Bivalves, brachiopods, and gastropods, oh my: three investigations into the morphology, physiology, and taphonomy of shelled invertebrates near Friday Harbor Laboratories, Washington, USA

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Marine Invertebrate Zoology
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Keywords: micro-CT, *Terebratalia transversa*, turbidity, live-dead analysis

Abstract:

I completed three research projects as part of the Summer 2025 Marine Invertebrate Zoology course. First, generating (to my knowledge) the first contrast-enhanced scan of a brachiopod, *Terebratalia transversa*, to visualize soft tissues. The specimens were stained in 1.75% Lugol's iodine in Sorensen's buffer for 48 hours, allowing for visualization of structures such as the lophophore, gonads, digestive tract, and shell adductor and abductor muscles. Second, I conducted an experiment investigating filter feeding rates in the brachiopod *Terebratalia transversa* and the bivalve *Mytilus edulis* under turbid conditions. Preliminary results suggest that both brachiopods and bivalves engage in particle sorting during filter feeding and that *Mytilus* is more effective at removing particles from suspension, although the latter finding was not statistically significant. Finally, I compared and analyzed a living and dead assemblage from a dredge sample taken from a shell gravel in San Juan Channel. I found that rank correlation between the live and dead assemblages was weak, but Chao-Jaccard similarity was high. These findings indicate that the death assemblage in this sample has high fidelity with respect to species diversity, but low fidelity with respect to relative abundance. The disagreement in rank abundance appears to be largely driven by rapid destruction of shells from thin-shelled gastropods such as *Calyptraea fastigiata*, *Crepidula perforans*, and *Hipponix cranioides*.

Project 1: microCT scanning of *Terebratalia transversa*

I CT scanned three *Terebratalia transversa* specimens using the Bruker Skyscan 1273 scanner at Friday Harbor Laboratories. The specimens were scanned twice, first at a voltage of 80 kV, tube current of 300 μA, and a voxel size of 35 μm, focusing on the hard structures (shell and brachidium). The specimens were then stained in 1.75% Lugol's iodine in Sorensen's buffer for 48 hours, then scanned again at a voltage of 130 kV, 70 μA, and voxel size of 13 μm with the goal of visualizing soft tissues. Reconstructed slices were visualized and segmented using 3D Slicer (Fedorov et al., 2012) and the SlicerMorph extension (Rolfe et al., 2021).

While other studies have CT scanned brachiopods, often to investigate the calcareous lophophore-supporting structures (e.g., Lopez Carranza and Carlson, 2019; Schreiber et al., 2014), to my knowledge this is the first time a CT scan targeting soft tissues in brachiopods has been performed. There is room for refinement in staining protocol, as some internal structures are still difficult to make out, but the lophophore, gonads, digestive tract, and adductor muscles are all visible in the scans of the stained specimens (Slides 15 and 16).

Project 2: comparison of brachiopod and bivalve filter feeding under turbid conditions

A large amount of paleontological literature has been devoted to comparing the biology of brachiopods and bivalves in an attempt to understand the factors controlling the relative dominance of these two groups in marine ecosystems over time. Prior to the end-Permian mass extinction, brachiopods were the dominant group occupying benthic, sessile, suspension-feeding niches. Following the end-Permian mass extinction, from the Mesozoic Era to the Recent, bivalves have been far more successful and have expanded to occupy many of the niches previously occupied by brachiopods. There continues to be debate over whether the success of bivalves and decreased diversity of brachiopods was simply the result of differential responses to the end-Permian mass extinction (Gould and Calloway, 1980), or if brachiopods have been directly outcompeted by bivalves (Liow et al., 2015). One argument often cited in favor of the competition hypothesis is that bivalve gills are more efficient for filter feeding than the brachiopod lophophore, in part because of the ability of bivalves to dynamically select food particles by size and/or quality (Ward and Shumway, 2004). However, observations of lophophore structure and current generation suggest that brachiopods may also have particle selection mechanisms that are in fact more efficient than bivalve ctenidia under certain conditions, such as high turbidity (Thayer, 1986).

I conducted an experiment to study the rate of removal of particulate matter from the water column by brachiopods and bivalves under different turbidity conditions. I hypothesized that (1) both brachiopods and bivalves have mechanisms for particle selection/sorting, and (2) brachiopods may have higher feeding rates than bivalves under high turbidity conditions. I conducted my experiment using the species *Terebratalia transversa* (brachiopod) and *Mytilus edulis* (bivalve). Each trial was conducted by mixing a slurry of <63µm sediment particles and water with filtered water in varying ratios to create conditions of different turbidity. I did trials using a 25:1 ratio of water to sediment (high turbidity), 50:1 (mid turbidity), and no sediment (control). For each trial, ~1L of the sediment-water suspension was created, then an individual animal was placed in an aquarium tank with the suspension. Starting turbidity was recorded by taking a photograph of a black and white camera calibration grid placed behind the aquarium. I allowed the animal to filter feed for 30 minutes, then removed the animal and recorded turbidity via photograph once more. Turbidity was measured from the photographs using the histogram function in Fiji (Schindelin et al., 2012) to extract the modal intensity within a single white square of the calibration grid. Statistical analysis was conducted in R (v. 4.5.0).

Qualitatively, I observed active sorting and rejection of particles in both taxa the form of pseudofeces for *Mytilus* and mucus streamers for *Terebratalia* (slide 19). These findings are consistent with Rhodes and Thayer (1991), who also report formation of mucus streamers by brachiopods in turbid suspensions. My quantitative results suggest that *Mytilus* may be more effective at removing particulate matter from the water column than *Terebratalia* at high turbidity levels (Slide 20; Table 1). However, this difference is not statistically significant (two tailed t-test p-value = 0.26). This is likely due to limited sample size (only three replicates) and the limited resolution of my method for measuring turbidity. Future experiments would benefit from more precise measurements of suspended particles using a particle counter or spectrophotometer, rather than a visual estimate which is less sensitive to small changes in turbidity and is easily affected by lighting and camera settings.

Project 3: live-dead analysis of a dredge sample from San Juan Channel

I conducted analysis of living and dead shell assemblages from a dredge sample taken in San Juan Channel near Lopez Island (48°29.431'N, 122°56.916'W to 48°29.281'N, 122°56.957'W; 57-62m depth). The sample consisted of shell gravel and was collected by rock dredge. The live assemblage of bivalves, shelled gastropods, and brachiopods consisted of 21 species and 184 individuals, while the death assemblage consisted of 34 species and 760 individual shells. There were 14 species found in both the live and dead assemblages, for a total of 41 species and 944 individuals and shells (Table 2). The analyses reported here use the raw counts of bivalve valve abundance in the death assemblage. Dividing the number of bivalve valves by 2 (to account for each individual producing 2 valves) did not significantly affect rank abundances or similarity index results (Slide 37). By far the most abundant species was *Pododesmus macrochisma*, with 23 live individuals and 437 dead valves. 88 *Pododesmus* valves (~20%) had obvious drill holes.

Rank correlation between the live and dead assemblages was weak (Spearman's rho = 0.2721, p=0.085), largely driven by underrepresentation of thin-shelled, limpet-like gastropods that attach to dead shells, e.g., *Calyptraea fastigiata*, *Crepidula perforans*, and *Hipponix cranioides* (Slide 34). This suggests bias resulting from weaker shells being destroyed shortly after death. However, similarity, or species overlap between the live and dead assemblages was high with a Chao-Jaccard similarity index of 0.9996 (Chao et al., 2004), implemented in the fossil package in R (Vavrek, 2020). The high similarity index suggests high fidelity of the death assemblage with respect to species diversity, despite the low fidelity with respect to relative abundance. The sample used in this project has been sent to Broc Kokesh (University of California, Berkeley) to be reposited at the University of California Museum of Paleontology (UCMP).

Table 1: turbidity experiment data

Turbidity level	**Taxon**	**Starting modal intensity**	**Ending modal intensity**	**Difference (end - start)**
high	brachiopod	147	144	-3
none	bivalve	178	189	11
mid	bivalve	161	164	3
high	bivalve	141	149	8
high	brachiopod	153	163	10
mid	brachiopod	175	205	30
mid	bivalve	184	184	0
high	brachiopod	168	194	26
mid	brachiopod	202	211	9
none	bivalve	206	206	0
mid	bivalve	180	216	36
none	bivalve	205	208	3
none	brachiopod	212	213	1
none	brachiopod	198	199	1
none	brachiopod	209	205	-4
mid	brachiopod	197	201	4
high	bivalve	168	205	37
high	bivalve	157	222	65

Table 2: live-dead analysis data

Phylum	**Class**	**Species**	**No. live individuals**	**No. dead shells**
Mollusca	Bivalvia	Lyonsia californica	1	0
Mollusca	Gastropoda	Scabrotrophon lasius	1	0
Mollusca	Gastropoda	Odostomia sp.	1	0
Mollusca	Bivalvia	Ciliatocardium ciliatum	2	0
Mollusca	Gastropoda	Harfordia harfordii	2	0
Brachiopoda	Rhynchonellata	Terebratulina unguicula	4	0
Mollusca	Gastropoda	Hipponix craniodes	6	0
Mollusca	Bivalvia	Mytilus edulis?	0	1
Mollusca	Bivalvia	Parvilucina tenuisculpta	0	1
Mollusca	Bivalvia	Mya truncata	0	1
Mollusca	Gastropoda	Eulima tenisoni	0	1
Mollusca	Gastropoda	Gastropoda indet.	0	1
Mollusca	Gastropoda	Acteocina harpa?	0	1
Mollusca	Gastropoda	Ceratostoma foliatum	0	1
Mollusca	Gastropoda	Lirularia parcipicta	0	1
Mollusca	Gastropoda	Puncturella cucullata	1	1
Mollusca	Gastropoda	Diodora aspera	1	1
Mollusca	Bivalvia	Tellina carpenteri	0	2

Mollusca	Bivalvia	Thracia sp.	0	2
Mollusca	Gastropoda	Epitoniidae indet.	0	2
Mollusca	Gastropoda	Gigahomalopoma luridum	0	2
Mollusca	Gastropoda	Crepidula perforans	8	2
Mollusca	Bivalvia	Leukoma staminea	0	3
Mollusca	Gastropoda	Colus griseus	0	3
Mollusca	Bivalvia	Gari californica	0	4
Mollusca	Gastropoda	Crepidula dorsata	0	4
Mollusca	Gastropoda	Trichotropis cancellata	0	4
Mollusca	Bivalvia	Compsomyax subdiaphana	0	5
Mollusca	Gastropoda	Neptunea smirnia	5	5
Mollusca	Gastropoda	Margaritacollonia lacunata	6	5
Brachiopoda	Rhynchonellata	Terebratalia transversa	17	6
Mollusca	Bivalvia	Coanicardita ventricosa	0	10
Mollusca	Bivalvia	Protothaca tenerrima	0	11
Mollusca	Bivalvia	Chlamys hastata	1	22
Mollusca	Gastropoda	Calyptraea fastigiata	80	23
Mollusca	Bivalvia	Semele rubropicta	2	31
Mollusca	Bivalvia	Keenocardium blandum	8	31
Mollusca	Gastropoda	Cryptobranchia concentrica	8	31

Mollusca	Bivalvia	Chlamys rubida	4	52
Mollusca	Bivalvia	Humilaria kennerlyi	3	53
Mollusca	Bivalvia	Pododesmus macrochisma	23	437

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Bivalves and Brachiopods and Gastropods, oh my!

Or, why thinking like a paleontologist matters (even if you don’t study fossils)

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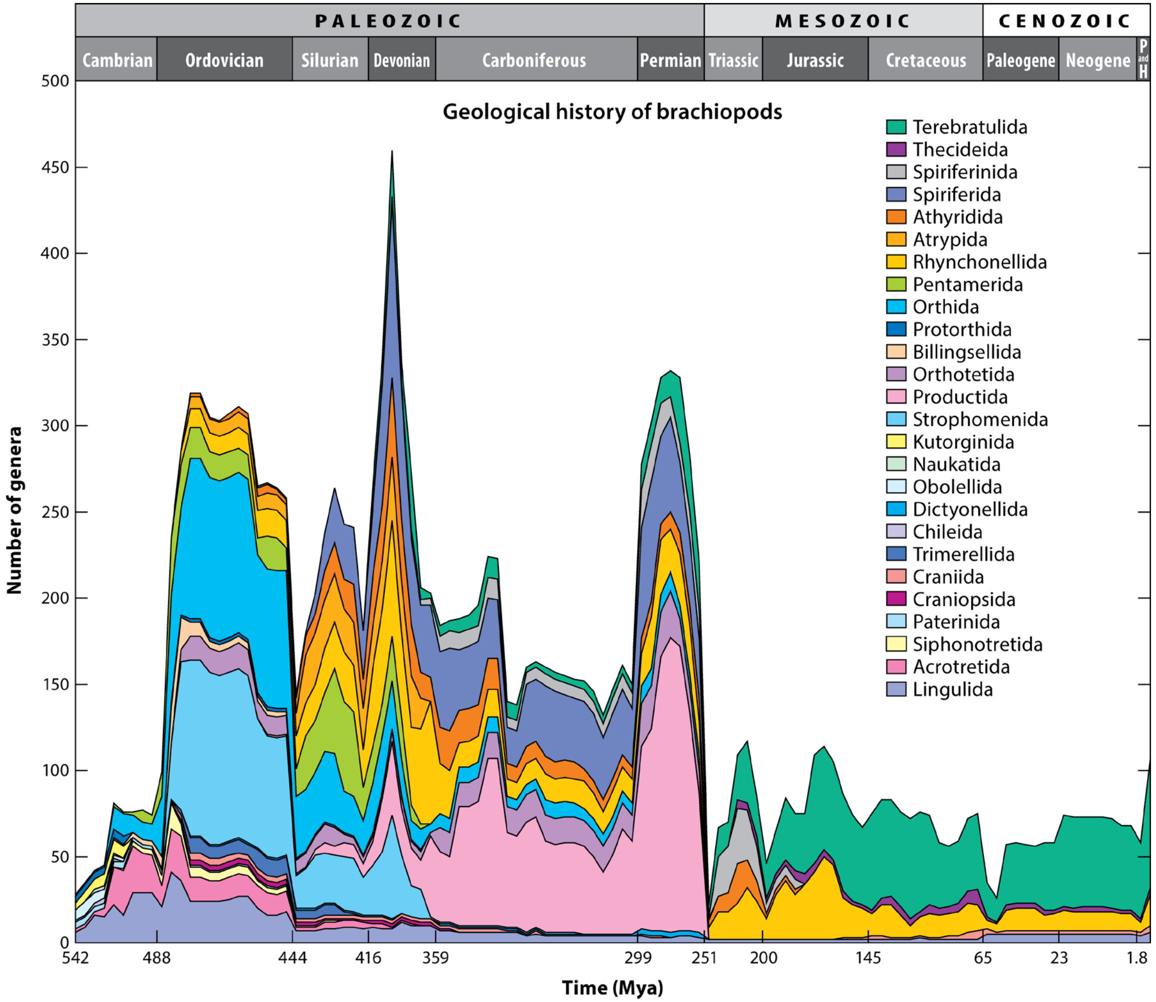
Brachiopods now

- ~400 species
- Relatively uncommon
- Largely unknown among non-paleontologists
- Mostly live in cold water, low light, low current/wave energy

Brachiopods then

- Diverse (~12,000 extinct species!)
- Over 95% of brachiopod diversity represented only in the fossil record
- Abundant
- Incredibly important group in the study of stratigraphy, evolution, diversity, ecology, and climate change in the fossil record



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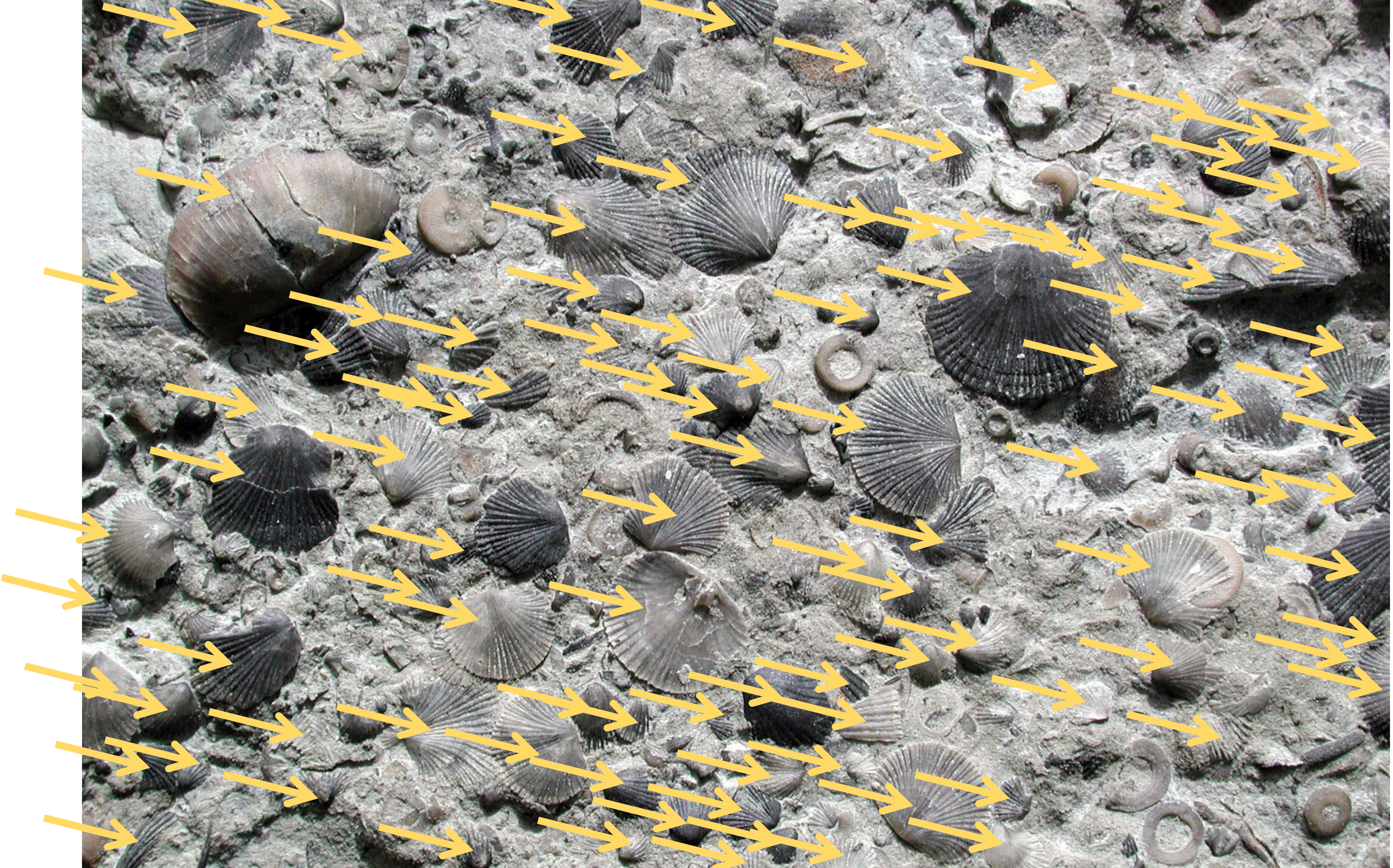
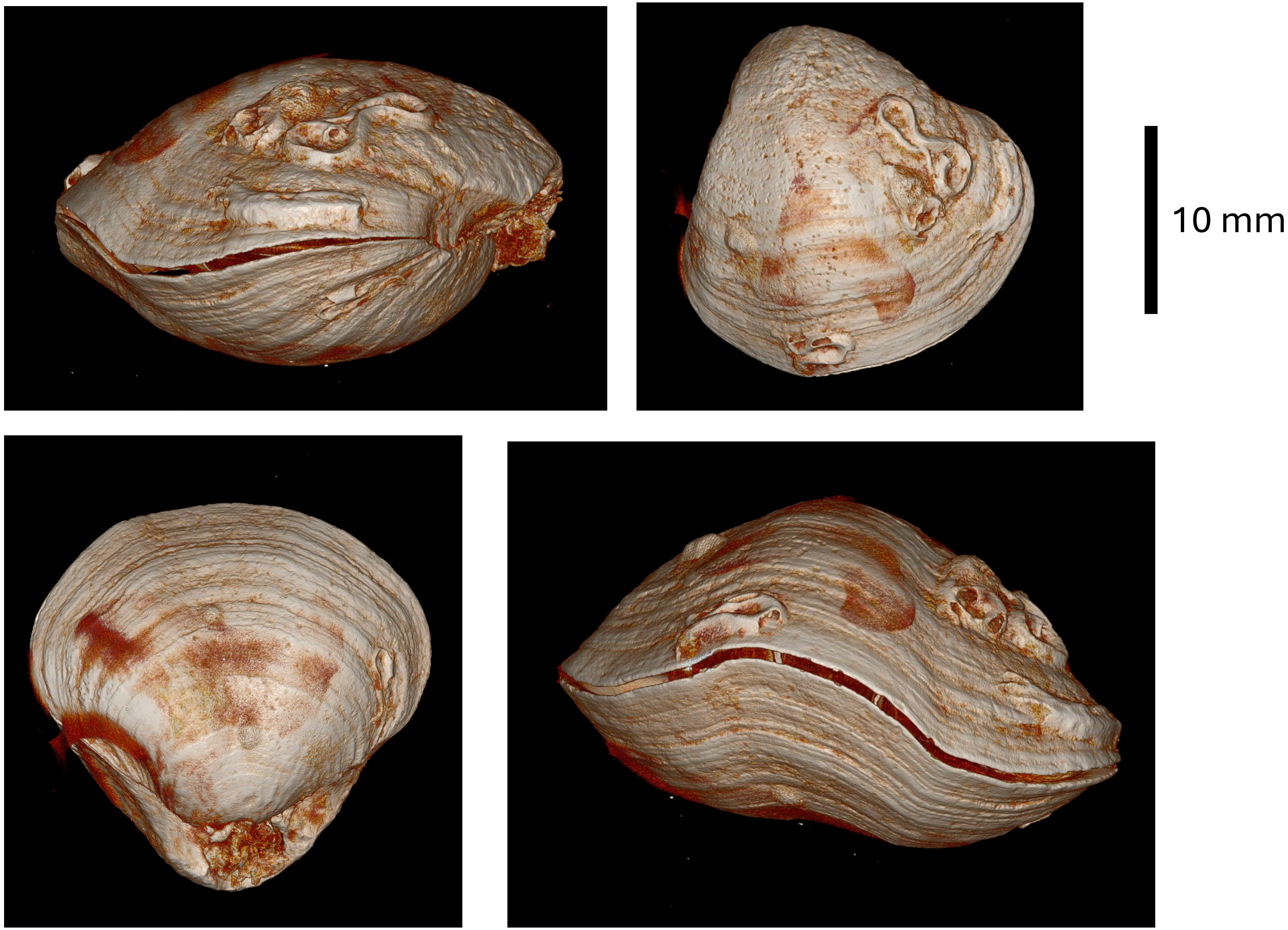


Project 1: CT scanning brachiopods

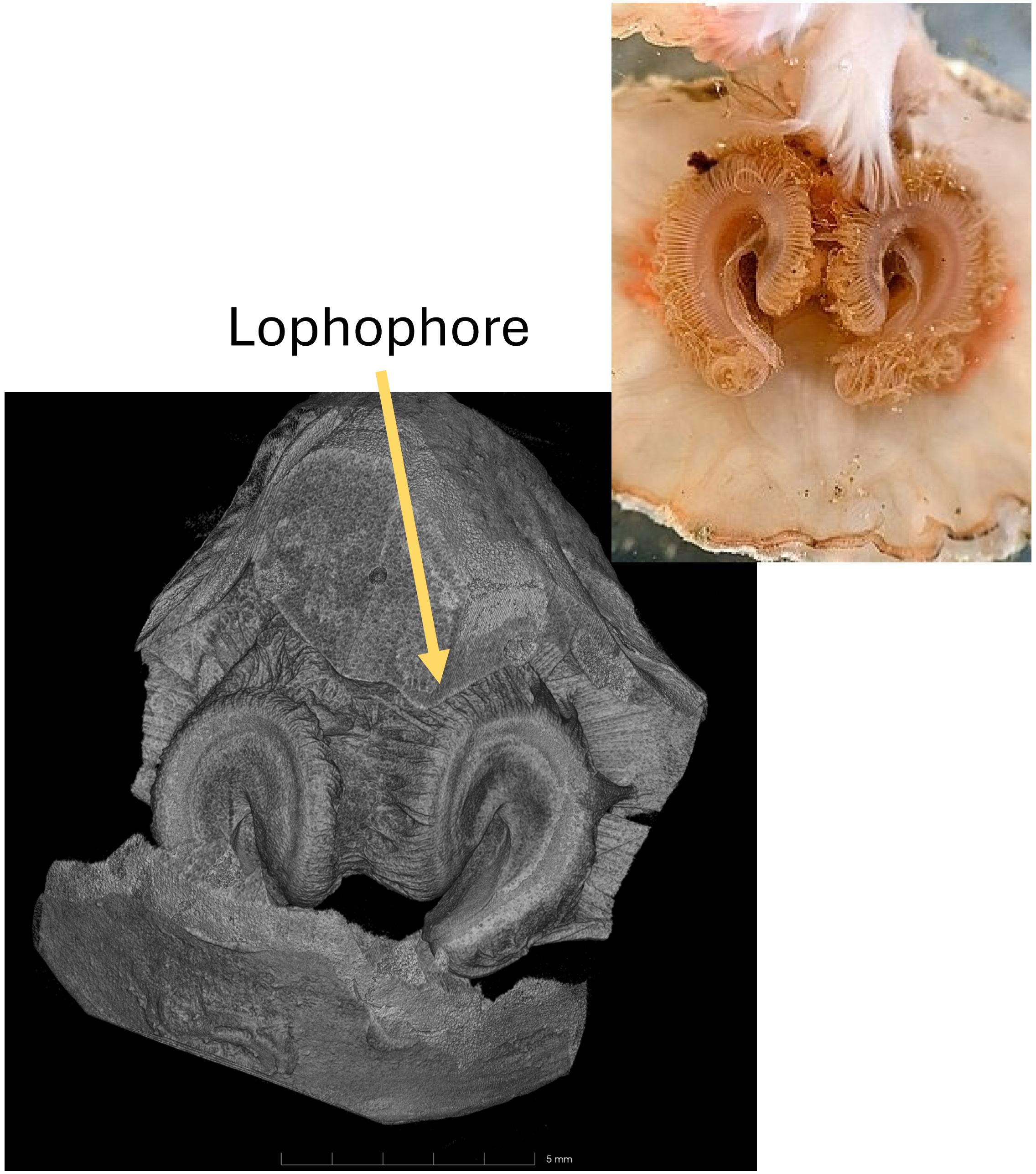


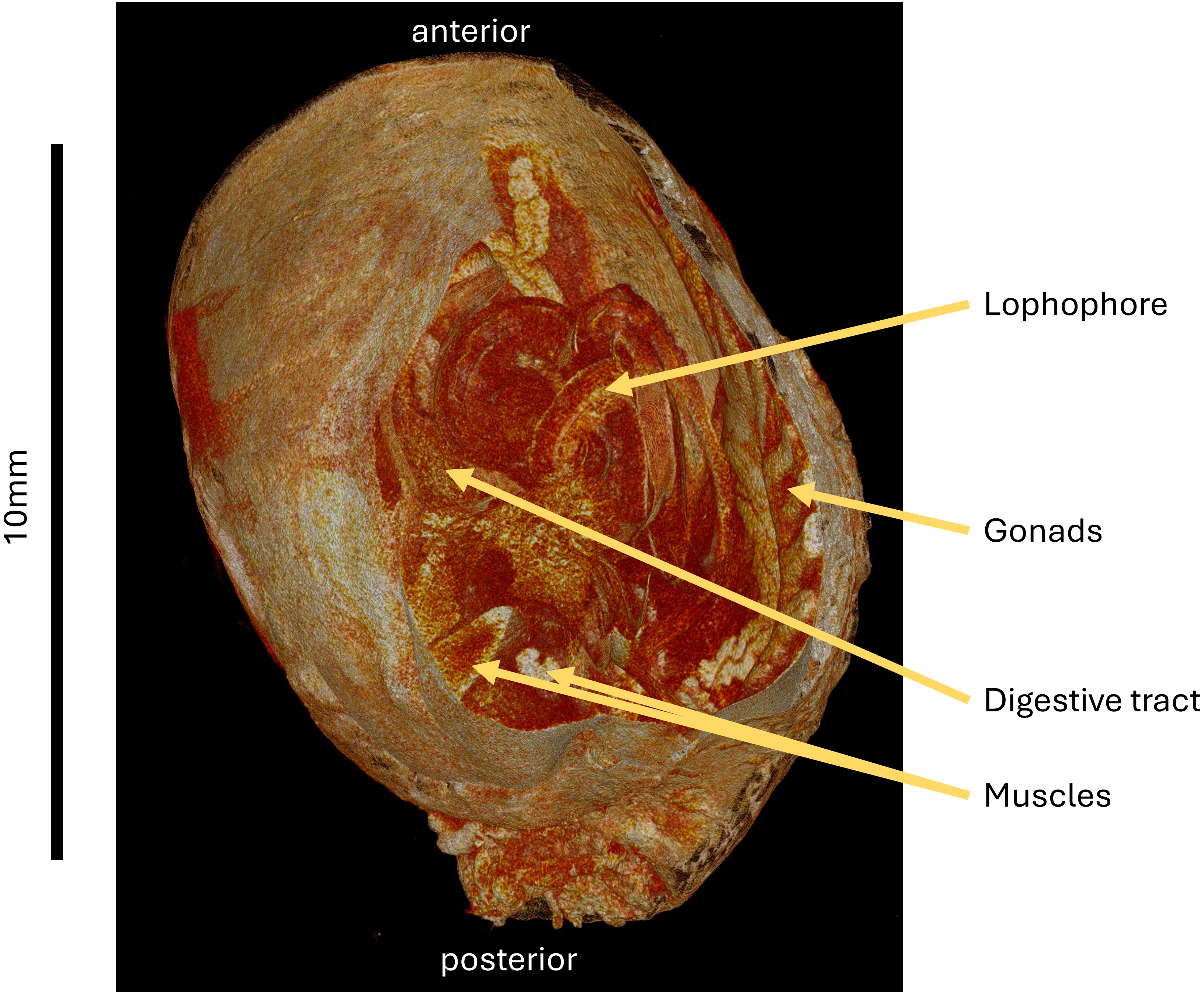
Internal anatomy

Brachidium

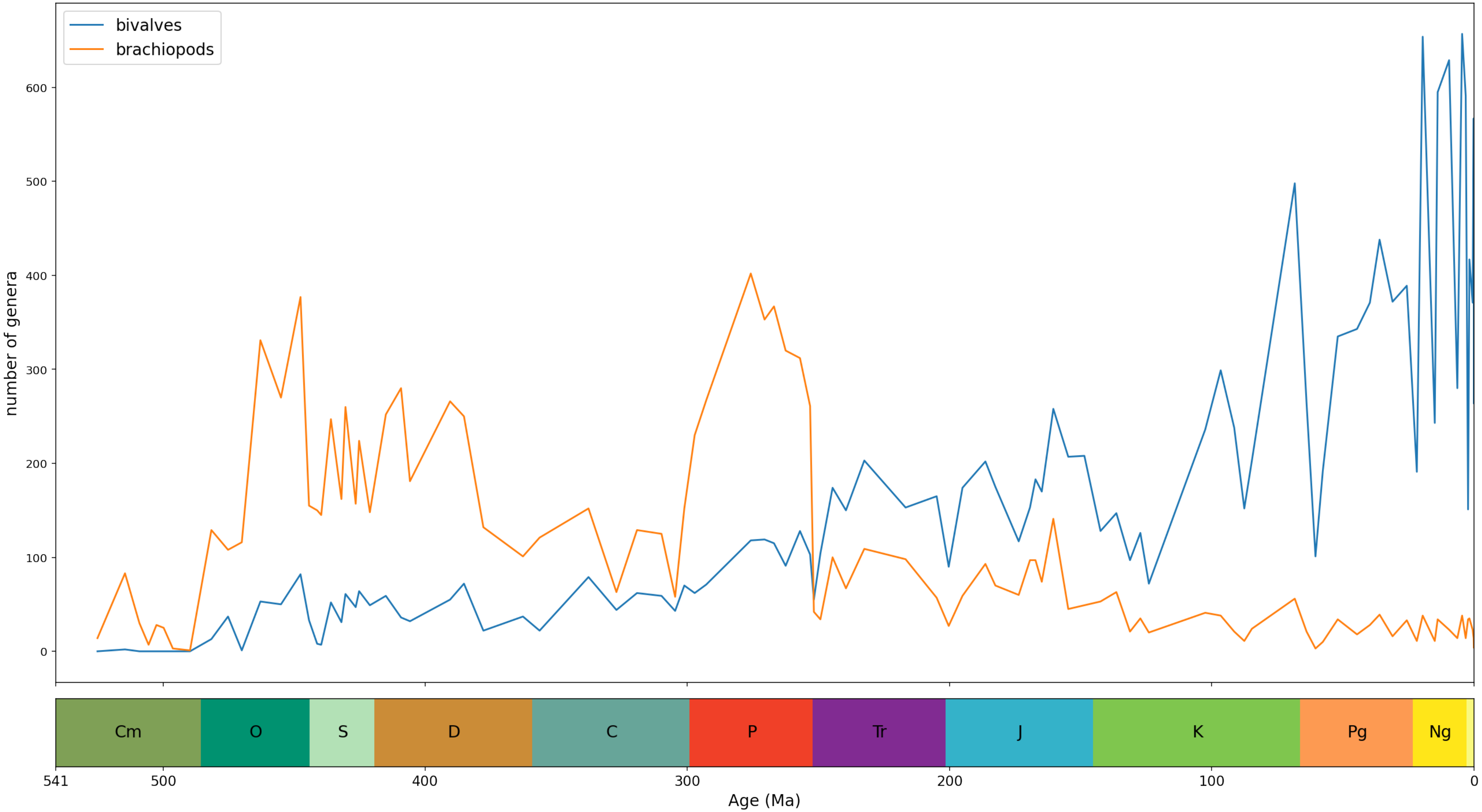
10mm

Lophophore



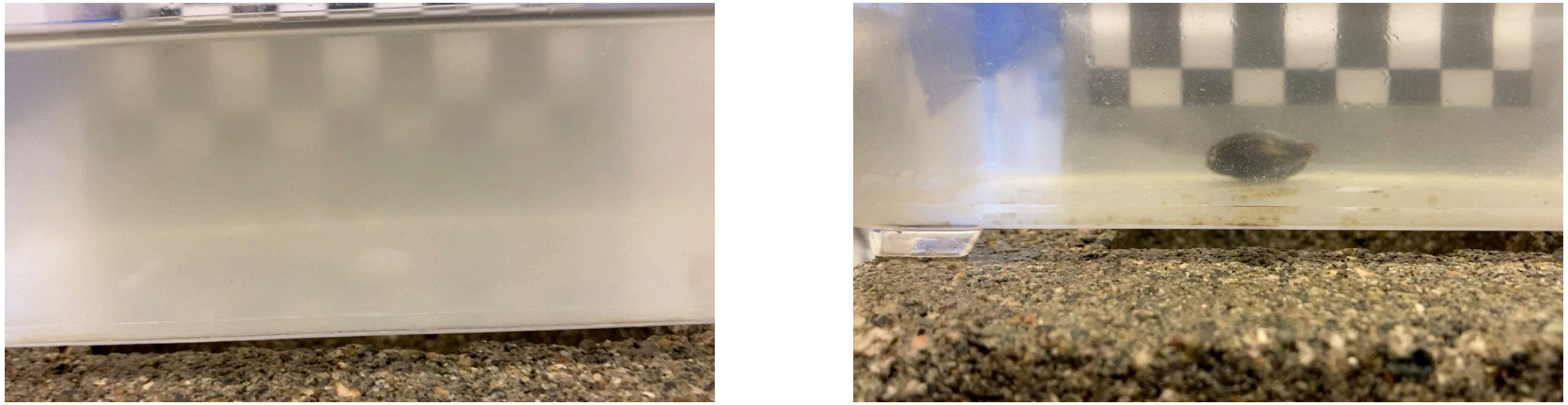

anterior
10mm
Lophophore
Gonads
Digestive tract
Muscles
posterior

Project 2: Comparing brachiopods and bivalves

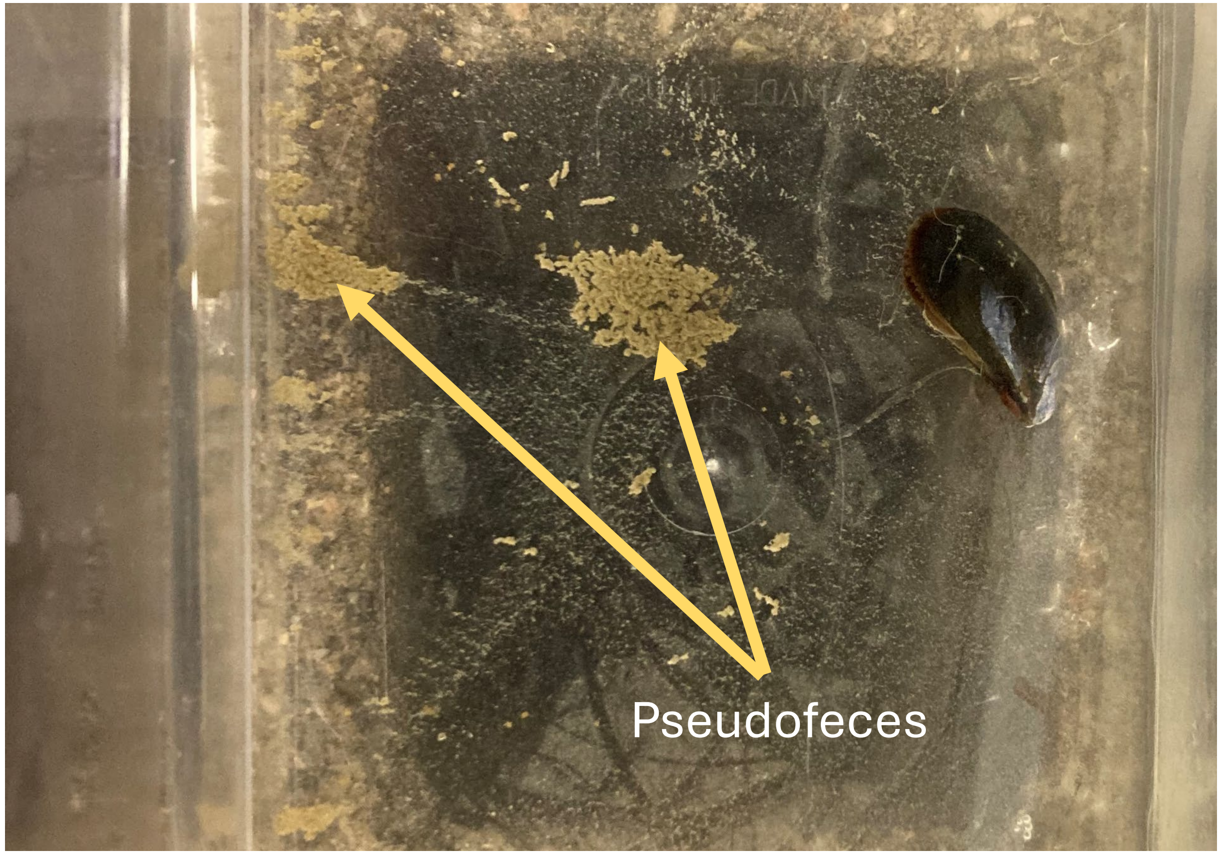


How does turbidity affect brachiopod and bivalve filter feeding?

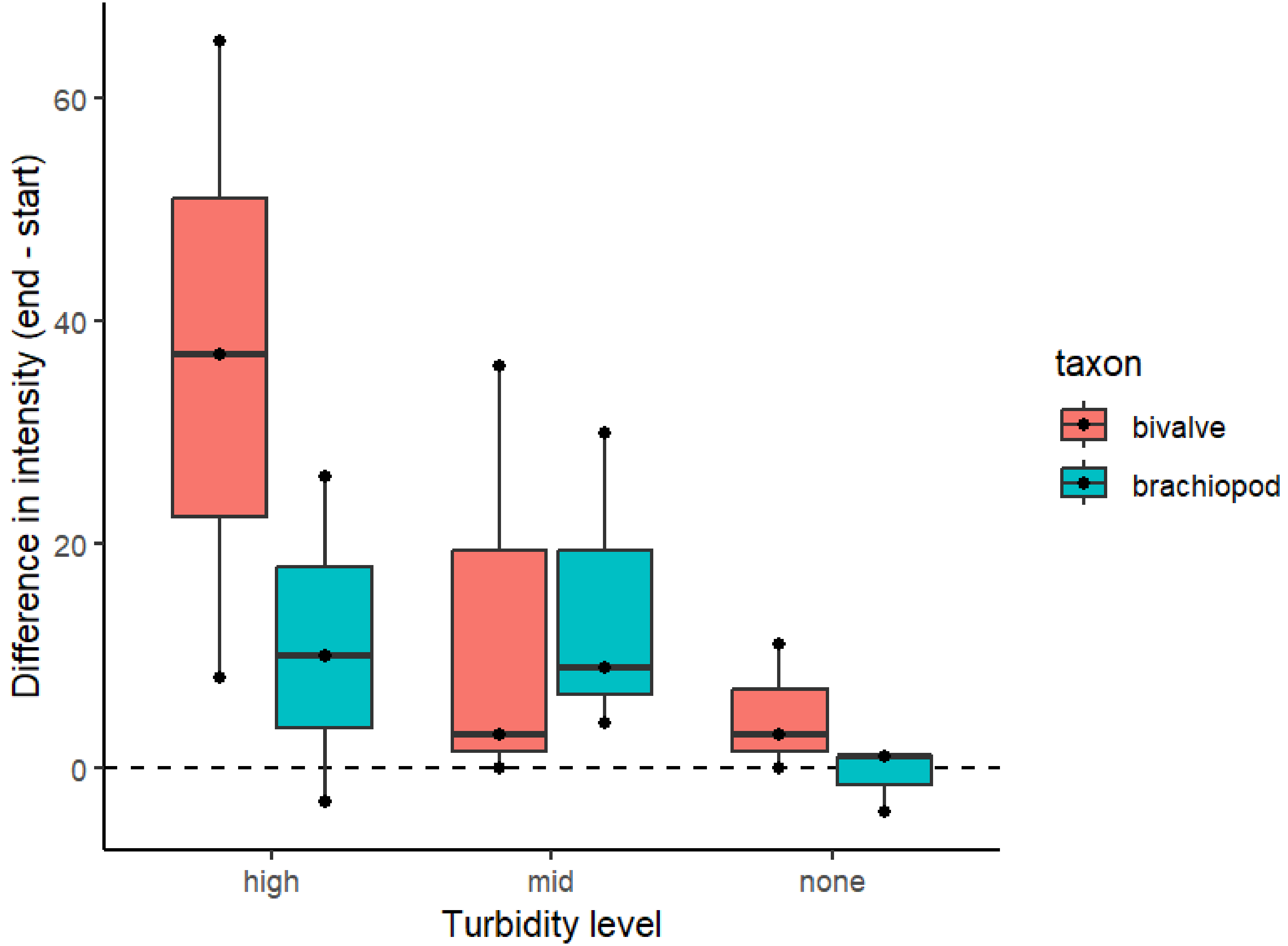
- Hypotheses:
  - Both brachiopods and bivalves have mechanisms for particle selection/sorting
  - Brachiopods may have higher feeding rates than bivalves under high turbidity conditions
- Methods:
  - Species: *Terebratalia transversa* (brachiopod) and *Mytilus edulis* (bivalve)
  - Sediment slurry (<63 μm) mixed with filtered water in ratios of 1:25 and 1:50 to create different turbidity levels
  - Control: filtered water only, no sediment
  - Single individual placed in tank w/ 1L of water/sediment mixture, allowed to feed for 30 min
  - Turbidity measured before and after each trial with a camera calibration card, intensity measurements in ImageJ



Qualitative observations



Bivalves decrease turbidity more than brachiopods



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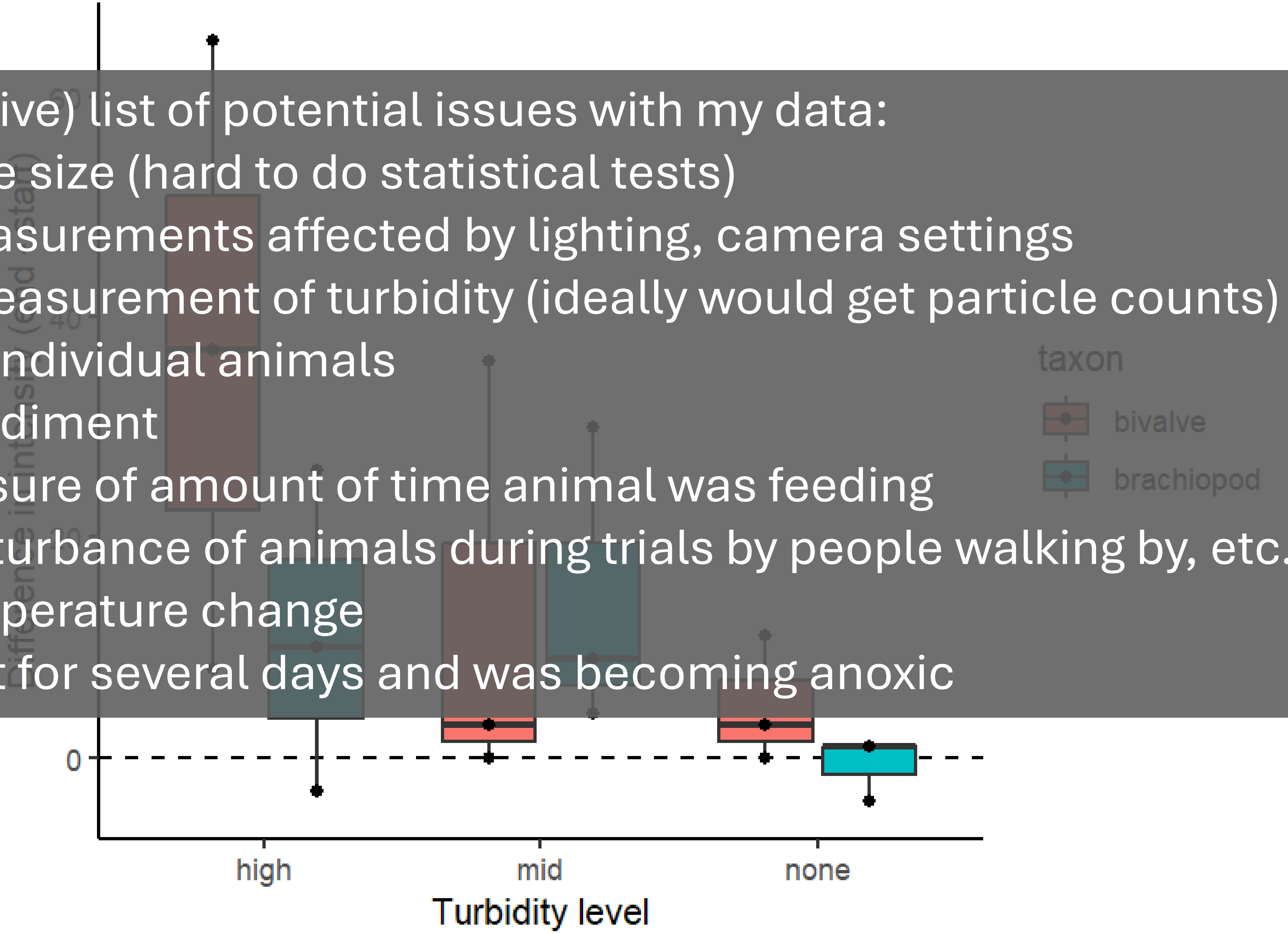

A (non-exhaustive) list of potential issues with my data:

- Small sample size (hard to do statistical tests)
- Turbidity measurements affected by lighting, camera settings
- Imprecise measurement of turbidity (ideally would get particle counts)
- Body size of individual animals
- Settling of sediment
- Inexact measure of amount of time animal was feeding
- Potential disturbance of animals during trials by people walking by, etc.
- Ambient temperature change
- Sediment sat for several days and was becoming anoxic

Project 3: live-dead assemblages

Comparing the live community with the one represented by dead shells

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Why do paleontologists care?

- Fidelity of the fossil record – how well does the fossil record capture actual living communities?
- Taphonomy – what processes affect shells before they get turned into fossils? Breakage, encrustation, etc.

Project 3: live-dead assemblages

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Why should modern biologists care?

- More complete sampling – shell assemblages can contain uncommon species that are hard to sample
- Time-averaging – communities change seasonally, annually, decadally, but shells persist!
- Changing baselines – shell assemblages can record community changes over hundreds or thousands of years

Summary stats

- Dredge taken in San Juan Channel, near Lopez Island (48°29.431’N, 122°56.916’W to 48°29.281’N, 122°56.957’W)
- Rock dredge in shell gravel
- 57-62m depth

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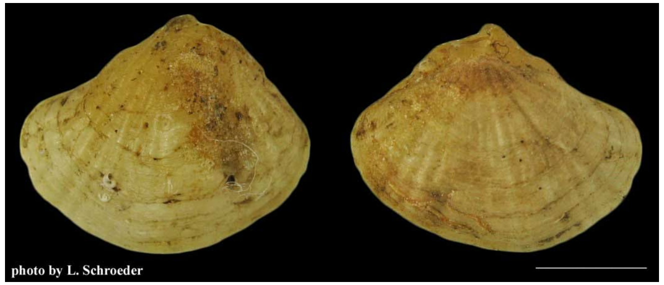
- Rock dredge in shell gravel
- 57-62m depth
- Live assemblage: 21 species, 184 individuals
- Death assemblage: 34 species, 760 shells
- **Total: 41 species (14 in common), 944 individuals + shells**

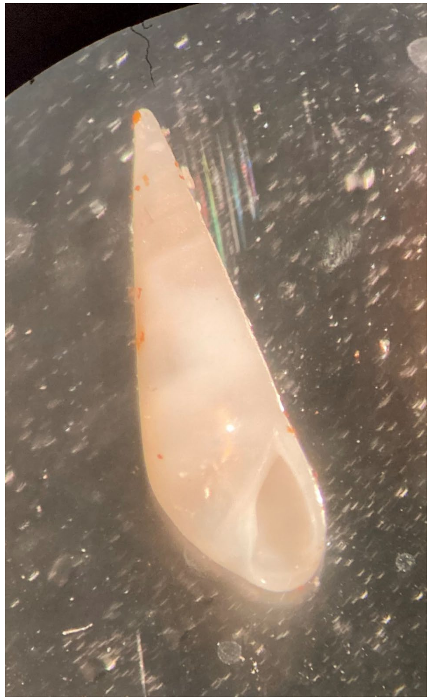
Species highlights

Most abundant species:
Pododesmus macrochisma (23 live + 437 valves)
Humilaria kennerlyi (3 live + 53 valves
Keenocardium blandum (8 live + 31 valves)
Chlamys rubida (4 live + 52 valves)
Chlamys hastata (1 live + 22 valves)
Semele rubropicta (2 live + 31 valves)
Calyptraea fastigiate (80 live + 23 shells)
Cryptobranchia concentrica (8 live + 31 shells)
Terebratalia transversa (17 live + 6 shells)



Species highlights: interesting weirdos

Eulima tenisoni
echinoderm parasite

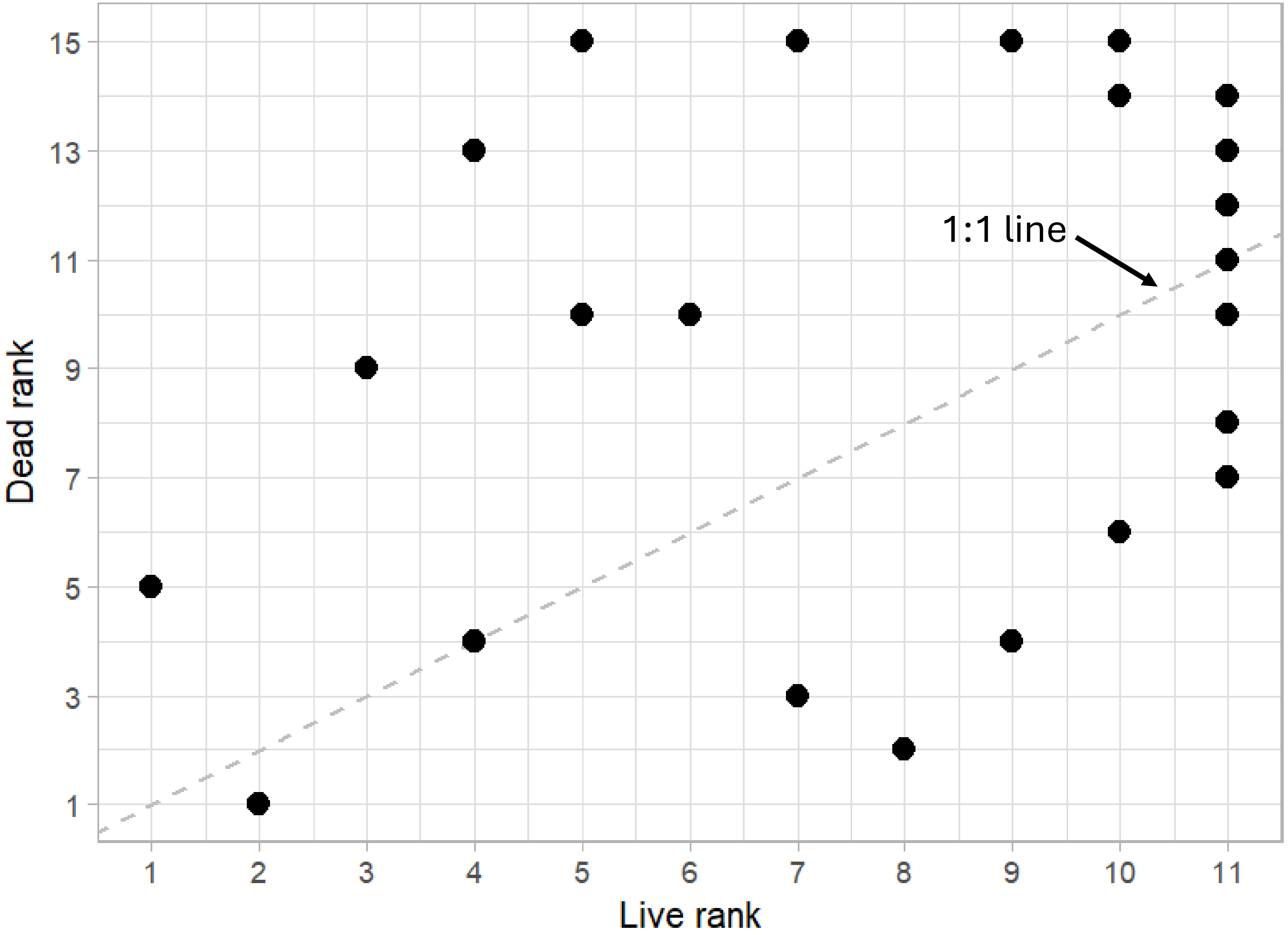


Odostomia sp.
bivalve ectoparasite

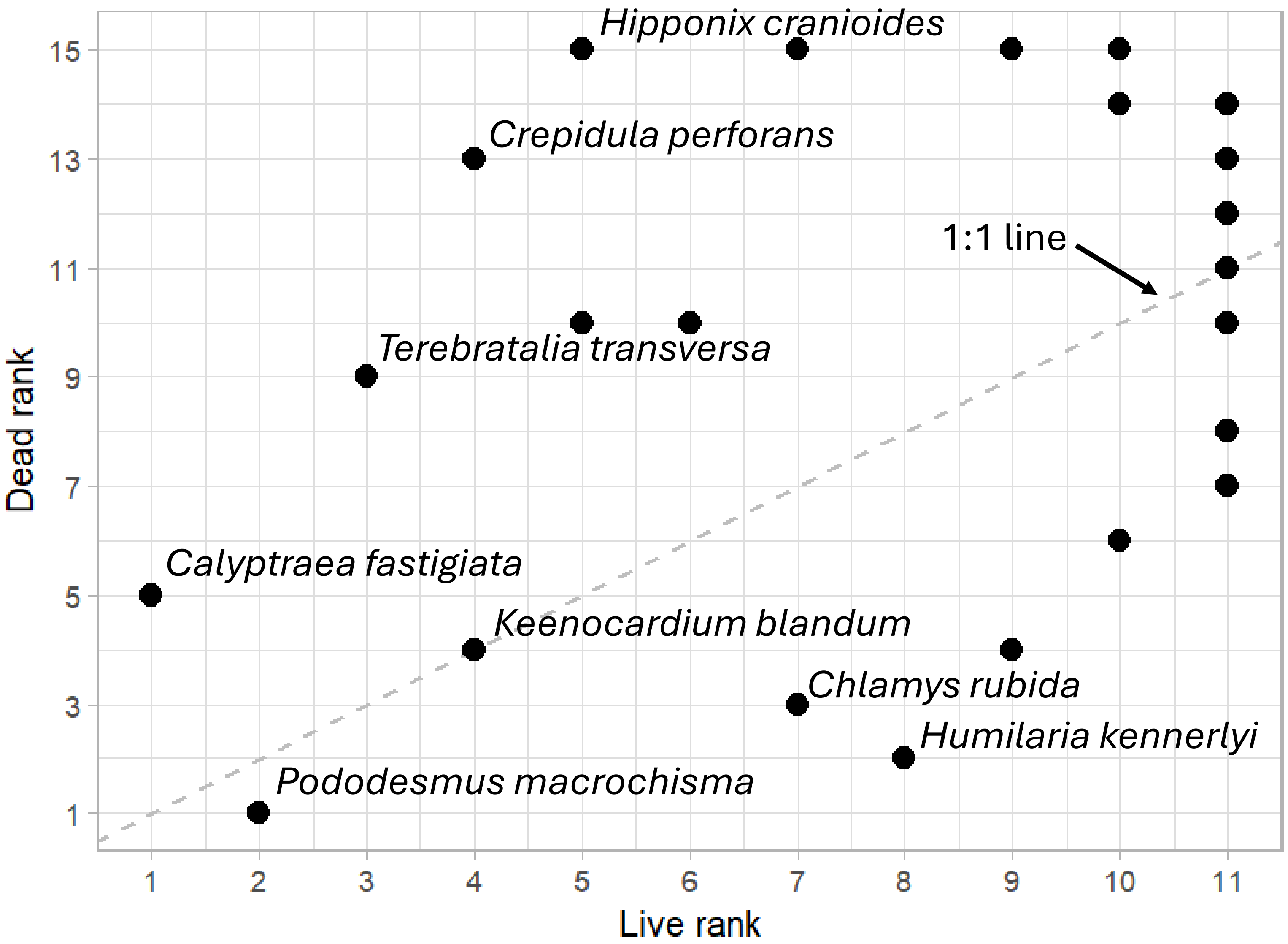
Terebratulina unguicula
another brachiopod species!

Lyonsia californica
anomalodesmatan bivalve

Comparing live and dead assemblages



Comparing live and dead assemblages



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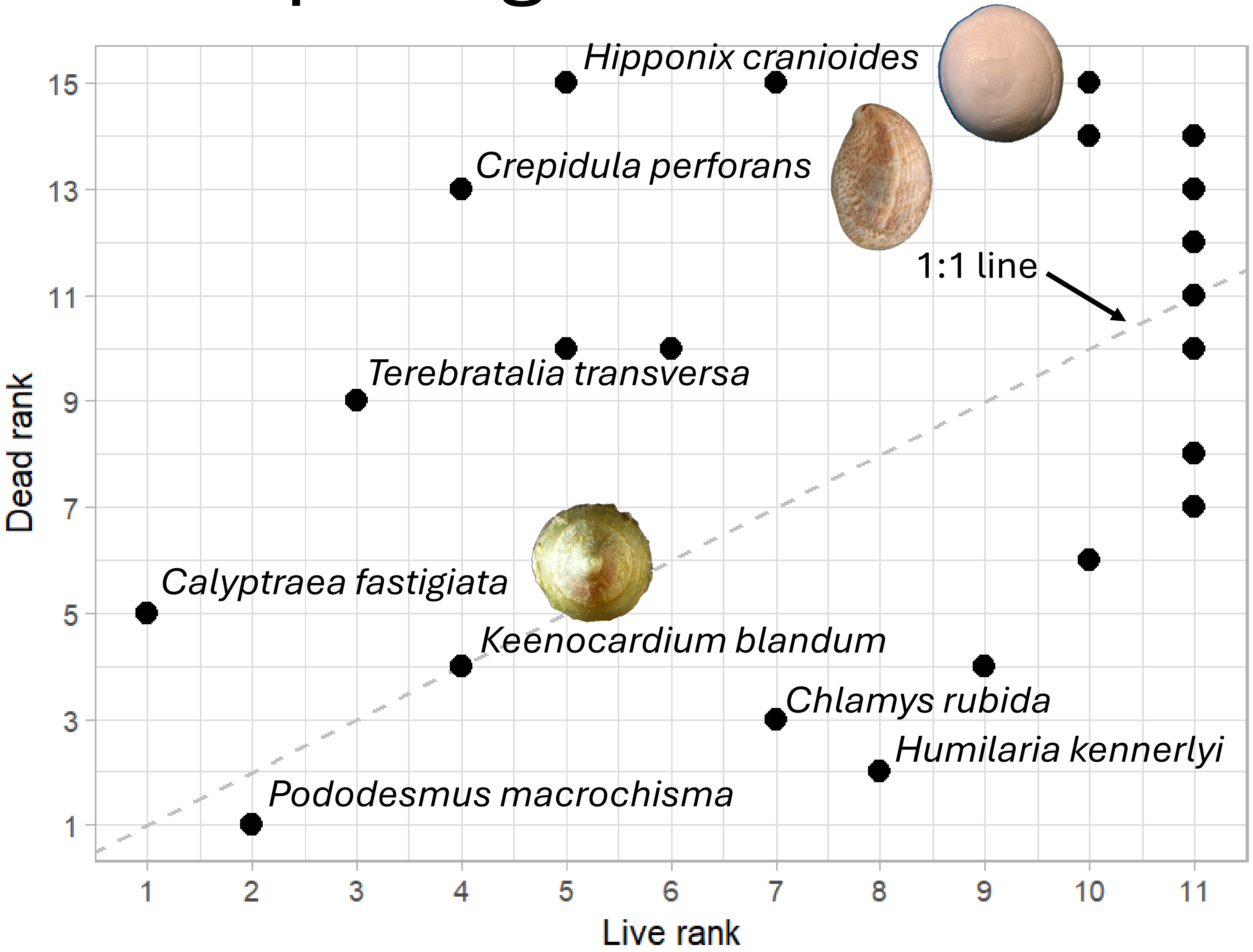

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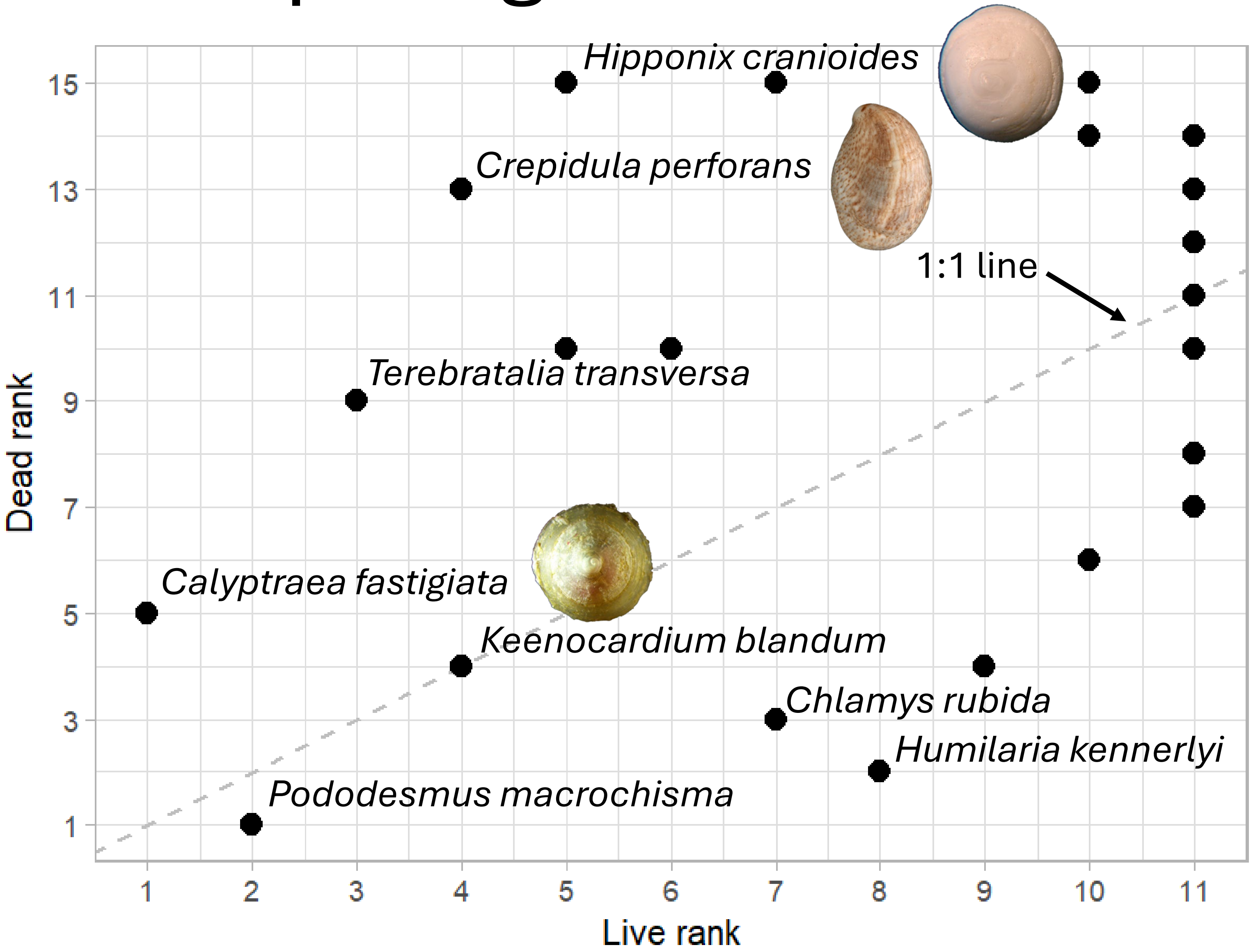
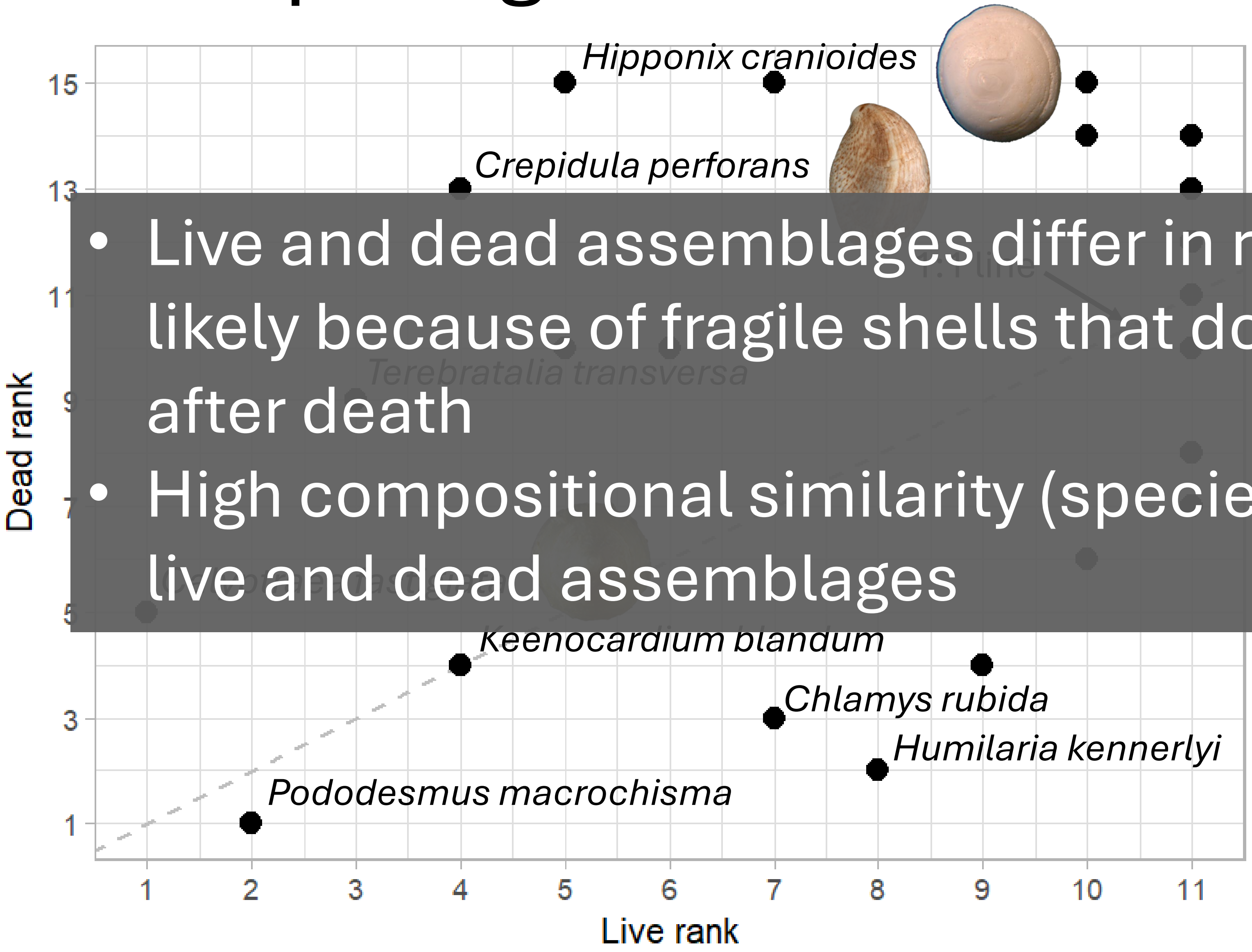


Spearman's rho: 0.2721, p=0.085

Chao-Jaccard similarity index: 0.9996

Comparing live and dead assemblages



Spearman’s rho: 0.2721, p=0.085

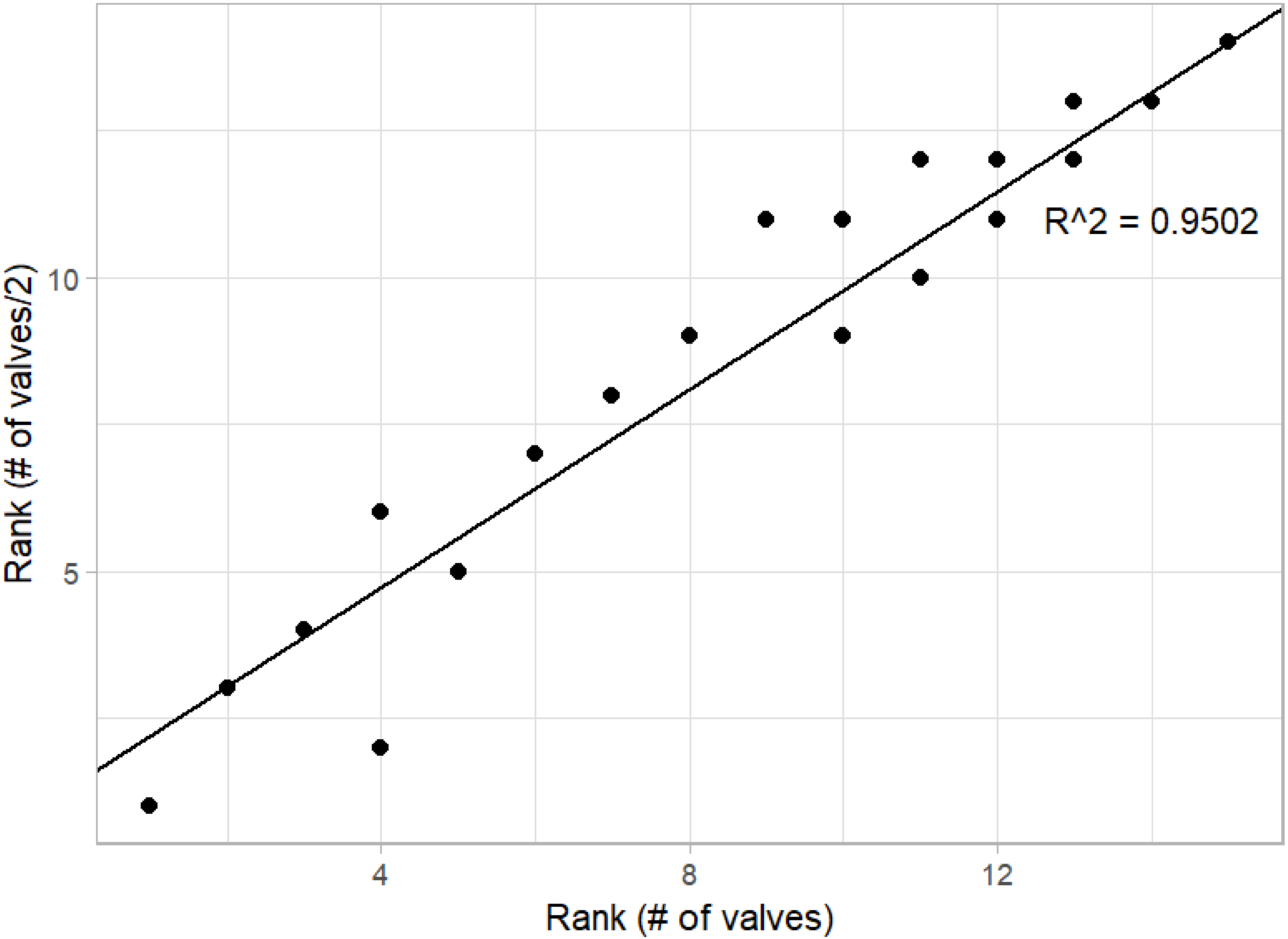
Chao-Jaccard similarity index: 0.9996

- Live and dead assemblages differ in rank abundance, likely because of fragile shells that don’t survive long after death
- High compositional similarity (species overlap) between live and dead assemblages

So, why should invertebrate zoologists care about paleontology?

1. Dead shells are biodiversity data too!
2. All of the diversity we’ve seen and talked about in this class represents only a tiny percentage of all biodiversity that’s ever existed. There are more things in heaven and earth than dreamt of in modern biology…

> **“I like to define biology as the history of the earth and all its life — past, present, and future.”**
>
> **– Rachel Carson**


R^2 = 0.9502
Rank (# of valves/2)
10
5
4
8
12
Rank (# of valves)