes bairdi*, were the most abundant organism, with 227 found in 24 pots (16% frequency of occurrence); sunflower sea stars (*Pycnopodia helianthoides*) were the most frequent (42%) occupant and second most abundant (189 in 62 pots). Octopuses (*Octopus dofleini*) were significantly associated with pots containing Tanner crabs. Occurrence of crabs in pots was primarily a function of background crab density and differed between the surveyed and nonsurveyed areas. Recently lost pots (< 1yr old) had significantly more male crabs, significantly larger male crabs, and contained seven times more total crabs than older pots (those lost two or more years prior to recovery). The proportion of pots with damaged webbing increased with pot age, but holes in pot webbing did not significantly affect catch per pot.

Winningham, M., Eisenlord, M. E., Gaydos, J. K., Montecino-Latorre, D., Nichols, J., Pattengill-Semmens, C. V., & Harvell, C. D. (2018). *A Tale of Two Sea Stars: Recovery (Ochre Star) of Endangerment (Sunflower Star) Following the 2014 Epidemic.* Paper presented at the Salish Sea Ecosystem Conference. Retrieved from https://cedar.wwu.edu/ssec/2018ssec/allsessions/527

During the summers of 2013 and 2014, populations of sea stars along the west coast from Alaska to Mexico were decimated by the sea star wasting disease (SSWD) epizootic. Two of the most highly affected species along this range are *Pisaster ochraceus* (the ochre star), the most common intertidal species, and *Pycnopodia helianthoides* (the sunflower star), the most common subtidal species, both of which are endemic to the western coast of the U.S. For the ochre star, in the San Juan Islands of Washington State, we measured high case fatality rates associated with disease prevalence over 90% during the summer of 2014. Low levels of disease were observed in the summers of 2015, 2016, and 2017. Population levels following the epizootic remain stable but small, and shifted in size structure from larger to smaller stars. At one site, a dramatic increase in both juvenile and adult ochre stars occurred in 2017, giving hope for future recovery. In contrast, the most common subtidal species, the sunflower star, also suffered catastrophic mortality in 2014. However, in this case, Citizen Science Monitoring in all oceanographic basins of the Salish Sea through 2017 shows an extraordinary decimation of this species, with no sign of recovery three years after the SSWD epizootic. Extremely low population size of sunflower stars raises concern about the capacity of this species to recover, as well as to resist other stochastic events in the future.