Journal for Oyster Reef Restoration Literature Review

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1 Introduction

2 Summary of Foundation Species Model

Oysters and oyster reefs are conceptualized using both the ecosystem services model and the foundation species model — sometimes in the same paper (Mercaldo-Allen et al., 2023). There is evidence in the literature to support the use of both of these models for understanding oyster ecology but the different models lead to different conceptualizations of the system. The foundation species model was originally described by Dayton (1972) and has been expanded to and developed into am more formalized description of ecosystems that are structured by a strongly interacting and numerically dominant species or assemblage of species (Ellison, 2019). What distinguishes foundation species from other strongly interacting species (e.g., keystone species, ecosystem engineers, etc. . .) is that foundation species are a dominant member of a community that, through the formation of substantial non–trophic interaction with other species in the community, strongly influence biodiversity, material and energy flows, and the physical and chemical conditions of the system (Ellison, 2019). Foundation species exert their influence through a complex network of interactions that often time can include other foundation species in a "facilitation cascade" (Angelini, Altieri, Silliman, & Bertness, 2011; Ellison, 2019; ?, ?). While Ellison (2019) provides a formalized definition of what a foundation species is, it is useful to describe the types of effects that foundation species facilitate in ecosystems to determine the unique community they create.

Although not specifically mentioned in the Ellison's formal definition of a foundation species, one of the main things that foundation species do is create biogenic structure that often substantially increases the complexity of the system (Ellison et al., 2005; Ellison, 2019; ?, ?; Fields & Silbiger, 2022). In contrast to other strongly interacting species that either create or modify the structure of the environment and facilitate other organisms (e.g., ecosystem engineers, cornerstone species, etc. . .), foundation species *dominate* the physical environment with their biogenic structure (Ellison, 2019). In fact Ellison

(2019) observes that foundation species are often the "defining" organisms of an ecosystem type, in that humans use the presence of the foundation species to define the system (e.g., a "coral" reef, a "mangrove" forest, etc. . .). The creation of the dominant habitat structure of the system, typically with their own biomass, allow for foundation species to form abundant interactions with other species (Ellison, 2019). Through these interactions, foundation species have a much larger effect on ecosystem diversity, structure, and function than even their substantial biomass would predict. , a reduction in the variation of physical stresses in the system (Ellison et al., 2005; Fields & Silbiger, 2022), a reduction in the velocity of material and energy cycling (Ellison et al., 2005; Ellison, 2019)

The foundation species model proposes that an ecosystem contains one or a few species that have a disproportional effect on community structure by altering the physical, chemical, and biological processes of an ecosystem to facilitate and stabilize a specific community (Fields & Silbiger, 2022). The presence of foundation species creates and stabilizes the physical environment by minimizing fluctuations in temperature, moisture, pH, or other physical parameters (Ellison et al., 2005). Foundation species can also alter ecosystem production through changes in nutrient cycling, in some cases increasing (Fields & Silbiger, 2022) or decreasing (Ellison et al., 2005) nutrient availability. A main effect of the foundation species is to literally build the three–dimensional habitat that other species require (Angelini et al., 2011). By facilitating the growth and persistence of organisms that would not be able to colonize a patch, foundation species create a unique, stable, and often more biodiverse community.

2.1 Oysters as Foundation Species

Conceptualizing an ecosystem based on the foundation species model, means understanding that system as being structured by the specific facilitation interactions of one or more numerically dominant species (Dayton, 1972; Ellison et al., 2005; Angelini et al., 2011). Because they are capable of building large biogenic structures that can persist for long time periods, sometimes centuries (Lockwood & Mann, 2019), of altering local physical conditions (Lenihan, 1999), and of processing large volumes of materials via filter feeding (Newell, 1988) oyster reefs can be conceptualized as foundation species where they occur. The three–dimensional structure of an oyster reef (mainly its height above the otherwise flat sediments) and its heterogeneous complex structure creates, a unique environment that facilitates the growth and persistence of the oysters themselves (Lenihan, 1999), sessile producers and consumers (), and mobile consumers (Smith, Lusk, & Castorani, 2022; Searles, Gipson, Walters, & Cook, 2022). This facilitation, in part, relies on the way that the reef alters the physical environment by altering flow around the reef to alter the temperature, dissolved oxygen, and other physiochemical factors (Lenihan, 1999). The reef also alters species trophic interactions by providing cover for both predators and prey organisms (Smith et al., 2022) and aggregating and increasing resources for consumers (Newell, 1988). As a result of these integrated effects oyster reefs support a unique community of sessile and mobile organisms who's growth and persistence is facilitated by the reef (Lenihan, 1999; Smith et al., 2022).

Consistent with the idea of a foundation species, when the reef structure is destroyed (mostly by destructive harvest methods), then the community becomes less diverse and dominated by non–reef–building organisms. Following the decline of oyster reefs in through the 19^{th} and 20^{th} centuries from overfishing, the habitats previously occupied by oysters became colonized by other benthic filter feeders (e.g., *Corbicula fluminea*) indicating a significant shift in the food web (Newell, 1988). The loss of the reefs also significantly affected material cycling within the esturine system, since the oysters were no longer concentrating phytoplankton biomass into feces and pseudofeces to provided resources to benthic consumers, benthic–pelagic coupling significantly decreased (Newell, 1988). What these observations support is the idea that the effect of the reefs on the system are due to emergent properties that result from the interactions between the oysters and other organisms in a "mature" reef. The function of oyster reefs is dependent on their structural development and complex ecological interactions, indicating that it is the creation of a particular habitat and its associated conditions that drives the effect. For example, Searles et al. (2022) found that reef-associated macroinvertebrate communities recovered on the interior of restored reefs but not their margins, suggesting that a certain oyster density and/or reef structure was required to facilitate the colonization of the specific assemblage of macroinvertebrates that typify a reef community.

One reason for this effect is likely that the alteration of the physical environment is a key factor in the way that oyster reefs create the specific ecological communities associated with them (Lenihan, 1999; Searles et al., 2022). Because the effects of the reef on the structure and function of the reef community are the result of emergent effects that result from the "physical–biological coupling" of the reef and the estuarine environment, the deconstruction of the reef by harvesting practices that destroy the three–dimensional characteristics of the reef, as well as remove individuals will result in the deminishment or elimination of the facultative properties of the reef (Lenihan, 1999). In this way the reef as a foundation species is defined by the emergent properties that arise from the integrated function of the oysters and the other organisms that are facilitated by the effects that the oysters have on the physical–biological coupling of the system (Lenihan, 1999; Ellison et al., 2005; Angelini et al., 2011).

3 Summary of Ecosystem Services Model

In contrast to the foundation species model, the ecosystem services model conceptualizes ecosystems based on the "services" that they provide, in particular services that are valued by humans (). In this conceptualization, the ecosystem is a source of unaccounted for value to the economic system by enhancing the surplus value of associated the economic system in ways that do not require payment (). The types and value of ecosystems services for many types of ecosystems have been extensively reviewed (Costanza et al., 1998). Costanza et al. (1998) estimated that the economic value of the total ecosystem services of the global biosphere was $33 trillion USD, which is 1.8 times global GDP at the time that the paper was written. The authors go even further to emphasize that their estimate represents the *minimum* value of ecosystems services provided by the world's ecosystems. Costanza et al. (1998) analysis highlights the enormous contribution that ecosystem services provide for human existence and that it is really impossible to truly account for these services economically. More practically the intent of the ecosystem services model is to translate the function of natural ecosystems into market value that can then be used to inform management decisions (). For example, Grabowski et al. (2012) found that the economic value the ecosystem services provided by restored oyster reefs exceeded the market value of the oysters harvested from them, indicating that from an economic perspective alone, oyster reefs should be restored and protected from harvest. Used in this way, the ecosystem services model can be used to calculate and communicate the way that the preservation and restoration of ecosystems adds economic value () and has been used successfully to justify the preservation of EXAMPLE ECOSYSTEMS.

The ecosystem services model has been applied extensively to oyster reef ecosystems and oyster reefs have been shown to provide shoreline protection, habitat creation for economically valuable fish species, water quality improvement through phytoplankton and excess nutrient removal, and carbon sequestration (Coen et al., 2007; Grabowski et al., 2012). Historically, oyster reefs have been seen as primarily just a source of oyster meat for consumption and shell for construction (). However, the increased recognition that oyster reefs provide a myriad of valuable ecosystem services has justified the restoration of reefs for more than just subsidizing harvest ().

4 Application of Models to Oyster Restoration and Aquaculture

5 Impact of Models on Understanding Oyster Management

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