Hitching a ride on Hercules: fatal epibiosis drives ecosystem change from mud banks to oyster reefs

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Best known as a ‘love them or hate them’ luxury food, or for their pearls, oysters are also ecosystem engineers, forming vast oyster reefs. Oyster reefs provide habitat for a myriad of species, and support fisheries, improve water quality and provide coastal protection. These services are estimated to be worth US$5500-$99,000 per hectare per year (Grabowski *et al*. 2012). Globally, oyster reefs have declined by 85% through destructive overfishing, coastal development, pollution, and introduced competitors, predators and diseases (Beck *et al*. 2011). Active restoration is becoming an increasingly popular tool to bring back lost oyster reefs and the ecosystem services they provide (Fitzsimons *et al*. 2019). However, restoration is not always successful, and knowledge about how reefs naturally form and function is vital to improve restoration success. Oyster larvae only settle on hard substrates. Reefs proliferate because oyster shells provide a settlement surface, and oysters provide chemical and sound cues that facilitate larval settlement (Lillis *et al.*, 2013). However, these reefs often form on intertidal sand and mud banks. This raises the question, how do oyster reefs form on mud banks in the absence of hard surfaces?

During research on the structure and population dynamics of remnant oyster reefs in Australia (McLeod et al. 2019), we observed many Hercules mud whelks (*Pyrazus ebeninum*) with oysters growing on their shells (Fig. 1, Video S1). These whelks are one of the most common large marine snails on the east coast of Australia. They grow to 100mm in length and feed on detritus and algae that grow on mud. We observed that individual whelks sometimes carried up to four large oysters on their shell, and as the oysters grew larger, it appeared that the whelks moved slower, and were pushed lower into the mud. We presumed that this would eventually lead to the death of the whelk and the formation of a new oyster clump. Evidence to support this presumption was gained when we investigated clumps of live oysters and found there was often a dead whelk shell in the center.

We searched for evidence of this process in the contemporary literature, and no record of whelks as a settlement habitat for oysters was found. Historical literature can be useful to regain information about historical baselines, especially when remaining reference ecosystems are degraded (McClenachan *et al*. 2012). By reviewing historical newspaper articles and fisheries reports some anecdotes were found. Fison (1887) reported "the best oysters, in clumps of four to five, each contain a whelk ~1.5 to 3 inches long attached to them by the back [...], as the oysters increase in size more recruits attach until the whelk is buried and dies". Saville-Kent (1891) similarly noted "bank oysters may attach to rocks, dead shell known as cultch or as more frequently, attach to the shell of the Hercules whelk, [...] and are ferried to various areas of the feeding grounds, until the whelk is overwhelmed and dies from the burden". An archaeological investigation into 1000-year-old Aboriginal rubbish heaps (middens) in southeast Queensland found that 7% of oyster valves showed evidence of being attached to Hercules whelks (Smith and McNiven 2019).

Complex physical habitat in coastal systems like rocky shores, subtidal reefs and mangrove roots are largely fixed in space and hence are a bottom-up limiting force for associated sessile invertebrates and reef associated communities. We hypothesize that Hercules whelks play a unique facilitative role for oysters as ecosystem engineers in sediment-dominated estuarine environments through epibiosis. Epibiosis is a relationship between two organisms, of which one lives on the other, but is not parasitic. Epibiosis differs from other interspecies relationships (Fig 2). For example, unlike *parasitism*, where one partner derives resources at the cost of the other, the majority of epibiotic organisms are facultative, and will attach to a wide range of hosts or inanimate hard surfaces (Wahl and Mark 1999). In contrast, both partners benefit in *mutualism*, while one partner benefits and the other is unaffected in *commensalism*. In *amensalism*, one partner is negatively affected but the other does not derive benefit nor harm.

There are thousands of examples of marine epibiosis that range from barnacles growing on whales and microcolonisers such as bacteria, and algal spores (Harder 2009). Epibiosis often harms host organisms by shading, increasing weight and friction, by reducing access to dissolved molecules, or through 'shared doom' by encouraging predation or herbivory (Wahl 1989). Conversely, hosts may benefit due to camouflage and protection against drying out, reduced friction, or providing physical defence. In the absence of hard surfaces on mud banks, epibiosis provides the only way for oysters to expand into these habitats. Subsequent generations of oyster larvae can then settle on oyster shells creating a self-sustaining ecosystem, no longer reliant on whelks as substrate. The Hercules-oyster relationship is significant because it appears to be facultative for an entire ecosystem and not just individuals.

Epibiosis as a driver of ecosystem change is likely to be under-recognised in the marine environment. For example, Pacific oysters are invasive in the Dutch Wadden Sea, and have overgrown and replaced native blue mussel (*Mytilis edulis*) beds by settling on their shells (Eschweiler and Christensen 2011). Pacific oysters also grow on the shells of the gastropod *Littorina littorea* (Periwinkles) reducing their ability to move and reproduce (Eschweiler and Buschbaum 2011). While the interaction between Hercules whelks and oysters is a similar process to these examples, the Hercules whelks and oysters are both native species in Australia. Therefore this is likely to be a natural process, as described in the historical literature. Only 10% of former oyster reefs remain in Australia (Gillies *et al*. 2018) and these ecosystems are often replaced by ‘bare’ soft sediments, with markedly less three-dimensional structure and habitat value (McLeod *et al*. 2019). Oyster restoration is rapidly scaling up in Australia, however there are few natural reference sites left to study to show how these ecosystems function (Gillies *et al*. 2018). This study shows the importance of understanding ecological processes including epibiosis, particularly in the context of the growing field of restoration. Further, it emphasizes the importance of going beyond the contemporary scientific literature in a rapidly changing world to include historical context from scientific naturalists for baselines and understanding natural ecosystem function.

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Figure Captions

Figure 1. A Hercules club mud whelk (Pyrazus ebeninum) with three oysters growing on its shell on a mud bank in Richmond River, New South Wales, Australia. Photo by Patrick Dwyer on 17 October 2015 at 28°50'55.4"S 153°34'22.3"E.

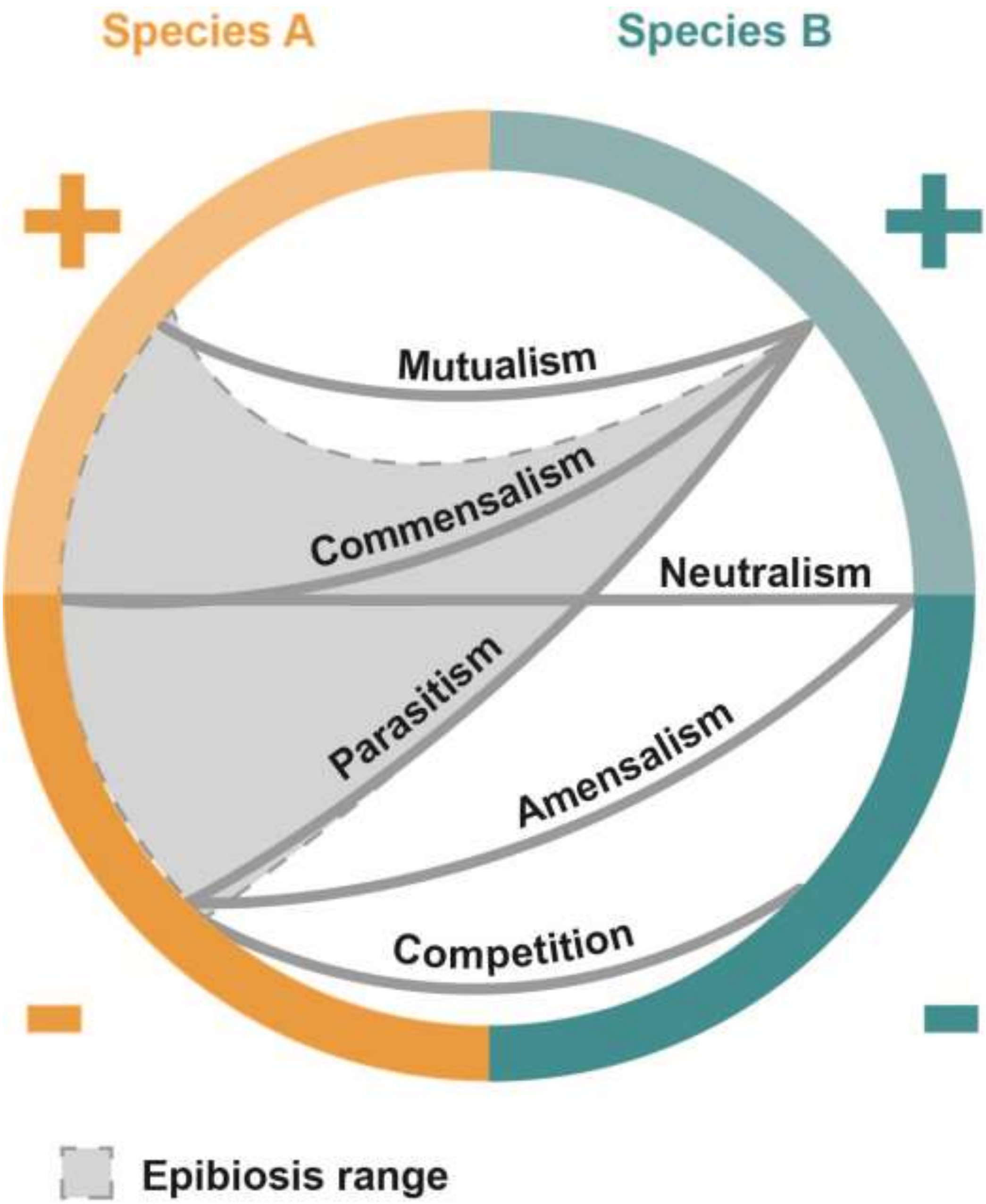

Figure 2. Interspecies relationships (i.e. symbioses) can take many forms, depending on the benefits and harm caused by the two species. The shaded area represents the potential range where epibiotic fits in to this schematic.