To Pen A Tale Of Pens…

By

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Life History

The term "life history" is really a misnomer. What the term really means is the generalized "story" of an average individual's life. Probably the animal whose life history is best known is the human. Broken down by geographical region, and other demographics, it is possible to predict with surprising accuracy the life span, as well as the major life experiences, such as the number of offspring, and when they occur, for the average individual of many human populations. In the case of humans, the driving force for the accumulation of such knowledge is not the desire for "abstract knowledge," but rather the desire to make a profit. On such knowledge is the insurance industry built, and it is based to a great extent on studies of human life history profiles extended to the greatest precision possible. We also know the life histories of a large number of other, mostly terrestrial, organisms. In these cases, biologists have spent a great deal of time studying populations of these animals and have noted when the animals are born, when they die, how long they live, when they mate, and so on. All of these data can be massaged and manipulated statistically to provide a good understanding of the essential experiences of an average member of those species.

However, once we pass out of the terrestrial realm and into the oceanic environment, our ability to see all of the relevant aspects of any given organism's life is significantly obscured by a wall of water. To accumulate the data and the observational knowledge to flesh out a "life history" takes good, down to earth (or ocean bottom), tedious, long-term, expensive and dedicated observational research. Because of the effort involved, such work has been completed for precious few animals, most of which are temperate, due primarily to the prevalence of marine laboratories in temperate regions.

The Story

In this essay, I summarize the results of a series of research projects concerning a temperate octocoral, the sea pen, *Ptilosarcus gurneyi*. This species has also been known as *Ptilosarcus quadrangulare*, *Leioptilus quadrangulare*, *Leioptilus guerneyi*, and *Ptilosarcus quadrangularis*, but these names have long been considered to be junior synonyms. Nonetheless, they still turn up from time to time, particularly in comments on the internet. The basic research on which this article is based was reported in two papers (Chia and Crawford, 1973; Birkeland, 1974), but in addition, there is a significant amount of my own hitherto unpublished research. For ease of readability, I will not cite either main reference again. If the reader is interested in more detail, please read these articles or contact me directly. In total, this information represents several thousand person-hours of observational time. As far as I know, no similar body of knowledge exists for any tropical octocoral, although there are similar accumulations of information regarding some Mediterranean gorgonians. I hope, however, that this example will give some appreciation for the life history of, at least, one type of octocoral. Perhaps, as well, this essay will present the types of data needed to discuss the biology of these animals.

Figure 1. A mature *Ptilosarcus gurneyi* individual extended about 50 cm out of the sediment. The primary polyp consists of the base which extends into the sediment, and the rachis or stalk extending from the base up between the "leaves." The gastrozooids or feeding polyps are found on the outside of the leaf edges, while the siphonozooids, or pumping individuals, are found in the orange regions on the sides of the rachis. The "warts" on a few of the leaves are caused by a parasitic isopod living inside the pen's tissues.

Figure 2. A portion of a sea pen bed in the central Puget Sound region, the depth was about 15 m. Water flow was from the left, and the foreground field of view is about 1.5 meters (5 feet) across.

Sea pens are octocorals. Taxonomically, they are placed in the Order Pennatulacea of the Subclass Octocorallia (= Alcyonaria), in the Class Anthozoa of the Phylum Cnidaria. All of this jargon means they are animals whose major body parts consist of modified polyps. Being octocorallians, their polyps show an octamerous or eight-fold symmetry most obviously manifested by the presence of eight tentacles around the mouth of the feeding polyps, or gastrozooids. These eight tentacles each have a series of small side branches, a condition referred to as "pinnate branching." Unlike other octocorals, sea pens are mobile. While they are sessile, living in unconsolidated ocean bottom sediments, they are not fastened to the substrate and at least some sea pens are capable of significant locomotion.

The adult sea pen is body considered to be comprised by the fused modifications of three types of polyps. The base and central stalk region, or rachis, is considered to be the modified original polyp. The feeding polyps possess tentacles are called gastrozooids and typically found either extending from the surface of the rachis much like the spokes of an umbrella, or on lateral extensions from the rachis, the "leaves". Depending on the sea pen species and the adult size, there may be from about ten to many thousand gastrozooids. Embedded in the rachis surface are the siphonozooids; modified polyps lacking tentacles. These structures consist of a "mouth" which is lined with microscopically sized, beating, hair-like projections called "cilia." Siphonozooids pump water into the body of the colony. The colony has quite an intricate system of channels which allow the movement of water and nutrients throughout the body. The forces necessary for the water movement comes from muscular contraction of the body and the beating of the cilia lining the water channels.

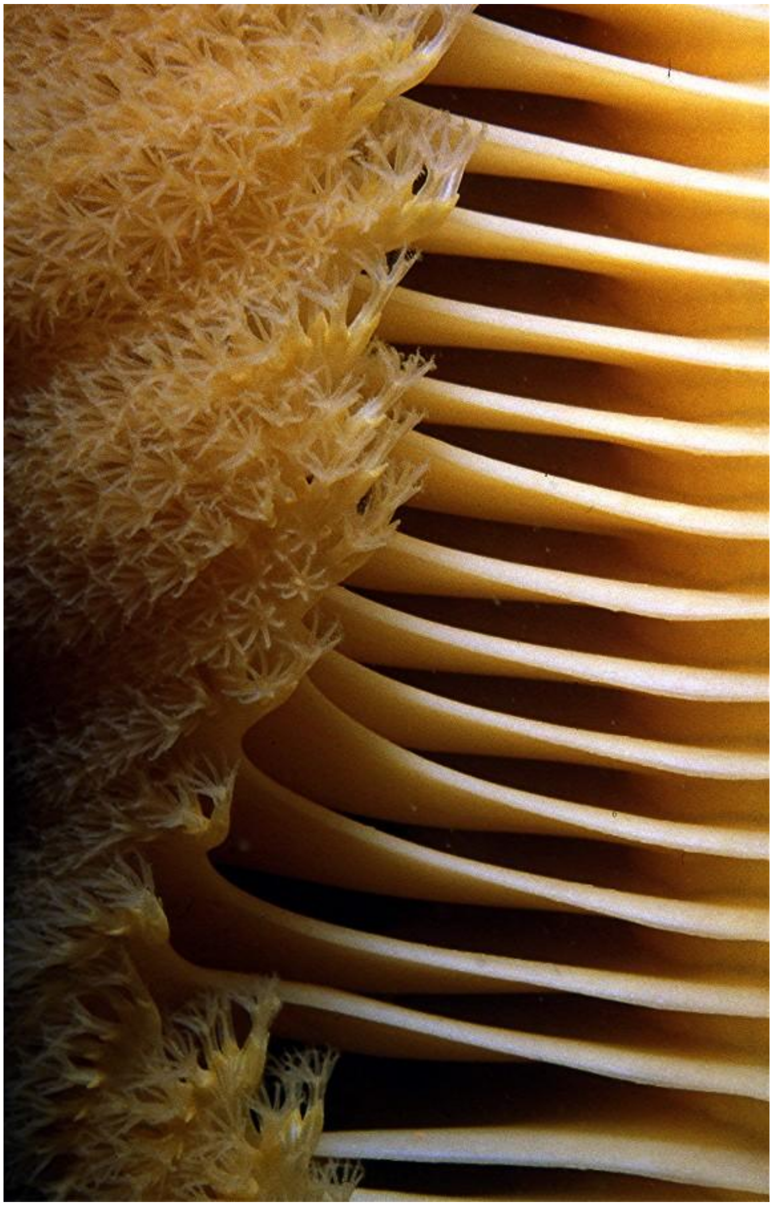

Figure 3. The "leaf" edges of a mature sea pen showing many gastrozooids. The leaves are oriented into the current, and can generate hydrodynamic lift. When the animals are disturbed, they may orient into the current, inflate, climb out of the sediment, and drift away in the current.

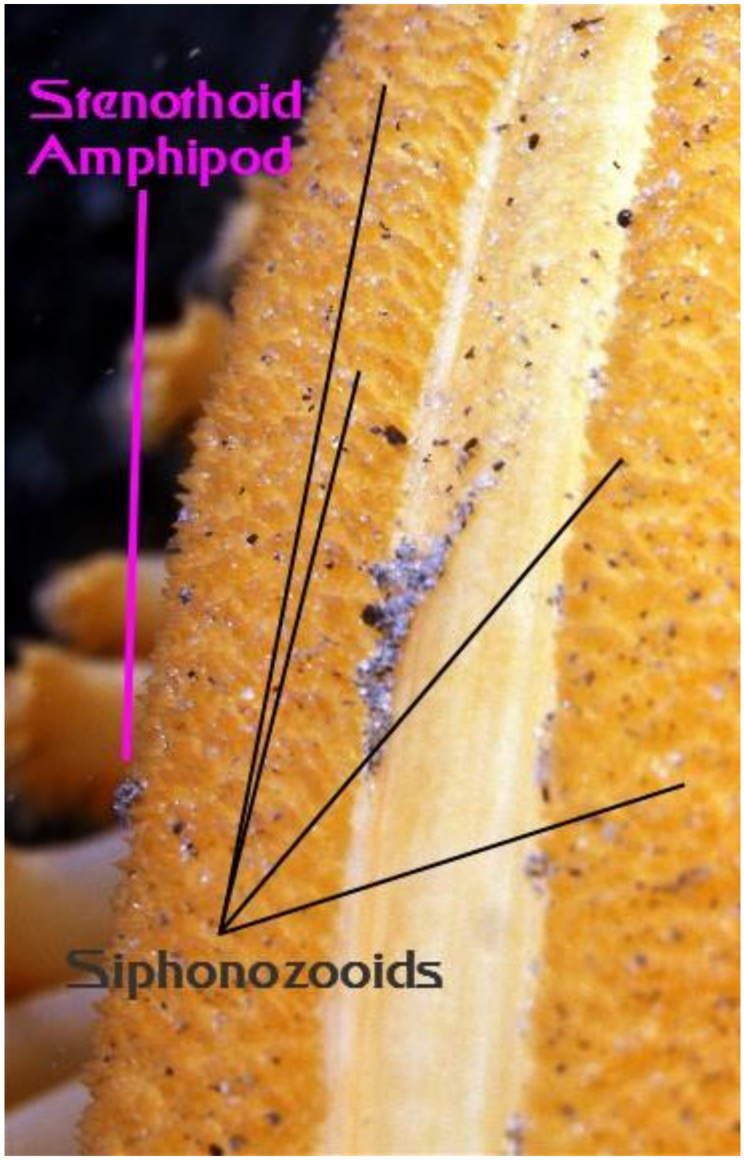

Figure 4. The siphonozooid region of a sea pen rachis; siphonozooids, basically polyps without tentacles, pump water into the pen. Small stenothoid amphipods are commonly found on the pen's surface.

Sea pens are like the late comic, Rodney Dangerfield, in that they "don't get no respect." They are often largely ignored in invertebrate zoology classes, and hardly discussed at all in many marine biology classes. Nonetheless, they are surprisingly abundant and, in fact, may be the dominant cnidarians over large regions of the earth's surface; areas where stony corals, other octocorals, and most sea anemones are essentially absent, the deep sea soft-sediment bottom. The largest of Earth's ecosystems, much of this area is characterized by the presence of sea pens. I doubt anybody has made the calculations, but I suspect that it would a sure bet to say that the biomass of sea pen living tissue exceeds that of all other benthic cnidarians combined.

Figure 5. A small sea pen that had been drifting across the bottom.

Ptilosarcus gurneyi, the subject of this article is found throughout the Northeastern Pacific from Alaska to Southern California. Fully expanded, large, adult individuals may extend for about 60 cm (2 feet) out of the sediments, with the base extending into the sediments another 15 to 30 cm (6 to 12 inches). Fully contracted, these same large adults will be about 15 to 20 cm (6 to 8 inches) long. The body color ranges from a pale cream to deep orange red. The body morphology may remind one of a fat, carrot-colored quill pen; hence, “sea pens”; alternatively, when contracted, they may remind one more, simply, of carrots. Internally, they contain a single large calcareous and proteinaceous style. The size of the style is related to the age of the sea pens, and measurements of it may be used to obtain ages of individuals in a population. *Ptilosarcus gurneyi* are found in shallow waters, ranging from the lowest intertidal zone to depths of about 500 feet, but are most abundant in shallow waters. And, the animals in this species may be amazingly abundant. In the Puget Sound areas studied by Birkeland, the number of sea pens averaged about 23 pens per square meter, with about 8 of these being three or more years in age. Sea pen beds typically reach depths in excess of 50 m, and extend laterally for dozens of kilometers, interrupted only physical features such as scouring by river currents, dredged harbors and the like. Although these beds are discontinuous, because of the currents in the area, they are not isolated from adjacent beds. Larvae are dispersed throughout the region, and even adult pens may move laterally great distances. The adults can crawl up out of the sediment, inflate with water, and drift along in the currents, much like an underwater balloon.

Figure 6. A sea pen photographed in the field, shortly after the spring equinox, a day or two prior to spawning, showing the eggs in the gastrozooids. The extended nature of the gastrozooids is visible in the image. Their guts extend through the leaves into the rachis where they meet and fuse with a large internal canal system that extends throughout the animal. The eggs are about 0.6 mm in diameter.

The sea pens have a cyclic behavior pattern of inflation, feeding, and then deflation. They may do this several times a day, and the rhythm appears more-or-less unrelated to feeding or available foods. At any one time, Birkeland found that only about a fourth of the pens were exposed, with the rest being completely buried in the sediments, often to a depth of 30 cm (1 foot) or more. The sea pens totally dominate and structure these communities. Very few other macroscopic animals live in the sediments of sea pen beds, possibly because the continuous bioturbation resulting from the movement of the sea pens.

As one might expect, the shear mass of sea pen flesh in these areas is a resource that has not "gone unnoticed" by predators. In fact, there is an amazing variety of predators that have become adapted and, in some cases, totally dependent upon the sea pen populations. In many respects, *Ptilosarcus gurneyi* in sea pen beds fills an ecological position similar to the huge herds of bison that used to occupy the American Great Plains or the grazing animals of the Serengeti. In each of these cases, whole food webs were built upon the basic primary resource species. Sea pens are suspension-feeders eating small organic particulate material, larvae, and other small zooplankton. In turn, they are the food of a wide variety of benthic predators. When small, they are eaten by several, mostly small, nudibranch species. As they grow they become too large for some of the nudibranchs, although others may still eat them. However, as the pens grow to maturity, they become the prey of several sea star species. At the apex of this food web is yet another sea star, which preys on those stars.

In The Water

Ptilosarcus gurneyi generally spawns in the first week following the spring equinox. In the laboratory during that time, sunlight hitting a tank of gravid sea pens that has been shaded will induce spawning. The eggs are large, about 600 µm across, and a mature female colony will produce upwards of 200,000 of them. Fertilization occurs in water column. Embryonic development occurs over about 3 days at 12º C, and results in a foot-ball shaped, mobile, non-feeding, planula larva about 1 mm long. After about five days, planulae raised in the laboratory begin to swim to the bottom of their containers. By inference, the same behavior in nature would move them toward the ocean bottom. In laboratory containers, they repeatedly swim vertically downward and touch their anterior end to the sediments. If the sediments are coarse sand, with particle diameters in the 0.250 to 0.500 µm range, they will stick to, and "settle" into that sediment and begin to metamorphose into a small sea pen. If appropriate sediments are not available, settlement and metamorphosis may be delayed for as much as a month. Without appropriate sediment, the animal will die. These pens are found in an areas dominated by vigorous tidal flows and offshore currents. In a month, the larvae could disperse over great distances.

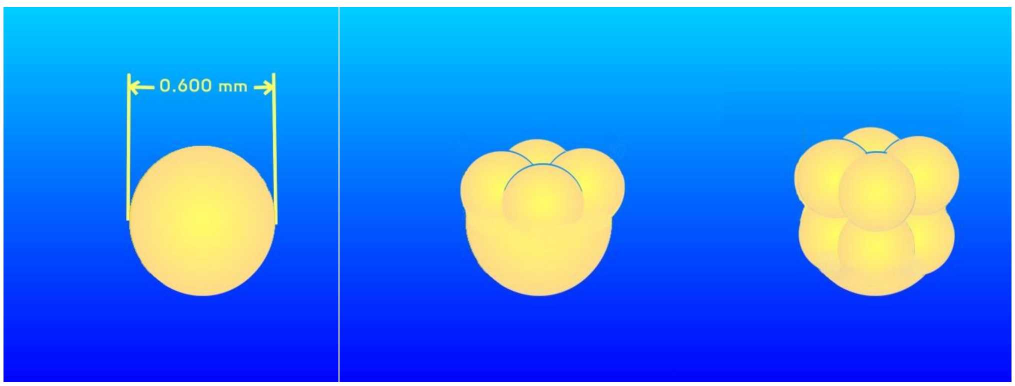

Figure 7. Drawings done from life of developing *Ptilosarcus gurneyi* embryos. Left. The newly released ovum. Center. Embryo at about the beginning of the 4-cell stage; about 4 hours old.

Cleavage is incomplete and doesn't extend through the embryo. Right: Embryo between the 4 and 8 cell stages, about 6 hours after fertilization.

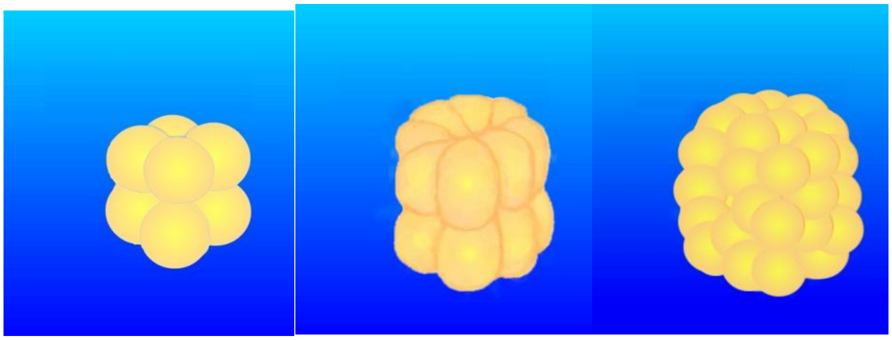

Figure 8. Drawings done from life of developing *Ptilosarcus gurneyi*. Left. The 8-celled stage is about the same diameter as a newly spawned egg; about 7 hours after fertilization. Center. The embryo is at the 16-celled stage; about 8 hours old. Right: This embryo is at the blastula stage, about 12 hours old.

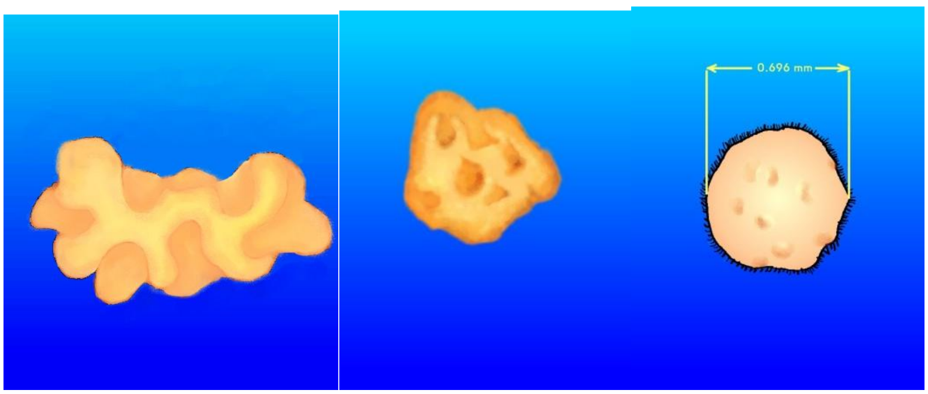

Figure 9. Drawings done from life of developing *Ptilosarcus gurneyi*. Gastrula stages; individual cells no longer visible. Left. Early gastrula, irregularly shaped, about 24 hours old. Center. Gastrula, about 36 hours old. Right: Late Gastrula, the embryo has become ciliated and is swimming; 2 days old.

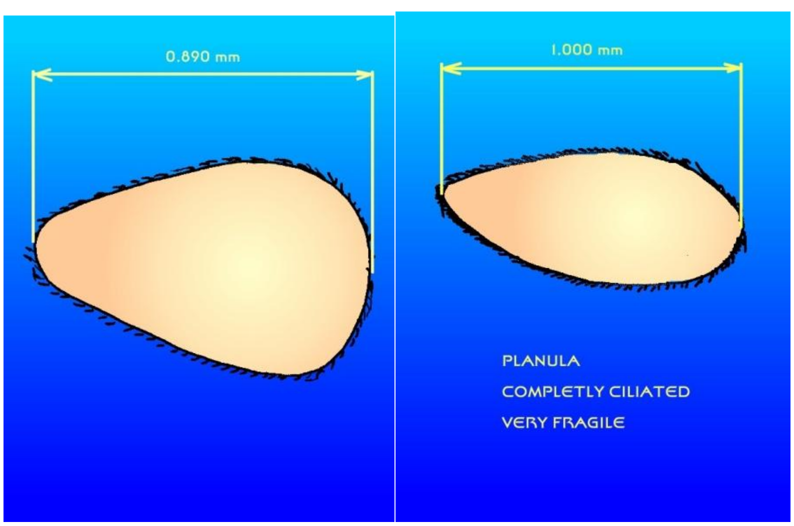

Figure 10. Drawings done from life of developing *Ptilosarcus gurneyi*. Left. Early planula, about 3 days old. Right: Planula larva at 4 days old.

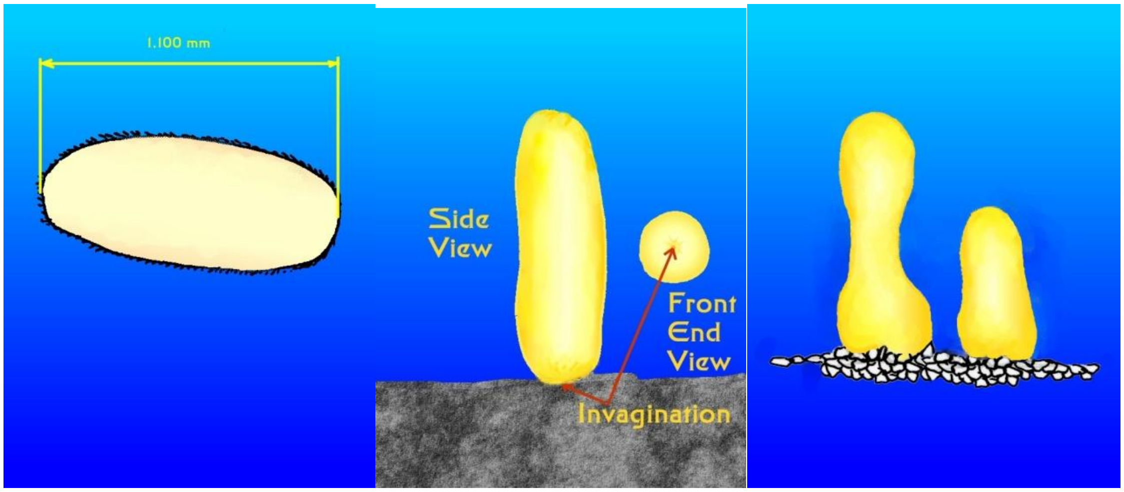

Figure 11. Drawings, done from life, of developing *Ptilosarcus gurneyi*. Left. Planula at 5 days. Center. Planula, settling, about 6 days. Right: Settled larva undergoing metamorphosis into a juvenile sea pen; about 8 days of age. The animal is capable of contraction and elongation.

Once metamorphosis begins development to a feeding individual is rapid, with the first polyp having functional tentacles within 2 weeks of spawning. Active feeding begins soon thereafter and given sufficient food, growth is relatively rapid. Once the sea pens have settled, they become potential prey for many predators. Birkeland found that small sea pens are eaten at the rate of about 200 per year per square meter by small nudibranchs. If they can survive this period, they get large enough to avoid becoming prey for the smallest of the nudibranchs, but they graduate into become food for sea stars. Sea pens grow at a relatively constant rate, reaching sexual maturity when they are about 24 cm (9. 4 inches) tall and five years old.

Both growth and predation rates are continuous; there is no cessation of growth upon reaching an "adult size." As with many cnidarians, no old age or senescence is demonstrable in these animals. Nonetheless, they don't live forever. In essence, *Ptilosarcus* life is an exercise in "beating the odds," and as in all such cases, the "odds," - in this case, the odds of being eaten by a predator - are too great for indefinite success. The life expectancy of an individual sea pen in the Puget Sound areas appears to be about 14 to 15 years. Older animals may be occasionally found but, if so, they are very rare. Predators aren't the only source of mortality in sea pens, nor are sea pens immune from parasites which may influence their growth and survival; however, these factors remain unstudied.

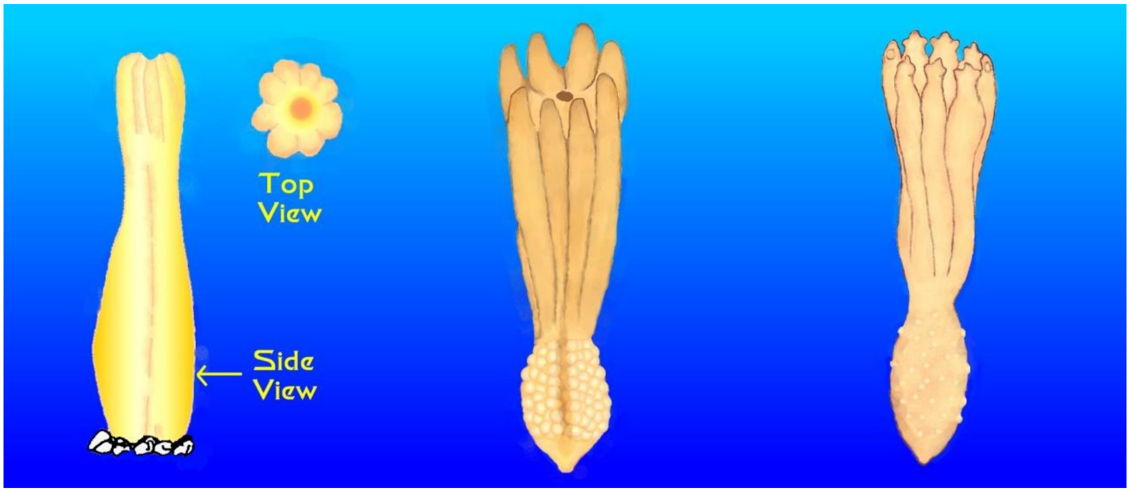

Figure 12. Drawings, done from life, of developing *Ptilosarcus gurneyi*. Larva undergoing metamorphosis. Left. 11 days. Center. 13 days old; tentacles clearly evident; bumps on body surface are of unknown function, spicules were not present; mouth is open and a gullet or gut is evident. Right: 15 days old; note the development of the first pinnae on the tentacles.

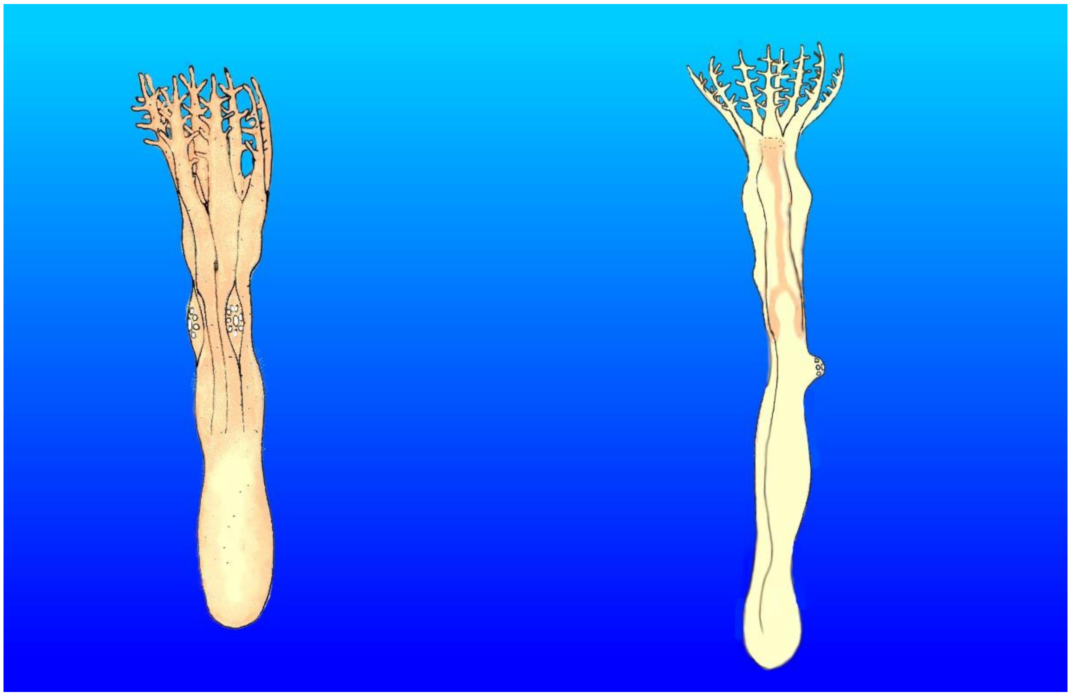

Figure 13. Drawings, done from life, of developing *Ptilosarcus gurneyi*. Two individuals about 3 weeks old; spicules are visible in the body wall. They have one complete feeding polyp, the primary polyp, and siphonozooids on the stalk. The animals were actively feeding at this time and were about 3.5 mm long. The extent of the visible gut is shown in the right individual. The individuals were settled and growing in coarse sand. At this point, I terminated this growth series and transplanted the juveniles to a sea pen bed in one of my benthic research study sites.

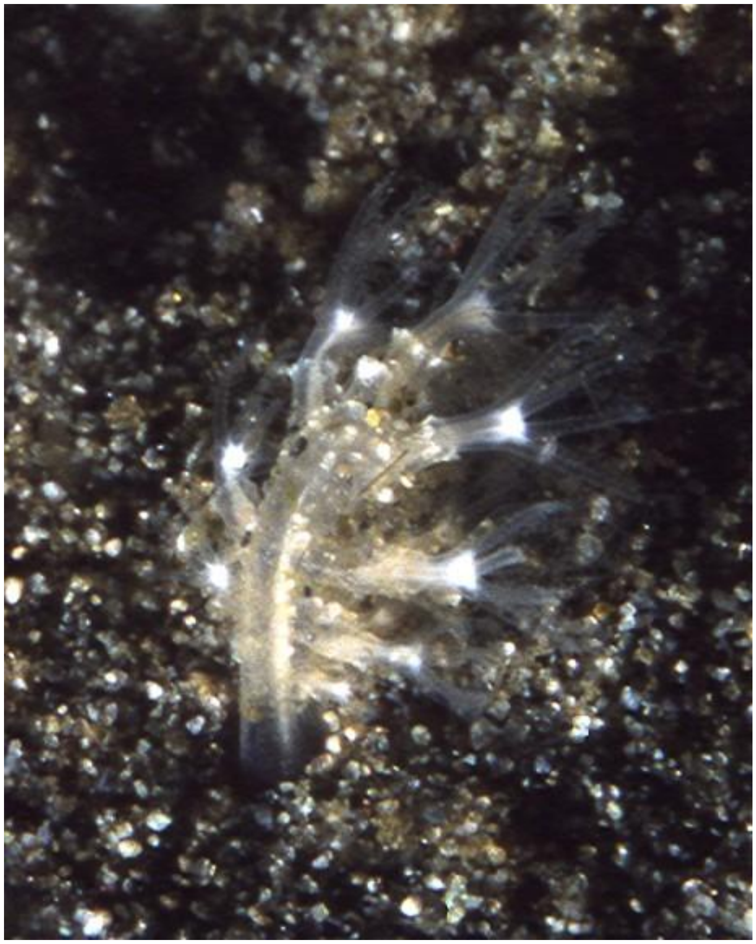

Figure 14. A juvenile sea pen, photographed in nature; depth about 15 m. The animal is an estimated one year old. It was between one and two centimeters (about 0.4 to 0.8 inches) high. Note gastrozooids, and the internal calcareous style (visible as a white band).

Figure 15. Juvenile sea pen, photographed in nature; depth about 15 m. This animal is about two years old. It was about 5 centimeters (about 2 inches) high. Note: the gastrozooids, the siphonozooids (visible as bumps on the stalk), and the developing leaves.

Figure 16. Older juvenile sea pen, probably about 4 years old, about 15 cm (6 inches) high. The internal style that can be used to age the animals is clearly visible as a white internal stripe.

Figure 17. Evidence of incomplete, or attempted, predation; in both cases these partially eaten sea pens probably were attacked by nudibranchs.

Figure 18. The Predators. These nudibranchs primarily eat the smallest pens and become common in sea pen beds shortly after the juveniles settle and metamorphose out of the plankton. Left. *Hermissenda crassicornis*. Right. *Flabellina trophina*. Both nudibranchs are small, reaching lengths that do not exceed about 4 cm (1.6 inches). These species are responsible for the deaths, on the average, of upwards of 200 sea pens per square meter, per year.

Figure 19. The Predators. This nudibranch, *Tritonia festiva*, reaches lengths of about 10 cm (4 inches) and primarily eats small to medium-sized sea pens, but will not hesitate to take a chunk out of a larger one, as the above individual is about to do.

Figure 20. The Predators. These two large nudibranchs, *Tritonia diomedia* (left) reaching lengths of 15 cm (6 inches) and *Tokuina tetraquetra* (right) reaching lengths in excess of 30 cm (12 inches) also eat sea pens. *Tritonia* is common in sea pen beds, *Tokuina* are uncommon in those areas, and tends to eat isolated sea pens growing in sediment pockets in rocks. Individuals of these two species can eat the largest of sea pens without any difficulty whatsoever.

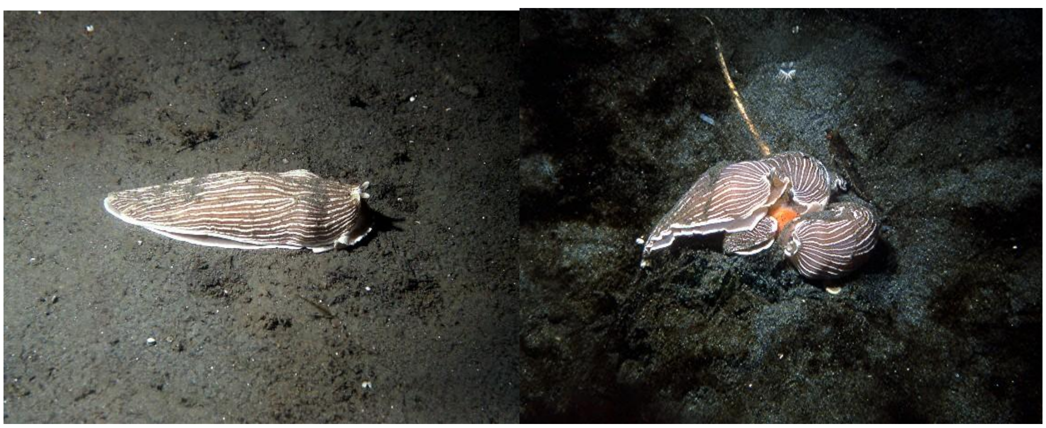

Figure 21. The Predators. These images show *Armina californica*, (left) probably the most abundant nudibranch predator that eats *Ptilosarcus*. Although solitary individuals are capable of eating a pen, these animals are gregarious and are often seen clustered over the remains of their prey (right). The nudibranchs are reach lengths of about 10 cm (4 inches) long, and will eat all size categories of pens.

Figure 22. The Predators. In the areas of the sea pen beds, about 50% of the food items eaten by *Crossaster papposus* are sea pens.

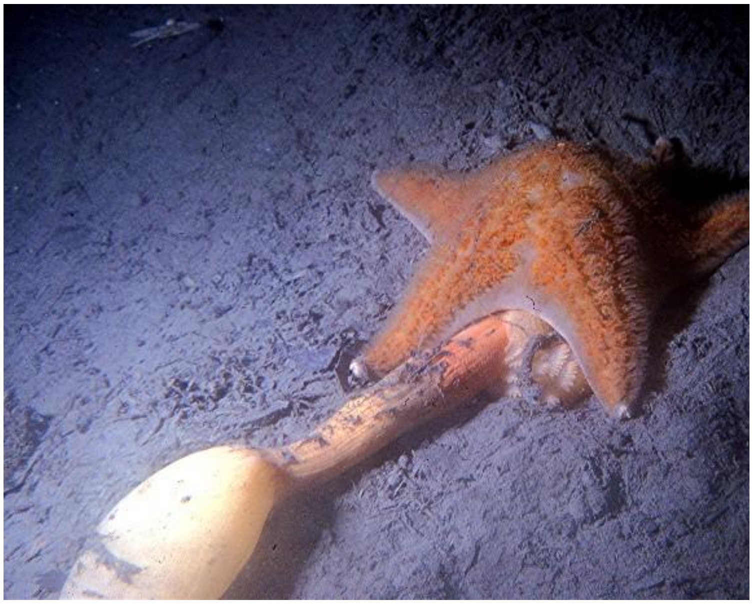

Figure 23. The predators. In the areas of the sea pen beds, about 98% of the food items eaten by *Dermasterias imbricata* are sea pens.

Figure 24. The Predators. ***Mediaster aequalis*** **is a predator of sea pens, among many other things. Here a sea star is hanging on to a previously buried sea pen that is expanding and trying to dislodge it. Pens bury into the sediments and, if stimulated, the pen will sometimes inflate, and expand in an apparent attempt dislodge the predator. Note that the pen has lifted the sea star totally off the substrate.**

Figure 25. The Predators. ***Hippasteria spinosa*** **eats only sea pens. It takes a full grown star about 4 to 5 days eaten a fully grown sea pen.**

Figure 26. The Predators. The end result of the effects of all of the predators is the style.

Figure 27. The Green Disease. As if predation wasn't enough, the sea pens are subject to other maladies. The green coloration in the pens above is caused by an endoparasitic green alga, which appears to kill the pens, albeit it takes several years to do so.

Figure 28. Not all *Ptilsosarcus gurneyi* in the Northeastern Pacific are found in dense beds. They may be found in many other habitats where sand pockets of the appropriate type occur. The anemones to the left are *Urticina piscivora*, and are about 30 cm (12 inches) across the oral disk.

During their lifetime, these pens probably reproduce about ten times. If the average number of eggs produced by one pen is 200,000, then each female will produce about 2,000,000 eggs over her life span. If the populations are assumed to be constant, neither shrinking nor growing, then over the life span of the female she must spawn the eggs to replace herself and her mate, indicating the odds of survival to successful reproduction by any given *Ptilosarcus gurneyi* individual in the Puget Sound region is about 1,000,000 to 1. Although those odds seem pretty slim, they are significantly greater than many other marine animals such as pelagic fishes.

Figure 29. Juvenile *Ptilosarcus* settle in dense assemblages; they have to, to be able to withstand the predation pressure of the array of predators that feed upon them.

To Take Home

There are some things that may be taken to heart from my tale of sea pen life and, mostly, death. First, despite their apparent simplicity, these are hardy animals capable of surviving much environmental perturbation; unless they are eaten, they have the potential of living a long time. Second, they are mobile and capable of movement, and will leave areas that are not to their liking. If someone attempts to keep a sea pen in a marine aquarium, the animals will have to be provided with a deep – really deep – 30 cm (1 foot) or more sand layer to allow their innate activity patterns to be expressed. Third, sea pens lack zooxanthellae, yet they have a rapid growth rate. Consequently, they will need to be fed – A LOT! The Puget Sound region, the so-called "Emerald Sea," is exceedingly rich in plankton. Sea pens obviously are so abundant in the region for a number of reasons, not the least of which is all of the potential food. They eat small zooplankton; in a marine aquarium, organisms much larger than newly hatched *Artemia* are likely to be too large for them. They probably will not eat much phytoplankton unless it is added as a dead suspension of clumped cells. Fourth, sexual maturity is likely to be reached when the animals are significantly less than full sized. Eggs, at least, will be quite noticeable as they develop in the "leaves" below each gastrozooid. Sperm may be difficult to see, but may be noticeable in similar body regions as white patches. Given the number of eggs released from even a small individual, it is likely that spawning events would significantly foul a small aquarium. If eggs are seen developing in a "pet" sea pen, then the aquarist must plan for the upcoming blessed event. Finally, these are very neat and strikingly beautiful animals. Additionally, they show activity patterns totally lacking in many of the other corals kept by aquarists. If the hobbyist is willing to accommodate their specific needs, primarily by providing a deep sand habitat for them to bury into, and an appropriate diet, they will likely thrive.

References:

Birkeland, C. 1974. Interactions between a sea pen and seven of its predators. Ecological Monographs. 44: 211-232.

Chia, F. S. and B. J. Crawford. 1973. Some observations on gametogenesis, larval development and substratum selection of the sea pen Ptilosarcus gurneyi. Marine Biology. 23: 73-82.

Kozloff, E. N. 1990. *Invertebrates*. Saunders College Publishing. Philadelphia. 866 pp.

Ruppert, E. E, R. S. Fox, and R. D. Barnes. 2003. *Invertebrate Zoology, A Functional Evolutionary Approach*. 7th Ed. Brooks/Cole-Thomson Learning. Belmont, CA. xvii +963 pp.+ I1-I 26pp.