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FHL 432: Marine Invertebrate Zoology Summer A 2025  
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### Epitoky, brooding, and precocial larvae in *Epigamia magna* (Polychaeta: Syllidae)

**Abstract:** Syllidae (Polychaeta) show a remarkable variety of reproductive strategies related to their transformation into the pelagic spawning epitoke form. Syllids can create epitokes through schizogamy, where stolons bud off, or epigamy, where the entire adult transforms in order to swim, and after fertilization they often brood their young with a variety of mechanisms. *Epigamia magna* (Berkeley, 1923) is a large syllid in the subfamily Autolytinae, and although its reproduction and larval development are poorly known, the subfamily is known for ventral brooding. I collected two fertilized female epitokes, one unfertilized female, and one male by night-lighting in late June and recorded their development. The fertilized females exhibited a long brooding period, at least 13 days, and the larvae which emerged from the brood sac were ciliated and highly developed, already at the 4-setiger stage. They quickly developed the fifth setiger within 2 hours, and grew to be 1100  $\mu\text{m}$  by hour 44. My observations of these larvae somewhat conflict with previous reports, as I found they were 800  $\mu\text{m}$  long at hatching, with six red eyes. *E. magna*'s large body size and long brooding period appear to allow heavy investment before larvae are released into the water column. I discuss a few of the many unresolved questions about this species' reproduction, including seasonal limits, the cues for swarming, and a potentially annual life cycle.

**Keywords:** epitoky, brooding, larval development, precociality, *Epigamia magna*, Syllidae

**Introduction:** The Syllidae can be identified by their proventricle and pharyngeal armature (Nygren 2004), but they are remarkable because of their enormous diversity of reproductive strategies. All syllids undergo epitoky, wherein adults dramatically alter their tissues to become a pelagic, sexually reproductive form. Besides the necessary gametogenesis, epitokes expand sensory structures and swimming chaetae, while degenerating the digestive system and other extraneous body parts (Fischer 1999, Aguado et al. 2012). Epitoky helps benthic worms find mates and disperse larvae, and it is linked to lunar, tidal, and diel cycles (Fischer 1999, Franke 1999). Syllidae can perform epigamy, where the entire organism transforms, or schizogamy, where sexual stolons break off swim independently. Some species return to the benthos after spawning, while others die after a single reproductive event (Franke 1999). Epitokes vary widely in their cephalization, sexual dimorphism, internal or external fertilization, hermaphroditism or gonochorism, budding patterns, and parental care (Giese & Pearse 1975, Aguado et al. 2012). Many syllids brood their young, in ventral or dorsal sacs, through modified nephridial pores, attached to chaetae or cirri, or internally (Aguado & San Martín 2009, Aguado et al. 2012).

The subfamily Autolytinae has brood yolky eggs in a ventral sac, with chambers linked to the parental segments. The largest species, *Epigamia magna* (Berkeley, 1923), is distributed from the San Juan Islands to Hokkaido, and lives among sponges and hydroids (Berkeley 1923, Imajima 1966, Nygren 2004). The sexually dimorphic epitokes are longer than the atokes, with three distinct body regions (Nygren 2004), and are documented February–June (Berkeley 1923, Imajima 1966). By reviewing iNaturalist observations, I have determined that the range extends south to Eureka, CA, and that while breeding peaks March–June, epitokes with ventral brood sacs have been found in November in Washington, and as late as August in Alaska.

All that is known about *E. magna*'s reproductive biology is that it is epigamous (Nygren 2004), and that 4-setiger larvae emerge from the ventral brood sac, about 600  $\mu\text{m}$  long, with 4 red eyes, apical tufts, ciliated bands, and a pharynx (Strathmann 1987). However, the congener *E. alexandri* has been studied in some detail: it breeds April–June, the chambers of the ventral sac develop asynchronously, and trochophore larvae emerge 6 days after fertilization, becoming 1-2 setiger larvae around day 10. The epitokes are phototactic, the females can hold sperm internally for several days, and brooding females coil

protectively around the sac if disturbed (Qian & Chia 1989). I expect that *E. magna's* reproduction is similar to *E. alexandri*, but because of the diversity within the family and *E. magna's* larger body size, I hope to provide a useful comparison by studying the larval development of *E. magna*.

Methods: I night-lighted around 11 PM nightly between June 20th and July 3rd, 2025 with a white light off the Friday Harbor Laboratories docks (48.54527, -123.01205) for 10–30 minutes. I captured *E. magna* with a jelly dipper and kept specimens in a sea table and observed them daily, until they died or until July 3rd. For the brooding females, day 0 was the day they were caught, June 20th. For larvae, day 0 was the day they hatched, because the day of fertilization was unknown.

Results: I caught two brooding females with enlarged ventral sacs on June 20th. One was more tan, and the other was bright orange. I caught a female on June 27th which had eggs inside the body in section b, but it did not have a brood sac, so I presumed it to be unfertilized. I also caught a male, with longer antennae and no sign of eggs on June 23rd. Only the females exhibited a defensive curl around the ventral region when disturbed. All epitokes swam constantly, especially under bright light. The male and unfertilized female did not show any noticeable changes over the two weeks. I tracked three groups of larvae, all from the tan female, which hatched on days 6, 7, and 8. These groups were combined for the results, because they did not show any differentiation.

The tan female released a few abortive eggs (diameter 60  $\mu\text{m}$ ) on day 5 which did not develop. On day 6, a chamber near the posterior opened, and white larvae began to spill out continuously through day 11. The female swam quickly while releasing larvae, which seemed to disperse them in the water. Section c broke off around when the brood sac began deteriorating. The female was noticeably weaker on day 8, as the sac was disintegrating, and continued to slow down and turn browner until day 12, when it died. The bright orange female began releasing a few under-developed, trochophore-like larvae on day 12, but was lost in the sea table drain on day 13, terminating the study. These premature larvae had 2 red eyes but no other noticeable features, though they may have been still encased in a fertilization envelope.

All larvae appeared similar on their day 0, which was set to each group's hatch time. At hatch, the larvae had four setigers and were developing a fifth, which did not yet have setae. They were about 800  $\mu\text{m}$ , and possessed ciliated akrotochs, prototrochs, gastrotrochs, and telotrochs. There were stereocilia on the first, asetigerous segment, and the pharynx was visible, as were six red eyes (four dorsal, two ventral). By hour 2, the fifth setiger was fully developed and the sixth had begun to form. The larvae mostly settled on the glass, especially concentrating at the water surface. The only noticeable development by hour 44 was that larvae reached 1100  $\mu\text{m}$ , with the sixth setiger still partially formed. This was the last time point recorded, because I attempted to feed the larvae brine shrimp food (Zooplankton Plus). Although they initially ate it, they all died within a few hours. I was unable to find any more study subjects, so with the initial batches of larvae dead and the second female lost down the drain, I ended my study.

Discussion: This study brings the number of *Epigamia* species studied for larval or reproductive development up to two, though more observational work is necessary to fully understand *E. magna*. A comparison to *E. alexandri* reveals that both species have similar breeding seasons (April–June), have a chambered ventral brood sac with the oldest larvae posterior, asynchronous development in the chambers, and quick settling of larvae (Qian & Chia 1989). The most striking difference is that *E. alexandri* larvae emerge as trochophores, whereas *E. magna* emerge as 4-setiger larvae. Additionally, the orange female survived in the lab for 13 days without releasing its larvae, and was already fertilized when collected, while *E. alexandri* only broods six days after fertilization (Qian & Chia 1989). *E. magna's* precocial larvae are presumably connected to body size and long brooding period, though details remain unclear.

My observations largely correspond to Strathmann's (1987) description, except I observed larger larvae (800 instead of 600  $\mu\text{m}$ ) with six red eyes, not four. Although occurrences of *E. magna* and swarming behavior peak February–June, iNaturalist shows that fertilized epitokes occur November–August. Swarms are seasonally restricted, but *E. magna* is apparently able to breed year-round except the hottest three months, and at higher latitudes the breeding season may be further extended. I also observed for the first time that *E. magna* can be found as far south as Eureka, CA. Although I only caught four specimens, I noticed that all syllids were rare during the new moon -- more work should be done to identify how lunar or tidal patterns drive *E. magna* epitoke behavior.

Both females appeared to release a few under-developed larvae just before they began releasing mature larvae. This may be a side effect of unsuccessful brooding, but some Autolytinae feed developing larvae with abortive eggs (Franke 1999), so it is possible that this was adaptive. Given that the species is epigamous, semelparous, mostly breeds February–June, it is plausible that *E. magna* has an annual life cycle, though this requires more investigation. The male and female epitokes which apparently failed to reproduce did not show any sign of deteriorating, which presents an intriguing possibility that unsuccessful epitokes can prolong their lives until another chance to breed occurs. In comparison to other members of its genus and subfamily, *E. magna* uses its large size to invest heavily in individual offspring, only releasing larvae when they are large, well-developed, and able to feed on prey items.

Although this study expands our knowledge about the reproduction of *E. magna*, many questions remain unresolved: Which cues trigger epitoke swarming? How common is it for female epitokes to be unfertilized, and is this related to the bounds of the breeding season? Why are under-developed larvae sometimes released? What does development look like inside the brood sac? Do females hold sperm for hours or days before fertilization, and if so why? These questions are just a sample of the many details that still must be elucidated to give a full picture of the reproductive strategies of this remarkable family.

## References

- Aguado MT, & San Martín G. 2009. "Phylogeny of Syllidae (Polychaeta) based on morphological data." *Zoologica Scripta* 38(4):379-402. <https://doi.org/10.1111/j.1463-6409.2008.00380.x>
- Aguado MT, San Martín G, & Siddall ME. 2012. "Systematics and evolution of syllids (Annelida, Syllidae)." *Cladistics* 28(3):234-250. <https://doi.org/10.1111/j.1096-0031.2011.00377.x>
- Berkeley E. 1923. "No. 11: Polychaetous annelids from the Nanaimo District.: Part I: Syllidae to Sigalionidae." *Contributions to Canadian Biology and Fisheries* 1a(2):203-218. <https://doi.org/10.1139/f22-011>
- Fischer A. 1999. "Reproductive and developmental phenomena in annelids: A source of exemplary research problems." *Hydrobiologia* 402:1-20. <https://doi.org/10.1023/A:1003719906378>
- Franke H-D. 1999. "Reproduction of the Syllidae (Annelida: Polychaeta)." *Hydrobiologia* 402:39-55. <https://doi.org/10.1023/A:1003732307286>
- Giese AC, & Pearse JS. 1975. *Reproduction of Marine Invertebrates: Volume III Annelids and Echiurans*. Academic Press, New York, San Francisco, and London.
- Imajima M. 1966. "The Syllidae (polychaetous annelids) from Japan (II): Autolytinae." *Publications of the Seto Marine Biological Laboratory* 14(1):27-83. <https://repository.kulib.kyoto-u.ac.jp/server/api/core/bitstreams/98a4eac9-d1cc-46b9-bc8b-211d2b1fb989/content>
- Nygren A. 2004. "Revision of Autolytinae (Syllidae: Polychaeta)." *Zootaxa* 680(1). <https://doi.org/10.11646/zootaxa.680.1.1>
- Qian P-Y, & Chia F-S. 1989. "Larval development of *Autolytus alexandri* Malmgren 1867 (Polychaeta, Syllidae)." *Invertebrate Reproduction & Development* 15(1):49-56. <https://doi.org/10.1080/07924259.1989.9672021>
- Strathmann MF. 1987. *Reproduction and Development of Marine Invertebrates of the Northern Pacific Coast*. University of Washington Press, Seattle.

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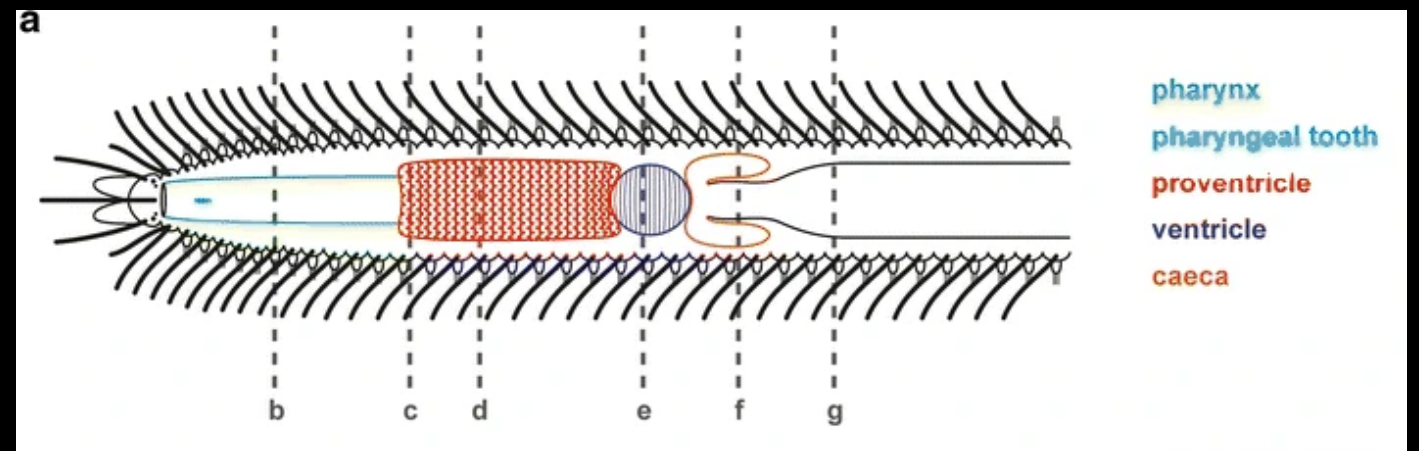
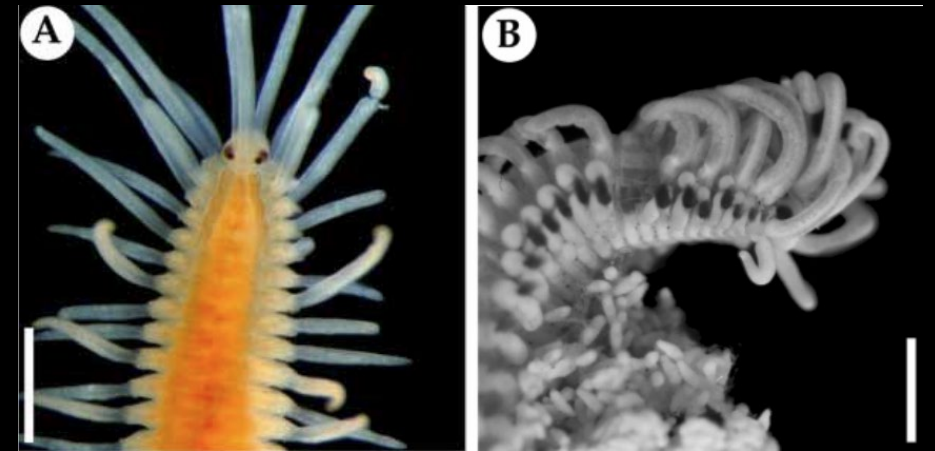
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FHL 432: Marine Invertebrate Zoology  
Dr. Megan Schwartz and Dr. Rebecca Varney, instructors  
Presented July 17<sup>th</sup>, 2025

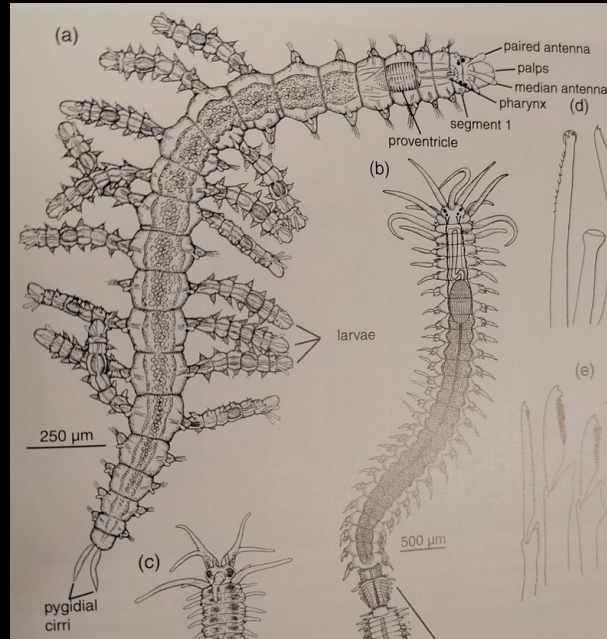


# Syllidae have diverse and specialized reproduction

- Polychaete family
  - Digestive proventricles
  - Pharyngeal armature
- Have long and cute antennae, tentacular cirri, often dorsal cirri



# Epitoky



- Widespread in Polychaeta
- Benthic adults transform into pelagic sexual form
- **DRAMATIC** alteration to tissues:
- Gametogenesis, expand sensory structures, expand swimming structures, reduce extraneous structures
- Useful for dispersal
- Keyed to lunar cycle (+diel +tidal)

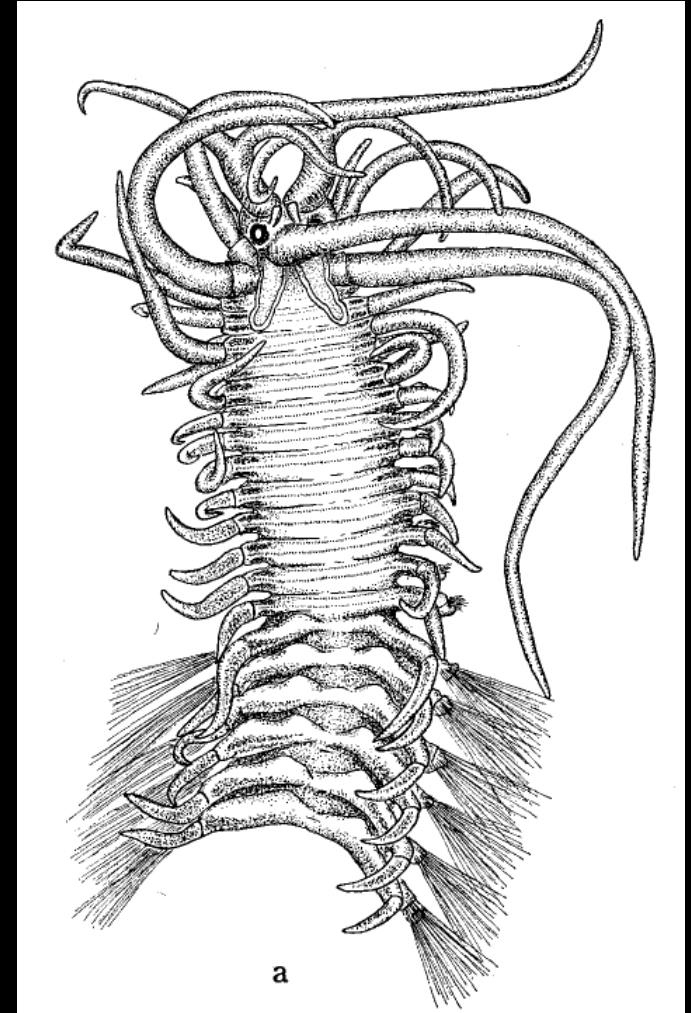


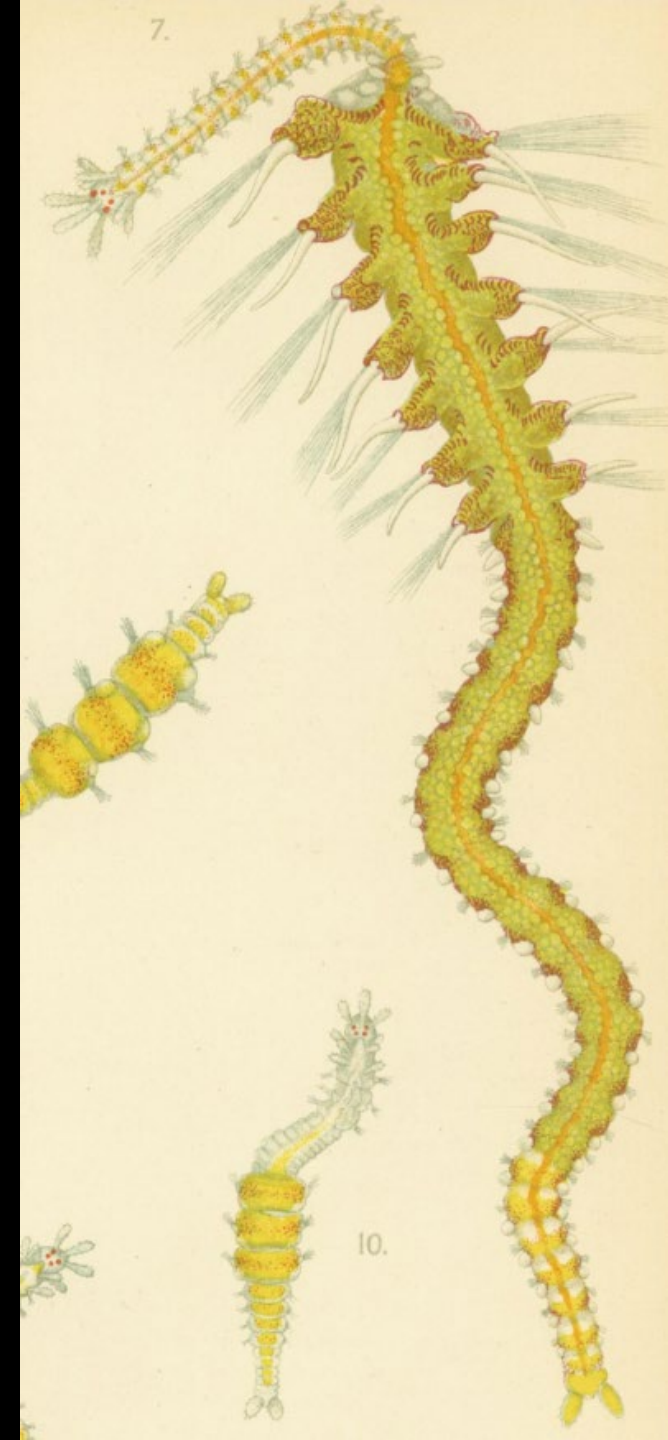
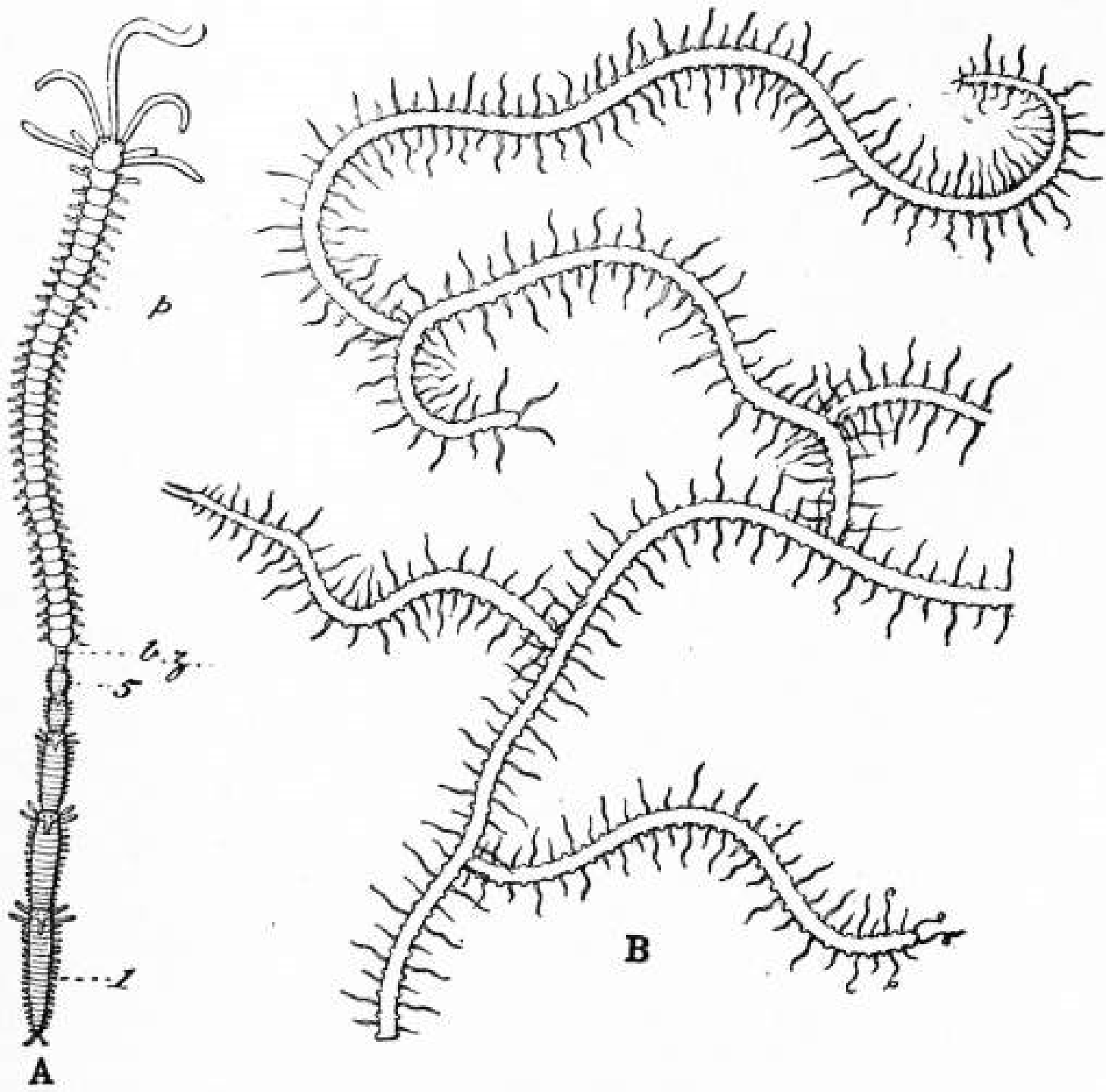
Fischer 1999, Rouse & Pleijel 2001, Aguado et al. 2012, Weidhase et al. 2016

# Schizogamy

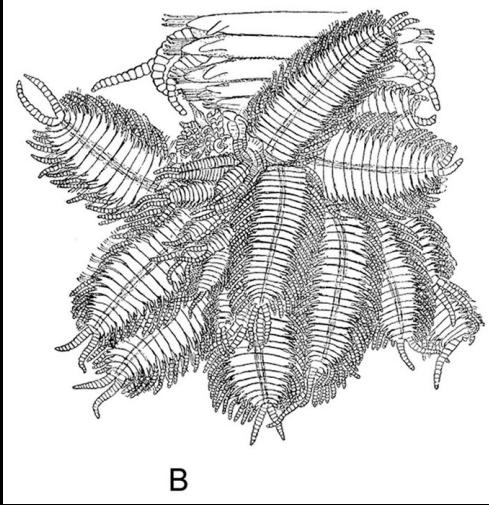


# Epigamy

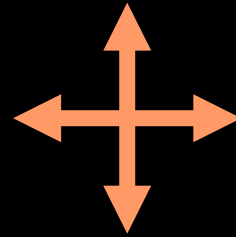
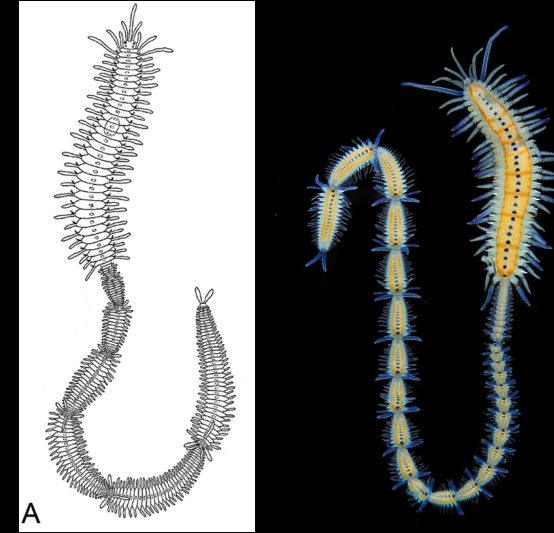




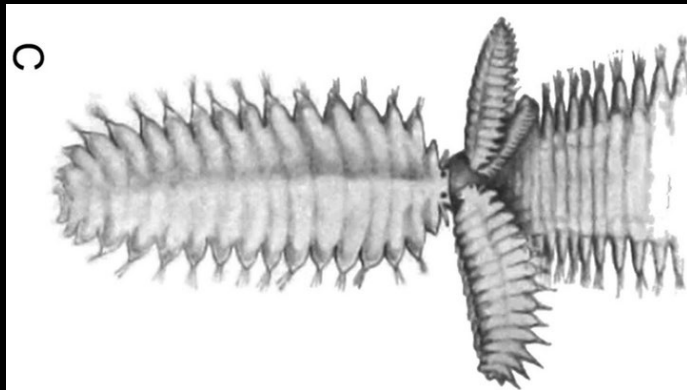
# Collateral Budding



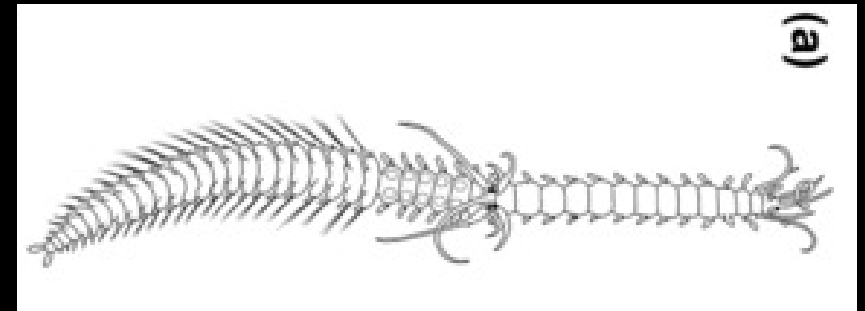
# Successive Budding



# Gemmiparous



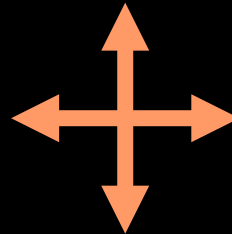
# Scissiparous



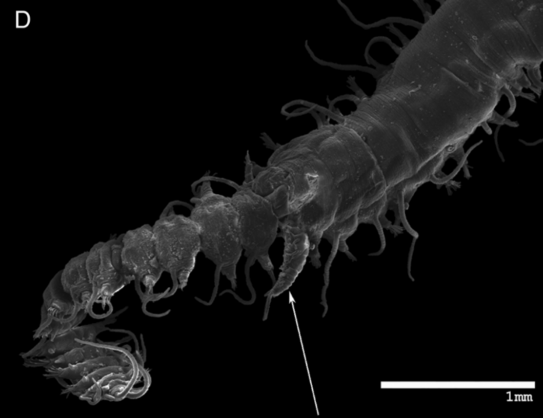
# Brood Sac



Brood on Cirri/Setae/  
Nephridial Pores



# Viviparity



Brood on Substrate

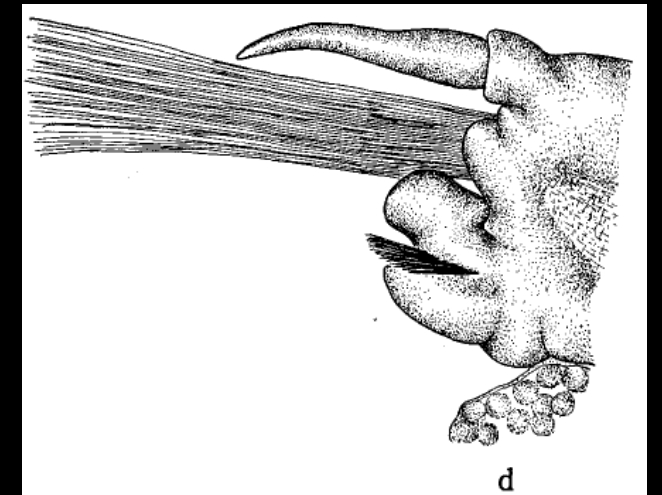
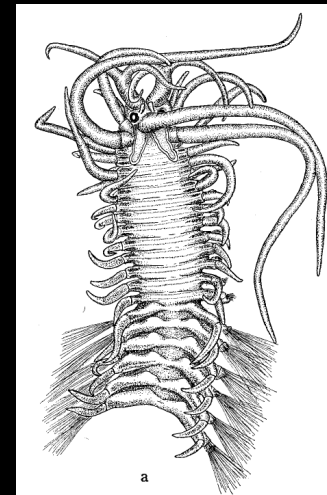
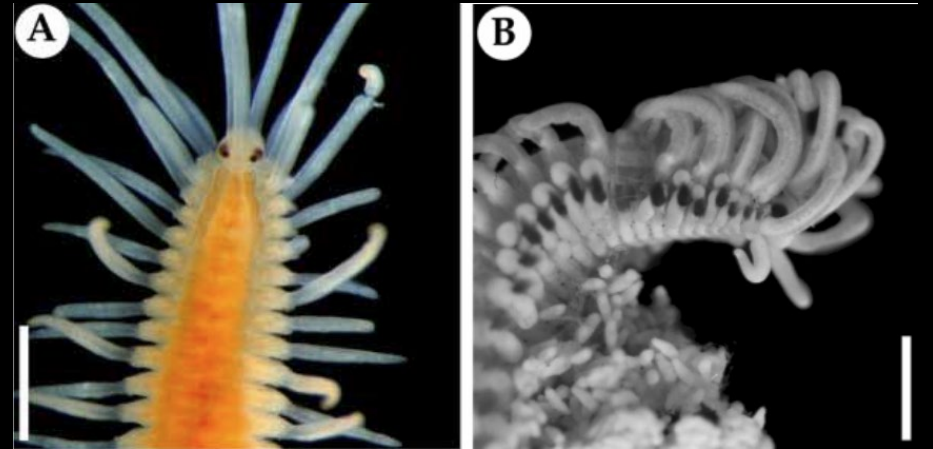


# And even more variety!

- Semelparous vs. Iteroparous
- Hermaphroditic vs. Gonochoristic vs. Parthenogenic
  - Sequential vs. Simultaneous hermaphroditism
  - Sexual dimorphism in epitokes
- Number of appendages on stolons (=schizogamous epitokes)
- Ent-aqua vs. Ect-aqua vs. Introsperm
- Co-parental care for brood
- Abortive eggs as food
- Annual, Lunar, Diel, Tidal cycle coordination

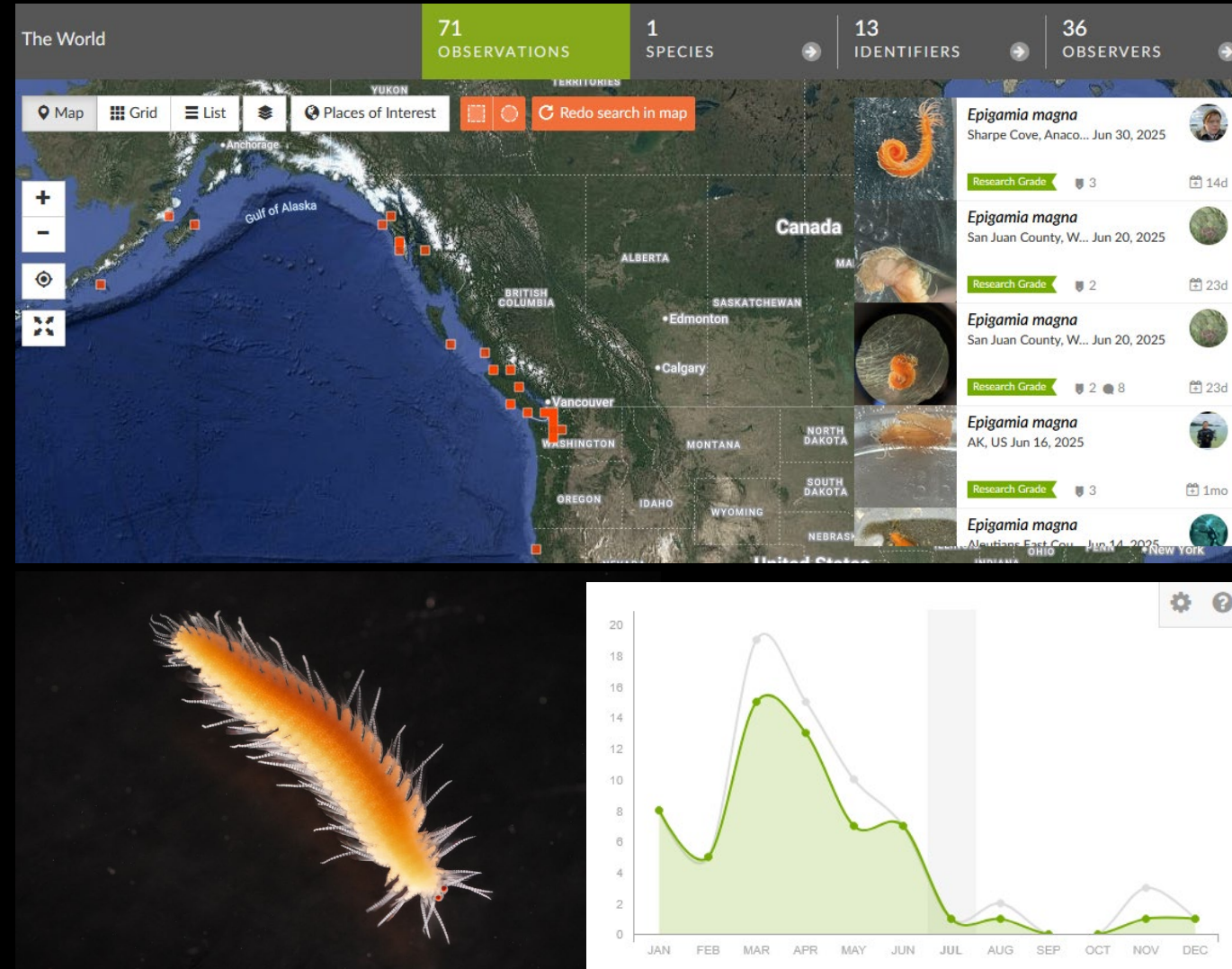
# *Epigamia magna* (Berkeley, 1923)

- North Pacific (San Juan Islands to Shirikishinai)
- Large (epitokes up to 48 mm), orange, dorsal cirri long, dorsal part of neuropodia very developed
- Atokes littoral to 56 m, among sponges and hydroids
- Epitokes longer than atokes
  - Three body regions with 14 / 29-41 / 16-41 segments



# iNaturalist data!

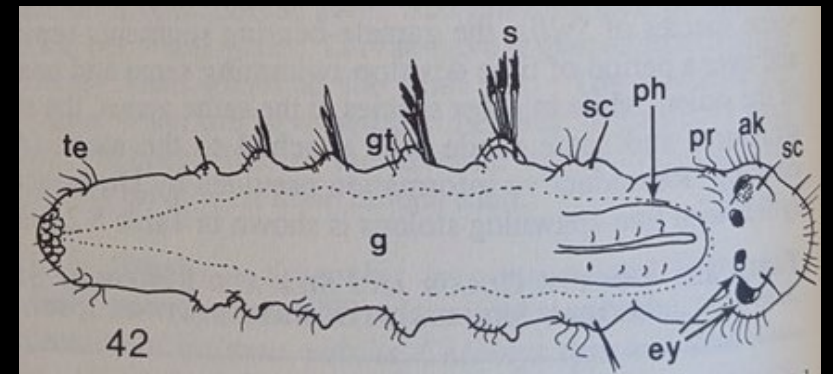
- Range larger than previously known
  - Found in Eureka, CA
- Epitokes found with brood sacs between November 17th and June 30<sup>th</sup>, until August 9<sup>th</sup> in Alaska
- Atoke found in January & November



# How do they reproduce?

- Seasonality
  - Epitokes collected in April and May in Hokkaido; February in Vancouver
- Larvae emerge from brood sac
  - 600  $\mu\text{m}$ , 4 setigers
  - Apical tufts
  - 4 red eyes
  - Prototroch, metatroch, telotroch, neurotroch, gastrotrochs
  - Developing pharynx
  - 3 compound and 1 simple setae
  - Attracted to light, glide

## Reproduction. Epigamy.

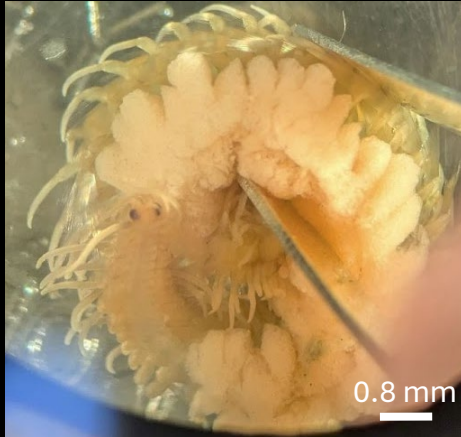


# Specimens collected by nightlighting



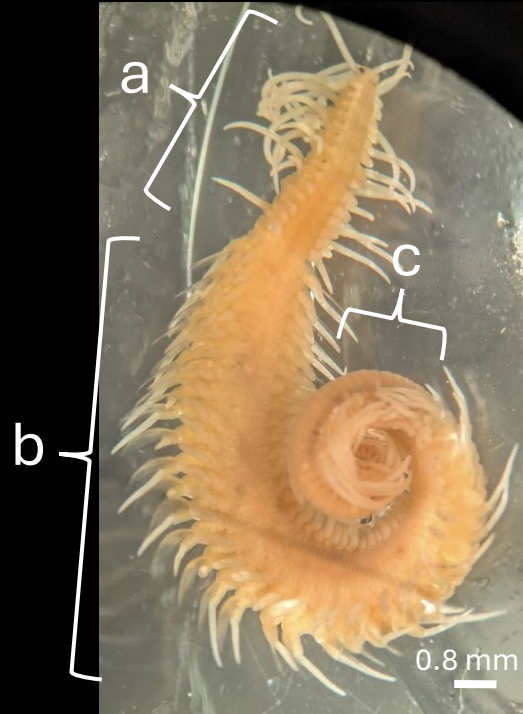
- White light for 10-30 minutes, around 11 PM
- Every night 6/20 to 7/3
- *E. magna* are distinctive, large, orange, swim slower than nereids
- Females especially awkward in swimming
- Best around high tide, with moon light

## 2 Brooding Females (2025-Jun-20)



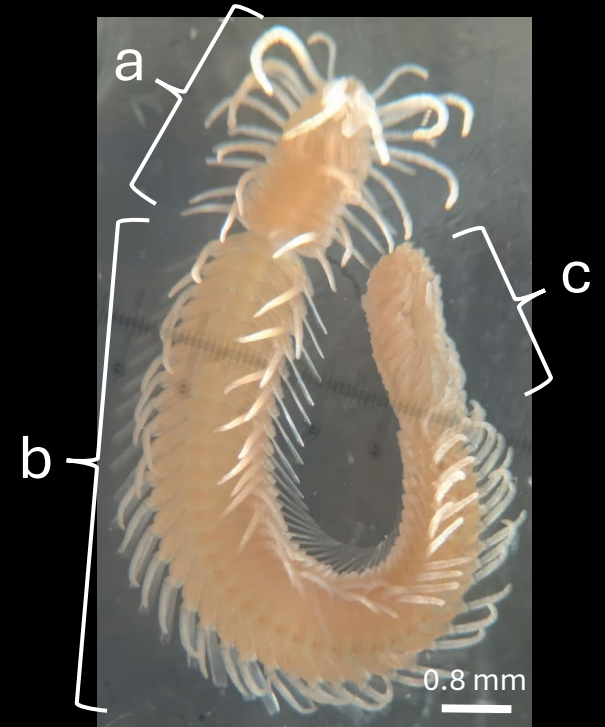
- Tan to orange ventral brood sac, chambers in section b
- Brood sac connected to parapodia, leads to much larger size and slower swimming
- Defensive curl

## Female (2025-Jun-27)



- Widened section b
- Parapodia flared outward
- Eggs visible in body
- Defensive curl

## Male (2025-Jun-23)



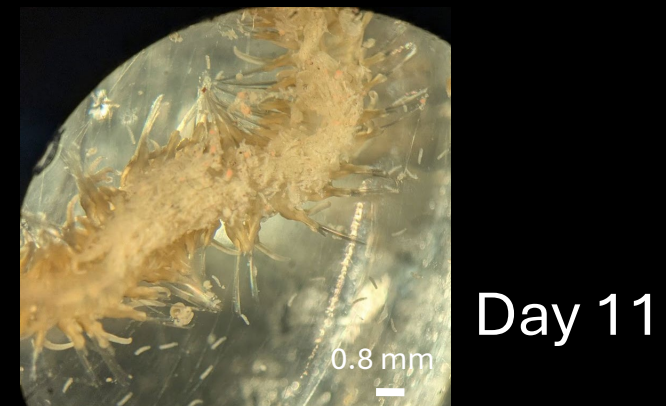
- Ventral surface concave
- Long antennae
- No defensive curl

# Epitoke development

- All epitokes showed near constant swimming behavior, especially toward light
- Male and unfertilized female showed no change over 2 weeks
- Fertilized females showed no change until brood sacs began hatching
- For tracking adult epitokes, days are measured from 2025-Jun-20 as day 0
- Fertilization date unknown, but ventral brood sacs were already developed when collected

# Female 1

- Released a few abortive eggs on day 5
- Began releasing larvae day 6
  - Swam very quickly
  - Started from the posterior-most chamber
  - Section c mostly broke off
- Weakening day 8, sac disintegrating
- Sac not pink day 9, often upside down
- Deteriorating day 11, weak and slow, last larvae released
- Dead day 12



# Female 2

- Brighter orange, coral color
- Began releasing a few under-developed, trochophore-like larvae day 12
  - Unclear if brood sac broke open
- Lost down the drain on day 13 :(



Day 3



Day 12

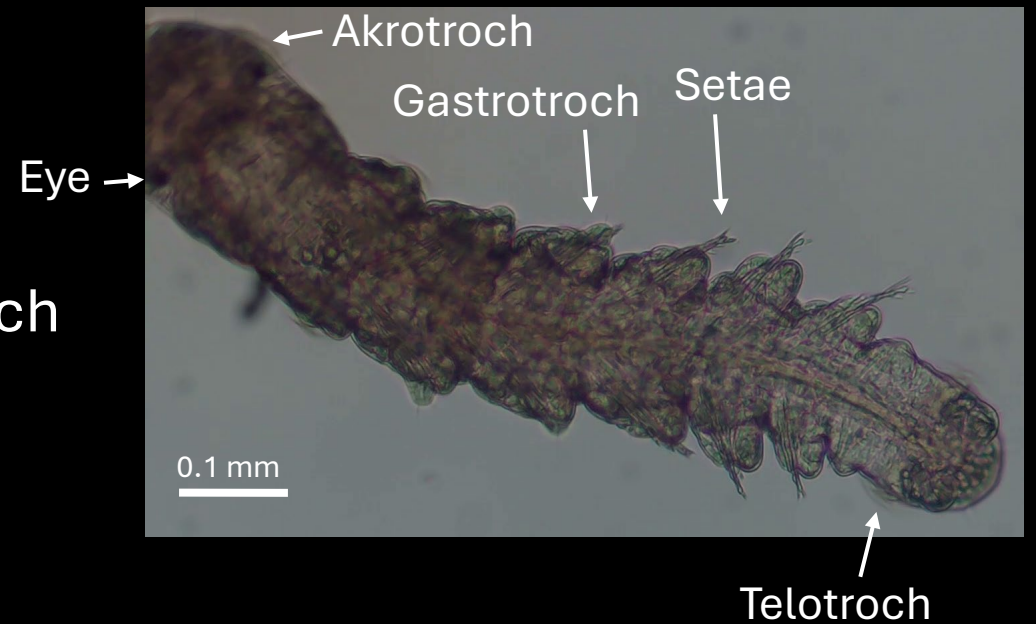
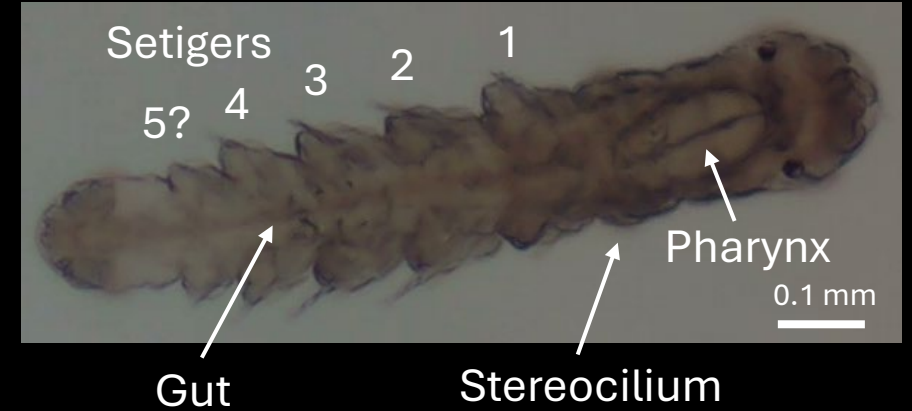
Day 12



Day 12

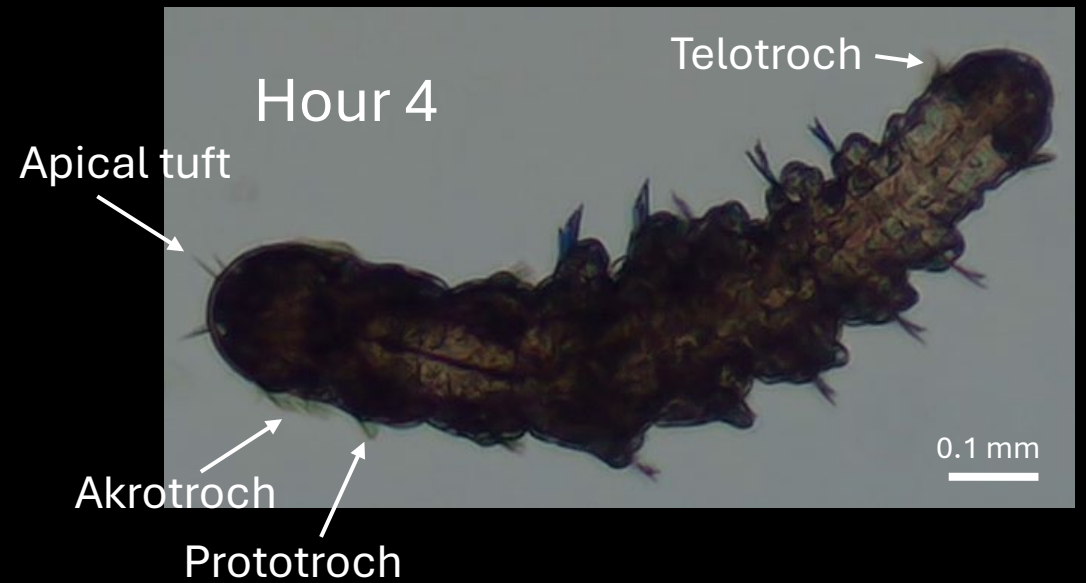
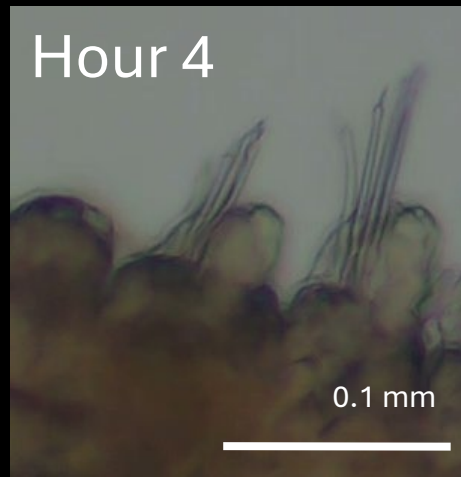
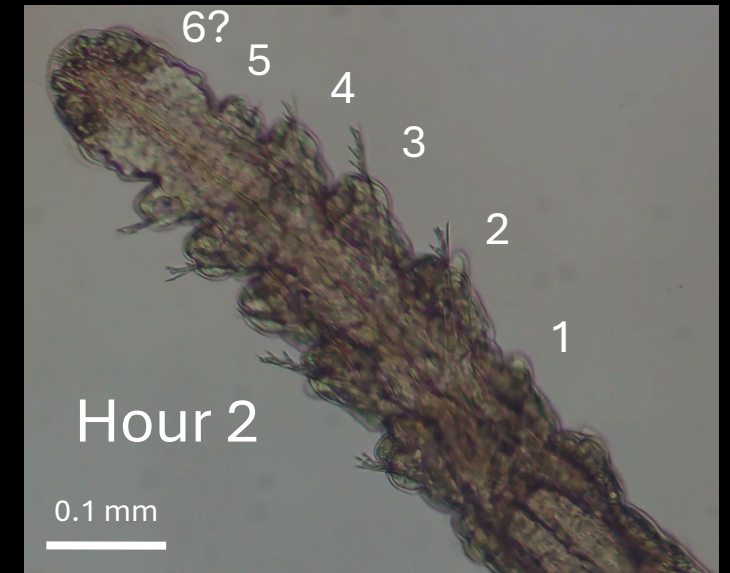
# Larval Sequence

- Combined from 3 separate hatch times
- Tracked relative to hatch time (hour 0)
- Hatch groups from days 6-8, all from female 1
- At hatch, 4 setigers and 5<sup>th</sup> developing
  - About 800  $\mu\text{m}$
  - Akrotroch, prototroch, gastrotroch, telotroch present
  - Stereocilia on first segment, pharynx developed
  - 6 red eyes (4 dorsal, 2 ventral)



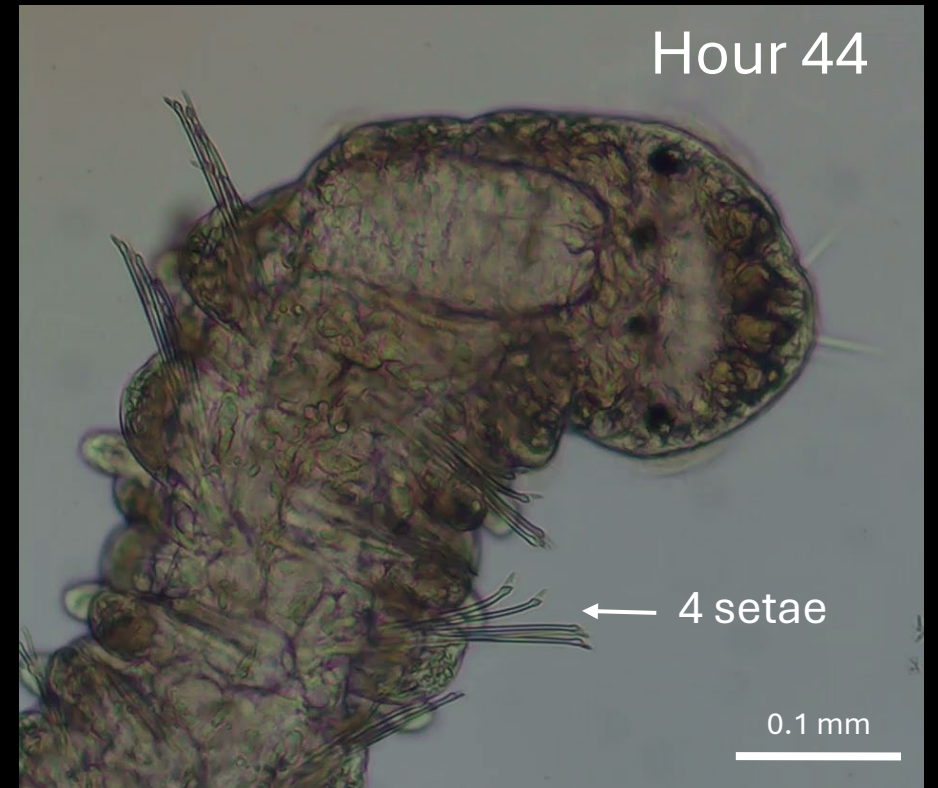
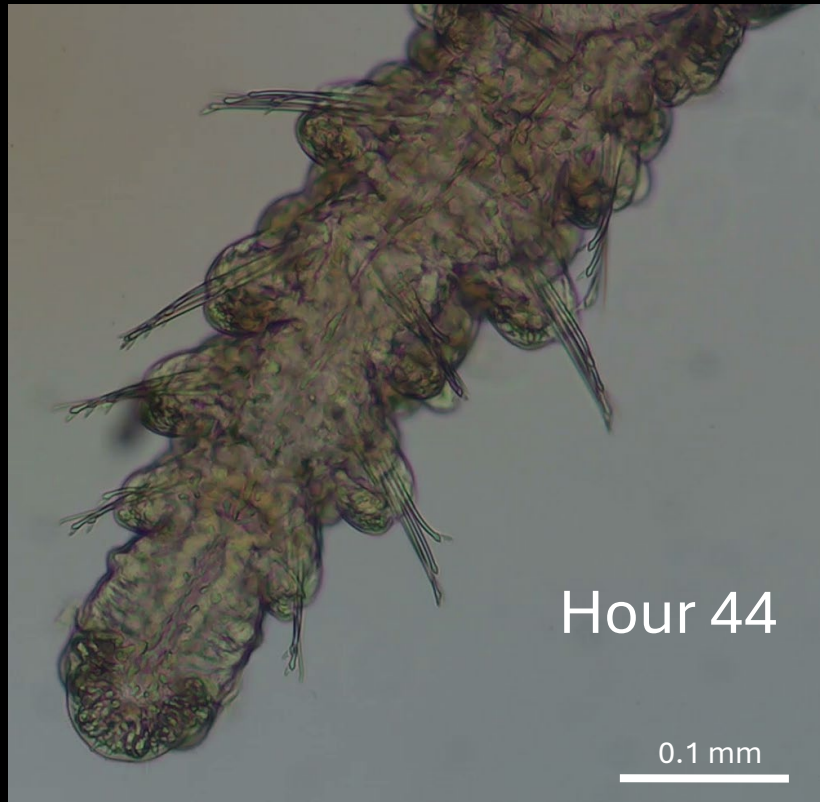
# Larval Sequence

- Hour 2, 5<sup>th</sup> setiger complete, 6<sup>th</sup> forming
- Cilia, setae, and eyes nicely visible
- Mostly settled on the glass dish and glided



# Larval Sequence

- Minimal change until Hour 44
- 1100  $\mu\text{m}$

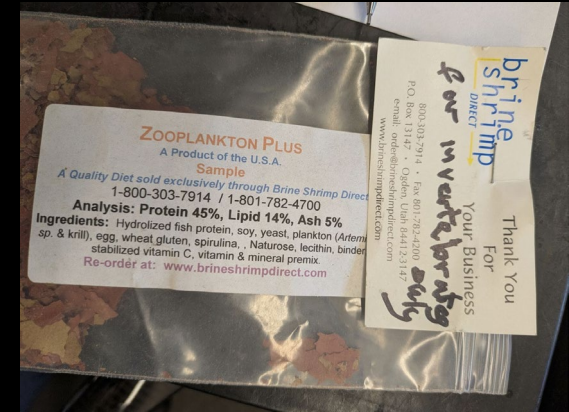


# Uh-oh... An Abrupt End to the Study

- Tried feeding them slurried brine shrimp food (based on Strathmann)
- Initially the larvae ate happily
- Within a few hours most movement stopped, many seemed deformed
- Soon all dead
- Find better food next time



(temporarily) happy larvae



hydrolyzed fish protein  
of doom



# Comparison to *Epigamia alexandri*

- Breeds April-June
- Chambered ventral brood sac
- Female can hold sperm internally for several days
- Asynchronous between chambers
- Trochophore larvae hatch from sac 6 days after fertilization
- 1-2 setiger at day 10

- 4-5 setiger larvae hatch an unknown time after fertilization, at least 14 days
  - Very precocial



# What have we learned about *E. magna*?

- Brooding period up to 14 days, potentially longer
- Larval release over 5 days, female dies immediately after
- 5<sup>th</sup> setiger forms in 2 hours, 6<sup>th</sup> setiger takes >44 hours
- Bigger than Strathmann describes, 6 larval eyes
- Breeding peaks March-June, but can be found November-August
- Range extends to far northern California
- Epitokes do not surface around a new moon



# Broader implications for *E. magna*

- Epigamous, semelparous, breed spring to early summer
  - Likely an annual life cycle
- Lifespan of epitokes that fail to spawn is apparently prolonged
- Breeding season likely shows latitudinal trend
- Long brooding and large body size allows females to invest in thousands of well-developed 4-setiger larvae
  - Much larger larvae than congeners or most Syllidae, even viviparous ones



# Open Questions

- Why were brooding epitokes swimming at night? Is swarming tied to lighting or to tides?
- How did I get an unfertilized female? Was it just unlucky and emerged at the very end of the breeding season?
- Why didn't the male and unfertilized female mate?
- Why are under-developed larvae sometimes released?
- What does development look like inside the brood sac? Are the posterior chambers actually oldest?

# Citations

Aguado MT, & San Martín G. 2009. "Phylogeny of Syllidae (Polychaeta) based on morphological data." *Zoologica Scripta* 38(4):379-402. <https://doi.org/10.1111/j.1463-6409.2008.00380.x>

Aguado MT, San Martín G, & Siddall ME. 2012. "Systematics and evolution of syllids (Annelida, Syllidae)." *Cladistics* 28(3):234-250. <https://doi.org/10.1111/j.1096-0031.2011.00377.x>

Berkeley E. 1923. "No. 11: Polychaetous annelids from the Nanaimo District.: Part I: Syllidae to Sigalionidae." *Contributions to Canadian Biology and Fisheries* 1a(2):203-218. <https://doi.org/10.1139/f22-011>

Fischer A. 1999. "Reproductive and developmental phenomena in annelids: A source of exemplary research problems." *Hydrobiologia* 402:1-20. <https://doi.org/10.1023/A:1003719906378>

Franke H-D. 1999. "Reproduction of the Syllidae (Annelida: Polychaeta)." *Hydrobiologia* 402:39-55. <https://doi.org/10.1023/A:1003732307286>

Giese AC, & Pearse JS. 1975. *Reproduction of Marine Invertebrates: Volume III Annelids and Echiurans*. Academic Press, New York, San Francisco, and London.

Imajima M. 1966. "The Syllidae (polychaetous annelids) from Japan (II): Autolytinae." *Publications of the Seto Marine Biological Laboratory* 14(1):27-83. <https://repository.kulib.kyoto-u.ac.jp/server/api/core/bitstreams/98a4eac9-d1cc-46b9-bc8b-211d2b1fb989/content>

Nygren A. 2004. "Revision of Autolytinae (Syllidae: Polychaeta)." *Zootaxa* 680(1). <https://doi.org/10.11646/zootaxa.680.1.1>

Qian P-Y, & Chia F-S. 1989. "Larval development of *Autolytus alexandri* Malmgren 1867 (Polychaeta, Syllidae)." *Invertebrate Reproduction & Development* 15(1):49-56. <https://doi.org/10.1080/07924259.1989.9672021>

Schiedges K-L. 1979. "Reproductive biology and ontogenesis in the polychaete genus *Autolytus* (Annelida: Syllida): Observations on laboratory-cultured individuals." *Marine Biology* 54:239-250. <https://doi.org/10.1007/BF00395786>

Strathmann MF. 1987. *Reproduction and Development of Marine Invertebrates of the Northern Pacific Coast*. University of Washington Press, Seattle.