11. A STABLE SYSTEM OF PREDATION ON A HOLOTHURIAN BY FOUR ASTEROIDS AND THEIR TOP PREDATOR

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SUMMARY

Seven species of asteroids feed on *Cucumaria lubrica*, but together they harvest only 3% of the population or 10% of the standing crop biomass per year at the locality of the study. The rates of predation by the asteroid *Solaster dawsoni* on the predators of *C. lubrica* are high enough and the rates of growth and successful recruitment into the area by the predators of *C. lubrica* are low enough to indicate that the predators of *C. lubrica* are possibly kept low in abundance by the higher predator *Solaster dawsoni*. *Solaster stimpsoni*, the most abundant predator of *C. lubrica* in the area, has a behavioural escape mechanism which becomes increasingly effective as *S. stimpsoni* grows large and when it is on vertical rock surfaces. While *S. dawsoni* removes about 24-32% of the *S. stimpsoni* population each year, probably preventing a buildup in numbers, the refuge in size of a reproductive stock allows the persistence of the long-lived, slow-growing, *S. stimpsoni*. *Dermasterias*, a predator of *C. lubrica* with a refuge in size but with no behavioural escape mechanism to *S. dawsoni*, is 0.07 times as common as *S. stimpsoni* with a size-frequency distribution represented predominantly by large adults. *Solaster endeca* and *Leptasterias*, predators of *C. lubrica* with no known refuge to *S. dawsoni*, are 0.004 and 0.008 times as common as *S. stimpsoni* and may be considered strays from other habitats. No significant changes in abundance were observed in the 3 trophic levels of the association from 1965 to 1976: *C. lubrica*, 4.4×10^3 m^{-2}; *S. stimpsoni*, 0.5 m^{-2}; *S. dawsoni*, 0.007 m^{-2}. The stability of the system results from different control mechanisms and refuges at each trophic level.

INTRODUCTION

In basic ecological theory, predator-prey systems have an inherent tendency to oscillate or to become extinct (Lotka 1920; Volterra 1926; Gause 1934; May 1973). In natural systems, populations usually fluctuate to a much lesser degree than would be expected (Murdoch and Oaten 1975). The factors preventing over-exploitation of a prey by its predators fit into two general categories (MacArthur 1972:31): (1) a refuge for the prey or (2) a factor limiting the predators to numbers low enough to prevent annihilation of prey (e.g., a higher level predator, a limiting resource other than the prey in short supply, cannibalism, territoriality, etc.). Prey refuges stabilize a community by providing protection for a reproductive stock but allowing relatively easy access of the predator to the "surplus" (Errington 1946) or excess "product" (Connell 1970; Smith 1972) of the prey population. For the simpler organisms in a heterogeneous environment, the susceptibility of prey to predation is usually inversely related to their abundance. The prey with the weakest escape or defence responses or those in the least safe location are caught first; so as prey become more scarce, only the less available are present. Also, scarcity and unpredictability can become refuges in themselves, even if site selection is disregarded (Smith 1968; Birkeland 1974). The effects of refuges are generally inversely related to prey population size and are thereby a stabilizing factor in predator-prey systems.

As pointed out by Elton (1927), species size distribution has a major influence on community organization. The "size of the prey of carnivorous animals is limited in the upward

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