Colonization of maritime heritage sites: Critical thinking exercises

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Scenario 1: Larval dispersal to island-like habitats

When surveying the seafloor, scientists observe that almost any hard object can serve as habitat. Stones, reefs, pilings, ships, and even lost shipping containers[1] become colonized by sessile invertebrates. Given enough time, it seems almost inevitable that a hard object will be colonized. The question then becomes: how do these animals arrive in their new homes? Mobile fauna such as crabs, sea stars, and fish can migrate from the surrounding area, but sessile fauna don't have that option. They must have dispersed there as larvae.

Most sessile invertebrates have short pelagic larval duration (PLD), meaning they only remain in the water column as larvae for short periods, a few days or weeks. They also generally stay close to the bottom to avoid dispersing very far from their parents. Sessile invertebrate larvae are adapted for short-range dispersal, and yet, we observe sessile invertebrate species on island-like habitats, far away from any source population. One example is *Boltenia ovifera*, a stalked sea squirt, which only disperses as a larva in the water column for 24 – 36 hours[2] but is found on shipwrecks throughout Stellwagen Bank National Marine Sanctuary, including the *Portland* and the *Palmer*/*Crary* wrecks.

Write a hypothesis to explain how sessile invertebrate larvae that only disperse for a short time reach island-like habitats, such as shipwrecks.
Design an experiment to test your hypothesis. If your hypothesis is correct, what effects could you observe? What samples will you need to collect, and how will you know that your hypothesis is correct?

Scenario 2: Community-level effects of long-range dispersal

Because maritime heritage sites are so isolated, not every species of larvae can reach these sites. Species that do disperse and settle on a shipwreck might experience a release – without their normal predators or competitors around, their population can grow unimpeded. Shipwrecks can serve as refuges for species that are subject to heavy competition or predation.

How would you expect communities of invertebrates to differ between shipwreck sites and natural hard-bottom reefs? Which species do you expect to be more abundant on shipwrecks?

Imagine a five-species community: a sponge, a mussel, an anemone, a sea squirt, and a sea star. The sponge and the anemone both overgrow the mussel; the anemone and the sea squirt compete for food; and the sea star is a predator of both the mussel and the sponge.

Which species would you expect to benefit most by dispersing to a shipwreck site? The least?

Scenario 3: Succession in island-like habitats

Succession is the process by which a community of organisms changes and develops over time. Usually, this process involves an increase in species richness, as more species arrive in a habitat and become part of the community. Sometimes, a species can get an early foot-hold by colonizing a new habitat before other species arrive, and in these cases, the early colonist could prevent other species from establishing themselves at that site. The course of succession and the community that ultimately results will look different from a community where that same species did not get an early foot-hold. Scientists refer to this as "multiple stable states."[3] What happens early in succession strongly influences the resulting community.

How do you think succession on shipwreck habitats might differ from succession on natural hard-bottom habitats? Will the process go faster or slower? Are shipwrecks or natural hard-bottom habitats more likely to have "multiple stable states"?

Design a research study on succession in island-like habitats. There are no time or resource limitations. What materials would you need? How will you conduct your sampling? What changes do you expect to observe over time?

References cited

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3. Sutherland, J. P. Multiple stable points in natural communities. *Am. Nat.* **108**, 859–873 (1974).

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Scenario 1: Larval dispersal to island-like habitats

Possible answers to this exercise are varied, and almost no answer is wrong. Below, I have listed a few "more correct" answers.

Hypothesis 1: Larvae are delaying metamorphosis to reach the shipwrecks. We should be able to observe carryover effects of delayed metamorphosis such as high juvenile mortality and reduced growth. Mortality is extremely difficult to quantify, but it is feasible to measure juvenile growth. You could go sampling at shipwreck sites and on natural hard-bottom reefs after the settlement season (most invertebrates reproduce in spring, so you should go sample in early summer) and measure the size of newly-settled juveniles. Assuming they are all the same size at settlement, their size shortly thereafter should represent growth. An alternative experiment would involve outplanting artificial settlement substrata (I use clay tiles or plastic panels), allowing juveniles to settle on them, then recovering the panels and raising juveniles in the lab to measure their growth.

Hypothesis 2: The current is actually faster than we think, so larvae are able to disperse very far despite only being in the water column for short periods. Current speed is relatively easy to measure. You would need to deploy current meters at various different depths at a location between a shipwreck and natural hard-bottom habitat that could serve as a potential source population. Then you would need to recover the current meters a few months or a year later, download the data, and calculate how far a larva dispersing at each given depth could travel before they are competent.

Hypothesis 3 (this is my real hypothesis): Populations of sessile invertebrates on shipwrecks are founded by just a few individuals. For some reason, these wayward larvae dispersed farther than their siblings and ended up at the shipwreck site. A combination of asexual reproduction (an animal splitting itself in half to make two individuals; anemones can do this) and philopatry (larvae spawned on the wreck settling near their parents) made the populations we see today. If my hypothesis is correct, evidence of this "founder effect" should be apparent in a genetic analysis, which would show lower genetic diversity in shipwreck populations than in populations of the same species on natural hard-bottom reefs. Currently, I am also testing this hypothesis with lab experiments, trying to see what factors might cause some larvae to disperse farther than others. I did an experiment this summer with the snail *Crepidula fornicata*, commonly known as the slipper shell, that showed mothers kept at colder temperatures spawned larvae that remained in the water column for longer periods of time. This means *C. fornicata* larvae spawned in early spring should disperse farther than larvae of the same species spawned later in the summer.

Scenario 2: Community-level effects of long-range dispersal

The questions in this scenario again have multiple right answers, and the only potential wrong answer is that communities on shipwrecks and natural habitats would be the same. For the first question, correct answers include:

- Shipwreck communities will have lower species richness (fewer species present) because not every species can disperse to the wreck.
- Shipwreck communities could have fewer trophic levels if predator species cannot disperse to the wreck.
- Shipwreck communities could have higher abundances of species that are poor competitors or prey.
- Shipwreck communities could be dominated by just a few species that experience a release from competition or predation on the wreck.

For the second question, it would be helpful to have students diagram the community. Use arrows to indicate which species affect which others via predation or competition (overgrowth is a form of competition). The species that would benefit the most from dispersing to a shipwreck is the mussel because it would escape both predators and competitors. The sponge, sea squirt, and anemone could each benefit by escaping a predator or competitor. The one species that will not thrive alone on a shipwreck is the sea star, because it relies on the sponge and the mussel for food.

Scenario 3: Succession in island-like habitats

The question of how succession differs between shipwrecks and natural hard-bottom sites is one that I am investigating as part of the Stellwagen Expedition project. Again, there are multiple right answers, and in this case, it is actually correct to hypothesize that succession will be the same between shipwrecks and natural hard-bottom habitats. Scientists know so little about succession in deep-water habitats (for the obvious reason that studies take a long time) that I cannot exclude the possibility that shipwrecks and natural reefs undergo the same succession process. Obviously, I hypothesize there are some differences, so other correct answers include:

- Succession will be slower on shipwrecks because their isolated, island-like nature means it will take a long time for larvae to reach them, and some larvae may never reach them.
- Succession on shipwrecks will be more variable and more likely to result in “multiple stable states.” Early-arriving species could build up large populations in the absence of their normal predators or competitors and have strong effects on the resulting community.

For the second question, there are infinite possibilities. The most obvious option is to create multiple new habitats and observe the process of succession over time. You would need to create artificial reefs using a standard design (to control for differences between construction materials) and deploy some close to a natural hard-bottom reef and some far away (mimicking a shipwreck). You would need multiple replicates, and you could observe the animals at each site using an underwater camera once per year.

Another possibility is to examine previously-recorded video footage to observe changes (that’s what I’m doing) or to find shipwrecks with different ages and compare their communities.