

Oysters in a New Classification of Keystone Species

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Keystone species are crucial in restoration ecology. Among all the keystone species known so far, live oysters are by far, the most efficient ‘keystone niches’, attracting hundreds of species to them. A new classification of keystone species is presented, including oysters as the best keystone niches.

Introduction

The concept and the role of keystone species in the food webs of an ecosystem were first developed by Robert Paine of the University of Washington, Seattle, USA¹. He defined keystone species are those that, despite low biomass, exert strong effects on the structure of the communities they inhabit. Keystone species have been variously defined by subsequent authors (Molles, Jr., [1], Bush [2] and Stiling [3]). In the light of recent experimental studies, keystone species in an ecosystem may be redefined broadly as those that influence species diversity either positively by attracting diverse species with niches that provide food or shelter or both, and negatively by foraging and predating on prey species or by modifying their habitats.

Paine developed this concept of keystone species originally based on his field experiments with the predator starfish *Pisaster ochraceus* in the intertidal rock pools of the Mukkaw Bay of the Northwest Washington State, USA. Later, he confirmed this concept through similar experiments with the starfish *Heliaster kubinjii* in the northern Gulf of California and also with the starfish *Stichaster australis* on the west coast of New Zealand. Other ecologists identified some more keystone species like the intertidal snail *Littorina*, the predator whelk *Conchlepas*, the steel-headed trout *Onchorhynchus*, the Nile Perch from Lake Victoria, insectivorous birds, fire ants *Solenopsis geminata* in South Mexico, African elephants, beavers, gray wolves and golfer tortoises of the southeastern United States.

¹ R T Paine, *American Naturalist*, 100, pp.65–75, 1966.
R T Paine, *American Naturalist*, 103, pp.91–93, 1969.

Keywords

Keystone niches, biofoulers, primary and secondary keystone species, restoration ecology.



Most such earlier studies however have been carried out only with keystone predators. Bush [1] states that “even primary producers can be keystone species” like the fig trees of the genus *Ficus* which are continuous fruit bearers for a diversity of frugivorous birds in the tropics. Today, besides the original predator type of keystone species, other types like the keystone prey (may be synonymous with keystone niches such as palm nuts, figs and nectar), keystone enemies (synonymous with keystone predators), keystone habitat modifiers (beavers and golfer tortoises) which are also called as the ‘ecosystem engineers’ [3], have been identified in various ecosystems.

Tribals, who disturb forest ecosystems by hunting the keystone wildlife, and today all of us humans who ‘alter the nature of their world’ [4], are said to be keystone habitat modifiers.

The amazing efficiency with which the keystone functions in setting up new ecosystems and food webs by coral skeletons and live oysters have not been fully highlighted. This article reviews the keystone functions of live oysters from all over the world, designating them as ‘keystone niches’ because of their providing habitats, or food or both, and accommodating them, along with the other types of keystone species, in a new classification of keystone species.

Oysters

In the intertidal waters, sessile filter-feeding organisms like the balanids of the genera *Balanus* and *Megabalanus*, green mussels of the genus *Perna* and oysters of the genera *Ostrea* and *Crassostrea* are generally called as biofoulers, since they colonise hard substrata in salt waters, sometimes to the extent of being a nuisance. Their hard shells also act, in turn, as substrata for a wide variety of other biofoulers, making up a uniquely rich micro-ecosystem. Wells [4] has recorded an amazing 303 different species of animal biofoulers alone (without plants), from the oyster beds of the estuary of the Newport River, in the Beaufort area of North Carolina, USA. Hence, oysters may be newly

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termed as 'keystone niches' that provide habitats, shelter and food for their associates. Although coral reefs provide a wider diversity of habitats for the incredible numbers of species it is chiefly their dead skeletons and not live polyps, as Schaeffer [5] states, that act as keystone niches to invite almost all aquatic biodiversity to their vicinity.

Why are Oysters such Efficient Keystone Species?

Live oysters are the most efficient keystone species because of the following reasons:

1) Normally, in coastal waters, biofouling is higher in shallow waters, directly exposed to the tidal impacts. As oysters inhabit bays (lagoons), estuaries and backwaters, tidal flushes that bring in fresh oxygen, planktonic and other microscopic food, lash against the oyster reefs (bars), aerating the waters by churning and mixing, so as to nourish the biofouler communities.

2) Live oysters are perhaps the most efficient filter-feeders, filtering about 15 litres per hour or about 50 to 55 gallons of water per day, which helps in,

- a) straining the detritus, planktonic and other microscopic organisms as food for the diverse biofouler communities, in and around the oysters, and
- b) filtering pollutants, both particulate as well as dissolved (Butler, [4] and Smith, [6]), so as to cleanse the waters and to attract a rich biodiversity. Hence oysters and their associates are said to be good 'ecological indicators' of the quality of brackishwaters they inhabit.

3) Large surfaces of the oyster, softer parts like the gills (ctenidia), labial palps and the inner, surface of the mantle, and their mucous lining entangle microorganisms as food for the commensals and browsers that enter the mantle cavity of the oysters, opened during their filter-feeding, at the high tides.



4) Marked seasonal biochemical changes taking place in the softer tissues of oysters, as observed by Thangavelu and Sanjeeva Raj [7] may release lipo-proteins and amino-acids into the surrounding waters, rendering them nutritiously/biochemically rich to attract biodiversity.

5) The rough and rugged outer shell-surface of oysters helps in the anchorage of sessile organisms. Besides them, the crevices of various dimensions, in between the oyster shells in a colony, provide ideal shelters and habitats for a variety of larger animals to inhabit.

Also, the sharp edges of the oyster shells prevent traditional fishermen from treading over the oyster-beds, thus providing security for the biofouler communities of the oyster reefs.

Thus, all the basic needs for survival-habitat, shelter and food – are supplied uniquely by the live-oysters to their associates, which the classical predator type or other types of keystone species do not provide. Hence, oysters may be ranked as the most efficient ‘keystone niches’.

Pre-requisites for Richer Associates at Live-Oyster Beds

Attracting a rich biofouler community at live-oyster beds, through observing the following parameters is crucial for biodiversity restoration in brackish waters:

- 1) The higher the salinity of brackish waters, the more would be the biodiversity of oyster associates (Wells, [4]).
- 2) Proximity to natural encrustations of sessile organisms would help in the recruitment of larvae and adults of biofoulers of oyster beds (Nair *et al.*, [8]).
- 3) Shallow brackish waters exposed directly to tidal impacts are more suitable for oysters and their associates (Hornell, [9]).
- 4) Less turbid (more transparent) brackish waters, proximity to a vast and pre-existing oyster-reef, protected from pollution and



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other human interventions, promotes richer oyster settlement and their biofouler communities (Sanjeeva Raj *et al.*, [10]).

A New Classification of Keystone Species

With the growing interest globally for biodiversity restoration, particularly in the tropics, the search for keystone species in the food webs of different ecosystems is crucial in restoration ecology. Stiling [3] warns us, ‘however, we should remain aware of the potential pitfalls of the imperfectly known webs’. Hence, there is a need to study food webs in depth, to identify new keystone species and to review and classify them in order to accommodate the functionally bewildering array of keystone species in nature.

Functionally, primary producers like the various species of fig trees and filter-feeders like oysters, green mussels and balanids, may be grouped under primary, or passive or positive keystone species, which will attract and promote species diversity in an ecosystem, directly.

On the other hand, predator type of keystone species like Paine’s original examples of the starfish *Pisaster* and others, habitat modifying keystone species like elephants, beavers and golfer tortoises may be grouped under secondary or active or negative keystone species, which would monitor the biodiversity composition of the ecosystem, indirectly.

Keystone species are ecosystem specific. The lower a keystone species is on the trophic level, the more efficient its keystone functions would be.

To support this new classification of keystone species, the functional differences of these two categories are listed in *Table 1*.

Restoration Ecology

“Keystone species offer great promise as focal points for conservation activity” (Stiles, [3]). Therefore, a knowledge of keystone species is indispensable for the successful restoration and man-

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Primary/Passive/Positive Keystone Species	Secondary/Active/Negative Keystone Species
1. Sessile, primary producers or filter-feeders; low on trophic level.	Mobile, primary consumers (herbivores) or secondary consumers (carnivores); high on trophic level.
2. These attract biodiversity directly, by providing habitats and food; they are highly efficient.	These attract biodiversity indirectly, by consuming some species and inviting others or by modifying their habitats; they are not so efficient.
3. These are easy to propagate and disseminate for restoration ecology; less liability for ecosystem managers.	These are difficult to be bred and disseminated for restoration ecology; more liability for ecosystem managers.
4. Even the dead components of these keystone animals help as keystone habitats.	Dead components of these are useless for the same keystone functions.
5. Total annihilation or restoration of these, results in total loss or total restoration of their associated biodiversity.	Total annihilation or restoration of these, results partially in influencing the biodiversity composition.

agement of degrading ecosystems. Oysters, as keystone species, are excellent tools for biodiversity restoration in degrading brackishwater ecosystems.

Table 1.

Oyster-spat can be collected on lime-coated roof-tiles (Thangavelu and Sundaram, [11]) for transplantation elsewhere. Even their dead components like oyster-shells make the best cultch, next to roof-tiles [11] for attracting the settlement of oyster-spat as well as for the succession of biofouler communities. Therefore, conservation of oysters, in protected areas or reserves in open brackishwater ecosystems, is a pre-requisite for the restoration and conservation of all the brackishwater biodiversity and fisheries. Traditional fishermen on the Pulicat Lake realised this truth long ago, that when oyster-shells were clandestinely exploited by contractors for burning them into lime, their traditional fisheries at the oyster-beds also disappeared.



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Hence, wanton destruction of any keystone species in an ecosystem is a serious ecological offence. However, in any ecosystem, if one keystone species is lost, there would be some alternate keystone species that would replace the lost ones and come to dominance. For instance, in the Pulicat Lake, when the dominant keystone oyster *Crassostrea madrasensis* (Preston) was lost, other primary keystone species like the balanid *Balanus amphitrite*, bivalves like the green mussel *Perna viridis* in the southern sector of the lake, and the secondary keystone species like the mud-crabs *Scylla tranquebarica* and *Scylla serrata*, all over the lake, replaced the keystone oysters, but on a less effective level. Thus, maintaining a diversity of keystone species also, in one and the same ecosystem simultaneously, is a management strategy to sustain ecosystems and their biodiversity.

In conclusion, restoration ecology should be on the constant search for newer and newer keystone species, as well as for saving the existing ones, in order to conserve biodiversity, particularly in these days, when ecosystems and their biodiversity are fast getting degraded. However, one should be cautious also, as not to introduce exotic keystone species into any ecosystem.

Suggested Reading

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