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Papers from the Echinoderm Conference

Edited by

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FOREWORD

Since the first major Symposium on Echinoderm Biology was held in London in 1966, sponsored by the Royal Zoological Society, at least six subsequent meetings have been organised by echinodermologists. These have been held in Washington D.C., U.S.A. (2), Rovinj, Yugoslavia (1), Sydney, Australia (1), London (1); the last two meetings (Sydney and London), within the same year (1978), and Brussels, Belgium. Also, at least four meetings are known to have been held in U.S.S.R. Such has been the surge of interest in the study of echinoderms over the past decade, that there is now a demand for the organisation of regular, and more frequent, meetings. The international representation at these meetings indicates the enormous involvement and co-operation which now exists between colleagues working in this exciting field, the world over.

It is more than evident that the satisfaction and pleasure expressed by Professor Norman Millott, in his foreword to the first Symposium volume (1967), at the resurgence of interest in Echinoderm Biology has been clearly justified and can continue so to be.

This volume presents twelve of the forty-one contributions offered at the Echinoderm Conference, Sydney, 1978. The papers are representative of the wide coverage of topics dealt with during the Conference, including echinoderm palaeontology, physiology, reproduction, ecology, behaviour and taxonomy.

To the speakers and chairmen, and to all those who attended the Sydney Conference, I convey my thanks. I must also thank my Technical Officer, Ms Jan Marshall, and Dr Susan Oldfield (Queen's Fellow at The Australian Museum, February, 1977-1979) for their unstinting assistance in the organisation of the Conference. Thanks are also due to the Department of State Fisheries (N.S.W.), Taronga Park Zoo, McWilliams Wines Pty, Leo Buring Wines Pty, Qantas Airways Ltd, and Trans-Australia Airlines (T.A.A.). To The Australian Museum Society (TAMS) I extend a special thanks for assistance.

This Conference could not have been held without the tremendous support and encouragement afforded to the organiser by Dr D. J. G. Griffin, Director, The Australian Museum, and the very generous financial support of the Trustees of the Museum, to both of whom I offer my very sincere thanks.

DECEMBER 1979   FRANCIS W. E. ROWE

CONTENTS

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 x 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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direction by the carnivore's strength and ability to catch the prey, and in the downward direction by the feasibility of getting enough of the smaller food to satisfy the carnivore's needs" (Elton 1927:60). A number of predators, even those quite generalized in their diets, will take only earlier age classes from the prey populations. Prey individuals that survive long enough will gain a refuge in size (Paine 1965, 1976; Dayton 1971). Many benthic marine invertebrates are characterized by the type III survivorship curve implying "extremely heavy mortality beginning early in life, but the few individuals which survive to advanced ages have a relatively high expectation of further life" (Deevey 1947:286). A refuge in size is prevalent among marine invertebrates (Thorson 1955, 1958, 1961; Paine 1965, 1976; Dayton 1971; Connell 1972). However, in cases in which effective refuges do not exist, populations which sustain mortality in all age classes could be composed largely of the young stages (Grassle and Sanders 1973). An age structure composed preponderantly of long-lived adults also could imply a crowded habitat governed by competitive interactions (Pianka 1970) or unpredictable reproductive success (Murphy 1968). Therefore, similar age structures could be the manifestations of very different processes. To be used as evidence for the effects of a process, age structures must be presented along with natural history information and ample data on the rates of the critical process. In this paper we examine a predator-prey system which displays remarkable constancy despite intensive predation at two trophic levels. Our goal is to elucidate the factors promoting stability.

In the San Juan Islands of Washington State, the holothurian *Cucumaria lubrica* H. L. Clark attains great population densities (4 to 6 x 10^3 m^{-2}) over extensive areas of rock or cobble substrata in shallow water (about 8 to 20 m depth). Within these areas, this holothurian species is preyed upon by 7 species of asteroids (3 of which are congeners) and forms the major portion of the diet of 4 of these predators (Mauzey, Birkeland and Dayton 1968). These predators are consistently common as a group and we have observed no major fluctuations in either prey or predator abundance over a period of eleven years. With this apparently opulent food supply, one would expect that total predator density might increase until the predators begin to eliminate their prey in local areas or at least seriously reduce its abundance.

OBSERVATIONS

Cucumaria lubrica is a small (up to 0.5g dry weight) dendrochirote holothurian which is numerically predominant over large areas of nearshore subtidal rock or cobble substrata in the San Juan Islands. The population density from November 1968 through May 1969 at Eagle Point (cf. Fig. 1, a map, in Mauzey, Birkeland and Dayton 1968) was estimated as 4420 ± 400 (±) m^{-2} from counts in eight 0.01 m^2 and four 0.06 m^2 quadrats. In the four quadrats of May 1969, an average recruitment of 7.7 x 10^3 m^{-2} additional tiny *C. lubrica* was observed. *Cucumaria lubrica* is thus numerically prevalent and, in fact, occupies up to 43% of the primary substrata in such areas as Black Rock (Fig. 1; Mauzey, Birkeland and Dayton 1968) and much of the area along the west shore of San Juan Island (e.g., Eagle Point and Edward's Reef). In 1972 the mean abundance from all samples from Eagle Point was 4380 m^{-2}, not significantly different from the 1968-1969 samples. Our observations over an eleven year period (December 1965 through August 1976) indicated that this is a stable condition; *C. lubrica* continued to occupy a major portion of the substrata at Eagle Point and Edward's Reef throughout this period. Like most dendrochirote holothurians, *C. lubrica* is a passive suspension-feeder, and a position with adequate access to the water current is potentially a limiting factor.

The size distribution of *C. lubrica* from dry weights taken on 239 specimens collected in November 1968 and February 1969 is shown in Figure 1. The size distributions from these two collections did not differ significantly, so the data from the two collections were combined. Five normal curves were extracted from the size distribution in Figure 1 by using the method of Cassie (1954). Assuming the different normal curves represent year classes, the longevity of *C. lubrica* was estimated as 5 years. Estimates of size classes derived from the method are given in Table 1.
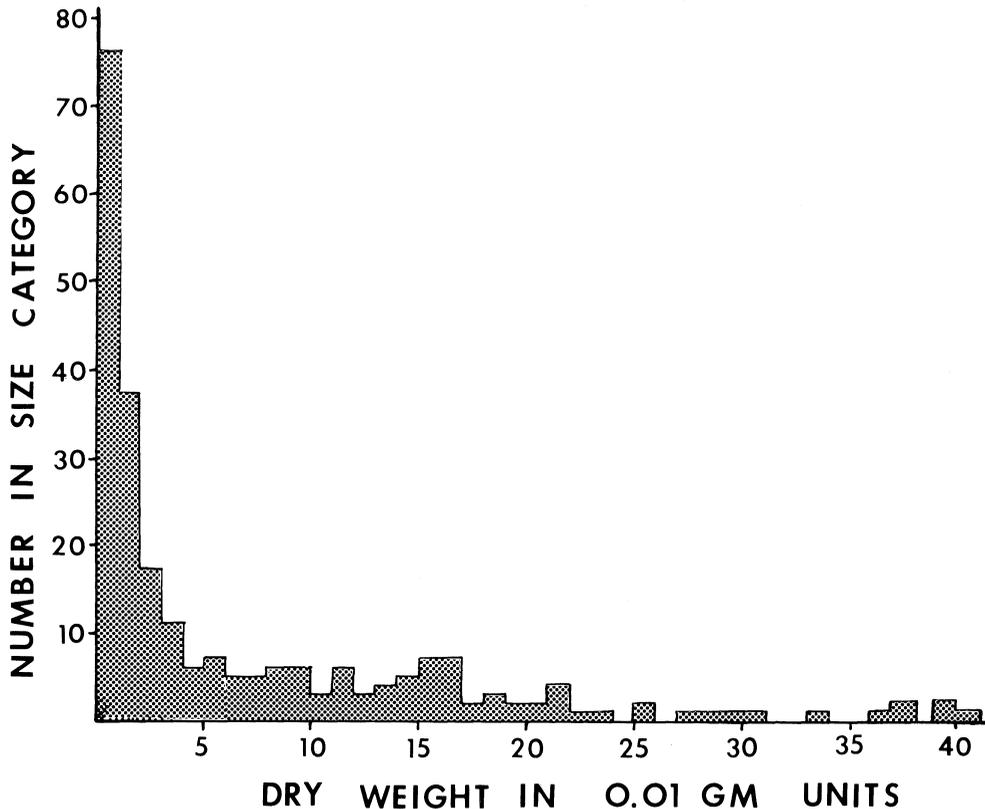
Fig. 1. Size distribution of *Cucumaria lubrica* at Eagle Point (at 10 m depth) from collections taken November 1968 and February 1969.

In areas in which it is predominant, this diminutive holothurian is preyed upon by seven species of asteroids (Mauzey, Birkeland and Dayton 1968): *Luidia foliolata* Grube, *Solaster stimpsoni* Verrill, *S. endeca* (Linnaeus), *S. dawsoni* Verrill, *Dermasterias imbricata* (Grube), *Leptasterias hexactis* (Stimpson) and *Pycnopodia helianthoides* (Brandt). While four of these species are generalists (*L. foliolata, D. imbricata, L. hexactis* and *P. helianthoides*) and prey upon organisms other than holothurians in areas where holothurians are not predominant, the abundances of the *Solaster* species appear to be related to the abundance of dendrochirote holothurians (Mauzey, Birkeland and Dayton 1968).

Luidia foliolata and *Pycnopodia helianthoides* only occasionally feed on *C. lubrica*. Forty-four percent of the observed prey items (N=61) of *L. foliolata* were holothurians and of these only about 47% (N=8) were *C. lubrica* (Mauzey, Birkeland and Dayton 1968). *Luidia foliolata* is characteristic of gently sloping or flat sand bottoms where it feeds on ophiuroids, holothurians and bivalves and is rare in current swept areas on solid substrata characterized by *C. lubrica*. Although large numbers of *C. lubrica* (17, 17 and 35) were found in *Pycnopodia* stomachs on 3 occasions, less than 2% of the feeding observations for *Pycnopodia* in the San Juan Islands included *C. lubrica* (Mauzey, Birkeland and Dayton 1968). Since *Luidia* and *Pycnopodia* only rarely eat *C. lubrica*, they will not be discussed further.

Table 1. Size class distributions of *Cucumaria lubrica* derived according to the methods of Cassie (1954).

Assumed Year Class	Dry Weight (10 mg units)		Standard Deviation	% of Total Collection*
	Mean	Range		
0	1.88	0.1 to 6.0	1.84	64.4
1	9.79	6.1 to 13.0	2.74	14.3
2	16.78	13.1 to 21.0	˙2.08	13.3
3	25.42	22.0 to 31.0	4.46	5.1
4+	38.30	34.0 to 41.0	4.49	2.9

*N = 239

Leptasterias hexactis and *Dermasterias imbricata* tend to specialize on *C. lubrica* in areas where *C. lubrica* is predominant, although they have very different diets in other areas. Small holothurians make up 82% of the diet of subtidal *L. hexactis* in the San Juan Islands (Mauzey, Birkeland and Dayton 1968), and *C. lubrica* comprises 85% of the holothurian prey or 69.7% of the total diet. In intertidal areas, however, *L. hexactis* feeds mainly on barnacles and molluscs (Menge 1972). In *C. lubrica* beds, 96.7% of the diet of *D. imbricata* (N=123) is made up of dendrochirote holothurians and of these, 92.4% are *C. lubrica* (89.4% of the total diet). In other areas, however, over 95% of the diet of *D. imbricata* may be made up of anemones, sponges, or pennatulaceans (Mauzey, Birkeland and Dayton 1968; Birkeland 1974) or 45% echinoids (Rosenthal and Chess 1972). Twenty-three *D. imbricata* contained from 1 to 30 + *C. lubrica* in their stomachs, with a mean of 7.7 *C. lubrica* per stomach.

Solaster stimpsoni and *S. endeca* feed mainly on dendrochirote holothurians (Mauzey, Birkeland and Dayton 1968). In the San Juan Islands, we recorded 424 feeding observations for *S. stimpsoni* (64% of the 656 *S. stimpsoni* examined were feeding). Holothurians made up 96% (or 408) of the feeding observations and of these, *Cucumaria lubrica* accounted for 93% (89.3% of the total diet), *Eupentacta* sp. and *C. miniata* (Brandt) 2% each and *Psolus chitinoides* H. L. Clark 1%. The *S. stimpsoni* preying upon *C. lubrica* were found with 1 to 8 specimens of *C. lubrica* per seastar or with a mean of 1.6 ± 0.9 s. *Solaster stimpsoni* spends 64% of its time feeding and 89% of its diet consists of *C. lubrica*. The average time required for digestion of a meal of *C. lubrica* was found to be 1.5 days for four observations in aquaria. Therefore, each *S. stimpsoni* eats about 222 *C. lubrica* per year. (This and similar calculations for the rate of predation on *C. lubrica* by the other species of asteroids are given in Table 2. The proportion of the *C. lubrica* population and biomass consumed by the combined activities of all asteroids is calculated in Table 3.)

One hundred thirty-eight *S. stimpsoni* were individually tagged with FD-67 Floy Tags. Within a year, most of the tagged seastars had disappeared, although many of these apparent disappearances could be simply a loss of tags with no sign of damage to the seastar. The *S. stimpsoni* recovered were individuals which had disappeared for several months, then reappeared. Other solasterids, *S. dawsoni* and *Crossaster papposus* (Linnaeus), are characteristically very motile (Mauzey, Birkeland and Dayton 1968; Birkeland 1974).

Although *Solaster stimpsoni* and *S. dawsoni* appeared to wander in and out of the area, they were relatively scarce in other areas and appeared not to be feeding as well in these other areas. We have examined many different habitats and localities between 1965 and 1976 (cf. also Mauzey, Birkeland and Dayton 1968). The percent of the *Solaster* that were feeding was lower in these other habitats (Birkeland 1974) and some of the prey items were of rather doubtful benefit to the *Solaster* (Mauzey, Birkeland and Dayton 1968; Birkeland 1974). For instance, *Solaster stimpsoni* feeds mainly on holothurians which were more scarce in these other habitats so the percent of the *S. stimpsoni* found feeding was lower. Sometimes *S. stimpsoni* was found with its rays wrapped around and its stomach extruded upon the surface of a sea pen, *Ptilosarcus gurneyi* (Gray), or over a tunicate, *Pyura haustor* (Stimpson). In these cases there was no sign of damage to the prey.

Although individual *S. stimpsoni* switched from "wall" to "wall" (areas in our study site) or disappeared while new individuals arrived in the area, the abundance of *S. stimpsoni* did not change significantly during the 9 year period (Table 4). The numbers of *S. stimpsoni* were counted on specific rock walls and on certain sections of horizontal cobble substrata in our study areas on 10 dates from 14 December 1967 to 13 August 1976. If we take dates as treatments or conditions and the six larger sample areas as subjects or replicates, we can use the nonparametric Friedman two-way anova by ranks (Siegel 1956) to test if the number of *S. stimpsoni* in the area varied significantly with time. Since the areas over which the counts were made must be complete matched sets for given dates, we tested the counts from the upper four rows (areas) in

Table 2. Rate of removal of *Cucumaria lubrica* by predation from six species of asteroids.

Predator Species	% of individuals found feeding (A)	% of diet consisting of C. lubrica (B)	Average No. of C. lubrica per stomach containing C. lubrica (C)	C. lubrica eaten per individual per year (365 ABC) 1.5*	C. lubrica eaten per 100 m² per year**
Solaster stimpsoni	64	89	1.6	222	10955
Solaster endeca	62	58	1.0	88	18
Solaster dawsoni	53	7	2.0	18	13
Dermasterias imbricata	64	89	7.7	1067	3522
Leptasterias hexactis	44	70	1.0	75	30
Pycnopodia helianthoides	51	1	26.0	32	97
				TOTAL	14635

*A consumption and digestion time for *C. lubrica* of 1.5 days is assumed for each species of asteroid based on the average of four observations in the laboratory for *S. stimpsoni* and five observations in the laboratory for *Dermasterias*.

**Calculated from data in Table 5.

Table 3. A calculated estimate of the proportion of *Cucumaria lubrica* biomass consumed by all six species of its asteroid predators.

Age Class	a no. m^{-2}	b no. eaten m^{-2}	c g m^{-2}	d g eaten m^{-2}
SET	2835	—	53.3	—
1 (yearlings)	626	36.6	61.3	3.6
2	589	36.6	98.8	6.1
3	221	36.6	56.2	9.3
4+	129	36.6	49.4	14.0
TOTAL	4400	146.4	319	33.0

a. No./m² determined by apportioning the abundance of 4400/m² according to the ratio of the numbers in year classes from Table 1.

b. No. eaten/m² acquired by evenly dividing the total from Table 2 among the larger year classes because *S. stimsoni* prefers larger *C. lubrica*.

c. G/m² derived by multiplying column a times the mean dry weight of each year class from Table 1.

d. G eaten/m² estimated by $\dfrac{\text{no eaten m}^{-2} \cdot \text{g m}^{-2}}{\text{no. m}^{-2}}$

Table 4 for all dates except December 1967 and January 1969 for which counts were lacking in one of the areas. Although there appears to be an increase in the numbers of *Solaster stimpsoni* over the nine year period (Table 4), the Friedman two-way anova by ranks test indicates that there was a seventy to eighty percent probability that the differences could have been greater by chance. On five dates, counts were made in all six areas. We compared October 1967, November 1968, February 1969, January 1972 and August 1976 for all six areas and found that there was a ten to twenty percent probability that the differences between dates would have been greater by chance alone. Therefore, the *S. stimpsoni* population seems to be characterized by a stability in numbers during a constant wandering of individuals in and out of a given local area. This is characteristic of several seastar populations (Menge 1974), including *S. dawsoni* (Birkeland 1974). The mean abundances of *S. stimpsoni* and the seastars relevant to our discussion are given in Table 5.

Seven tagged *S. stimpsoni* were recovered after one year, three of these after 2.6 years, but no predictable growth patterns could be observed. After reaching a diameter of about 25 cm, *S. stimpsoni* may increase or decrease in size. Those seastars which decrease in total diameter (tip of ray 1 to tip of ray 6) look "unhealthy"; the rays are particularly thin and occasionally even have concave grooves. From these few data (Table 6) we estimated the growth of adult *S. stimpsoni* (excluding from the analysis those decreasing in size) at 2 cm total diameter per year. Presumably, small individuals would grow at a greater rate.

About 21% of the *S. stimpsoni* at Eagle Point during 1968 and 1969 (N=74) were infected with a parasitic green alga *Diogenes* sp. Two of the six tagged *S. stimpsoni* that decreased in size were heavily infected; none of the six that grew were infected. Both of the *S. stimpsoni* had been infected by *Diogenes* sp. during the entire observation period, so *S. stimpsoni* is able to survive with *Diogenes* sp. for at least 32 months. One untagged *S. stimpsoni* was observed to be very green and very near death, motionless with concave grooves in its thin rays.

Of a total of 42 field observations on *Solaster endeca*, 27 were feeding: 16 on *Cucumaria lubrica*, 3 on *C. miniata*, 2 on *Psolus chitinoides*, and 6 on bryozoa, tunicates and unidentified organisms. *Solaster endeca* was very rare in our study areas with 0.004 times the abundance of *S. stimpsoni* (Table 5).

Of 138 field observations on *Solaster dawsoni*, 65 (47.1%) were feeding: 39 (60% of those feeding) were feeding on *S. stimpsoni*, 5 on *C. lubrica*, 4 on *Crossaster*, 3 on *Dermasterias*, 3 on *Leptasterias*, 3 on *Mediaster*, 3 on arms autotomized from *Evasterias*, 2 on arms autotomized from *Pycnopodia*, and 1 each on *Henricia*, *Balanus crenatus* Brugiere and *Solaster dawsoni*. *Solaster dawsoni* is cannibalistic and will defend itself against predation by others of its own species with a response similar to that used by *S. stimpsoni* (cf. Fig. 2 in Mauzey, Birkeland and Dayton 1968).

The recorded diameter ratios of prey *S. stimpsoni* to predator *S. dawsoni* which had successfully captured them were 0.38, 0.72, 0.90, 0.94, 1.00, 1.00, 1.02, 1.03, 1.08, 1.09, 1.10 and 1.14; the prey-predator diameter ratios recorded for attacks in which *S. stimpsoni* ultimately escaped were 1.18, 2.18, 2.23 and 2.23. The probability of the 4 escapes of *S. stimpsoni* being only by those greater than 1.15 times the diameter of their predator while the 12 successful captures of *S. stimpsoni* were only by those less than 1.15 times the diameter of their predator was due only by chance would be P=0.0011 by a two-tailed Fisher exact probability test (Siegel 1956). From this we conclude that the defence response of *S. stimpsoni* is effective only in combination with a refuge in size of approximately 1.15 times the diameter of the *S. dawsoni* attacking it.

Since *S. stimpsoni* and *Dermasterias* have refuges in relative size, the number of asteroids available as prey to *S. dawsoni* increases as *S. dawsoni* grows larger. The *S. dawsoni* feeding on *C.*

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Table 4. Counts of *Solaster stimpsoni* present on specific topographic areas at the Eagle Point study site during a 9 year period. The hyphens mean that no counts were made on the area on the given date.

SITE NAME	AREA (m²)	14 X 67	11 XII 67	15 IX 68	10 XI 68	16 I 69	22 II 69	10 V - 2 VI 69	5 I 72	6 VII 74	13 VIII 76
WALL No. 1	40	26	22	12	15	19	14	22	30	24	40
WALL No. 2	40	10	13	12	10	7	9	9	15	16	27
FLOOR	32	8	—	12	14	8	7	9	8	26	32
OFFSHORE ROCKS	16	10	3	12	9	—	12	16	7	3	1
WALL No. 3	35	16	26	—	8	—	13	—	23	—	50
WALL No. 4	28	9	—	—	14	—	4	—	4	—	12
MEAN No./m²		.41	.49	.38	.37	.30	.31	.44	.46	.54	.85

Table 5. Mean population densities at Eagle Point of the seastars involved in this study.

Topography	Total area sampled (in m²)	Mean densities (No./100 m²)					
		S. dawsoni	S. stimpsoni	S. endeca	Dermasterias	Leptasterias	Pycnopodia
Rock wall (vertical)	985	0.2	52.0	0.1	3.6	0.2	2.3
Cobble floor (horizontal)	1102	1.1	47.0	0.4	3.1	0.6	3.6
Total	2087	0.7	49.4	0.2	3.3	0.4	3.0

Table 6. Growth of tagged asteroids at Eagle Point.

Diameter in mm (tip of ray 1 to tip of ray 6)		Time interval (months)	Growth rate (mm/mo.)
beginning	end		
		Solaster stimpsoni	
218	252	14.1	2.41
257	287	14.1	2.13
277	270	6.6	-1.06
279	328	15.3	3.20
290	314	32.4	0.74
304	263	9.9	-4.14
304	312	9.9	0.81
315	302	6.6	-1.97
320	308	13.5	-0.89
325	339	10.4	1.35
328	320	31.8	-0.25
340	294	32.6	-1.41
Mean and standard deviation of growth rates		Only positive data included	1.77 ± .97
		All data included	.08 ± 2.10
		Dermasterias imbricata	
163	191	7.4	3.78
353	366	37.9	0.34
388	350	39.7	-0.96
Mean and standard deviation of growth rates		Only positive data included	2.1 ± 2.4
		All data included	1.1 ± 2.4

lubrica for which we have measurements were 9.2, 12.5 and 16.7 cm in diameter. Since only small *S. dawsoni* have been found feeding on *C. lubrica,* we interpret this to mean that *C. lubrica* probably serves as only an alternative food for small *S. dawsoni* which would prey upon asteroids if they could capture them. Indeed, a *S. dawsoni* 4.8 cm in total diameter was found consuming a 4.9 cm *S. stimpsoni.* When *S. dawsoni* is in areas where dendrochirote holothurians and asteroids of accessible size are rare, it will resort to cannibalism (Birkeland 1974). Food availability and cannibalism are the only factors we have found so far that might set an upper limit to the abundance of *S. dawsoni,* a top predator.

The time necessary for capture and consumption of asteroid prey by *S. dawsoni* was measured in the field and the average time required was found to be 4.5 days (Birkeland 1974). However, when the prey to predator diameter ratio for *Crossaster,* which uses the typical solasterid defense response, increases to about 0.7, *S. dawsoni* requires 6 days to complete the attack and consumption. In our single accurately timed field observation of *S. dawsoni* preying upon *S. stimpsoni,* 6 days were required for a 23.8 cm *S. dawsoni* to capture and consume a 16.5 cm *S. stimpsoni.* Six days could be a general underestimate of the time required because the above prey to predator diameter ratio (0.7) is fairly low for a successful attack.

Assuming that *S. dawsoni* requires about 6 days to capture and consume a *S. stimpsoni* and assuming 47% of the *S. dawsoni* are feeding, then *S. dawsoni* spends an average of approximately 7 days between meals or eats 1 meal every 13 days or 28 meals per year. Since 60% of the diet of *S. dawsoni* consists of *S. stimpsoni,* each *S. dawsoni* eats about 17 *S. stimpsoni* per year. There are 0.7

S. dawsoni per 100 m² (Table 5), so *S. dawsoni* predation removes about 12 *S. stimpsoni* per 100 m², or about 24% of the standing crop of *S. stimpsoni* per year.

There may be a bias in our calculations towards an overestimate of the number of *S. stimpsoni* consumed by *S. dawsoni* because the measured times required for consumption were obtained from situations in which the prey: predator diameter ratios were low. However, there may also be a conservative bias in our calculations towards fewer *S. stimpsoni* eaten per year because we may tend to find larger *S. stimpsoni* as the prey of *S. dawsoni*. Smaller *S. stimpsoni* take less time to digest and we have less chance of recording them. If we assumed *S. dawsoni* takes 4.5 days to capture and consume a meal (the average time recorded in all our field observations) then by the same calculations as above, *S. dawsoni* predation would remove approximately 32% of the standing crop of *S. stimpsoni* per year. Similar calculations for *S. dawsoni* estimate that 44 to 59% of its standing crop is possibly removed by cannibalism each year.

DISCUSSION

Theoretical reviews of predator prey systems usually discuss systems with either one predator-one prey or one predator-several alternative prey species interactions (e.g., Murdoch and Oaten 1975). A common system is structured with several predator species obtaining the majority of their food from a single prey species (Elton 1927; Feeney 1970; Birkeland 1974). The prevalence of this several predators-one prey system is often referred to in the general ecological literature (Elton 1927; Smith 1972; Birkeland 1974) but avoided in theoretical reviews of predator-prey interactions.

In order for several of the predators to specialize on a single prey species, the system must be stable enough to provide a dependable food supply to the predators. We have investigated this asteroid-*Cucumaria lubrica* system in an attempt to discover the possible mechanisms that prevent the expected over-exploitation of this single resource under the combined pressure from a variety of predators and which provide the stability to the system.

The asteroid-*Cucumaria lubrica* system is not closed and the individual seastars will wander in and out of the area although the species are always present as a group. Some of these species probably obtain a significant proportion of their diet from other areas and from prey species other than *C. lubrica* in these other areas. But this doesn't answer the question of how *C. lubrica* can remain so abundant under the constant predation pressure of this variety of predators. The alternative prey in other habitats could tend to increase the effectiveness of the predators in keeping the population of *C. lubrica* at lower levels of abundance (Flaherty 1969), at levels too low to support those predators such as *S. stimpsoni* that specialize on them. *Solaster stimpsoni* is relatively scarce in other habitats where they don't feed as frequently and their alternative prey are sometimes of dubious value to them.

As is often the case in temperate marine communities, the diets of these predators diverge when they are found in different habitats but converge on a single resource when they are found together for long periods of time (Birkeland 1974). The resource, *Cucumaria lubrica*, is an example of what Elton (1927: 57) termed a "key-industry" species and the several predators that rely heavily upon it make up a "guild" in the sense of Root (1967). *Cucumaria lubrica* does not have any behavioural, structural or chemical defence or escape mechanisms. Unlike the other dendrochirote holothurians in the area, it does not often live in crevices or partially under rocks, but lives in abundances of four to six thousand per square metre out on open flat exposed rock or cobble surfaces. Food resources that are abundant, palatable and easily accessible to predation are often thought to have a refuge in "unpredictability" (cf. Coe 1956; Smith 1968; Janzen 1970, 1971; Birkeland 1974). This would not seem to apply to *Cucumaria lubrica* because *C. lubrica*

broods its offspring (Atwood and Chia 1974). Recruitment from an abundant brooder presumably occurs usually within an area in which the adults already occur. The abundances of thousands per square metre were maintained with remarkably little fluctuation in the same areas through our eleven years of observation.

The combined predation pressure from all the asteroid species is estimated by the calculations in Table 2 as removing 146 *C. lubrica* per m^2 per year. The mean abundance of *C. lubrica* was 4420 m^{-2} in 1968-1969 and 4380 m^{-2} in 1972. Predation by asteroids accounts for only about 3% of *C. lubrica* mortality or removal of only about 10% o the total standing crop in gms (Table 3). Thus it appears that asteroids which feed on *C. lubrica* have a consistently available food supply. It is most likely that some factor other than food availability must be restricting the increase in abundance of the predators of *C. lubrica*.

Our calculations for the rate of predation by *S. dawsoni* indicates that 24 to 32% of the standing crop of *S. stimpsoni* could possibly be removed during a year. The portion of the size distribution of *S. stimpsoni* greater than 18 cm resembles a single normal curve (fig. 2). If we assume that this represents the "reproductive stock" population while the smaller individuals represent "recruitment", then recruitment replaces less than 15% of the standing crop. The slow growth rate of seastars suggests that this "recruitment" may represent the recruitment of several years. If this is so, then our estimate of the impact of *S. dawsoni* predation on *S. stimpsoni* is an underestimate. Our calculations imply that *S. dawsoni* should be causing the local extinction of *S. stimpsoni*. This is clearly not occurring (Table 4). *Solaster stimpsoni* is over 70 times as abundant as *S. dawsoni* (Table 5) and remains consistently common (Table 4). Therefore some of the prey may not be available to *S. dawsoni*.

The size distribution of *S. stimpsoni* is predominated by the larger individuals (fig. 2) despite the very slow growth rate of adults (Table 6). Although the young *S. stimpsoni* are generally available as food for *S. dawsoni*, the defense response of *S. stimpsoni* evidently provides a refuge from *S. dawsoni* with a diameter less than 87% of its own. Further, *S. stimpsoni* has a refuge from *S. dawsoni* in space as well as size. It can be seen from the data in Table 5 that about 5 times as many *S. dawsoni* are found foraging on horizontal surfaces compared with vertical surfaces. When *S. dawsoni* commences an attack on *S. stimpsoni* and the latter begins its defense response, the leading rays of both individuals are lifted from the substratum. We have not actually observed an attempted attack by *S. dawsoni* on a large *S. stimpsoni* taking place on a vertical surface. However, if *S. dawsoni* ever made such an attempt, the outcome would likely be that both predator and prey would tumble from the wall. If they were separated during the fall, the *S. dawsoni* would probably lose the *S. stimpsoni* since it locates prey by chance physical contact (Feder and Christenson 1966; Mauzey, Birkeland and Dayton 1968). Small seastars (*Leptasterias* and small juveniles of other species) are susceptible to *S. dawsoni* predation on vertical surfaces since capture and consumption of them does not require *S. dawsoni* to release its hold on the substratum. Most instances of *S. dawsoni* feeding on *C. lubrica* were observed on vertical surfaces.

The rate of mortality of *S. stimpsoni* due to infection by *Diogenes* sp. is insignificant in comparison with the rate of mortality due to predation by *S. dawsoni*. We have observed that a *S. stimpsoni* can survive at least 32 months while heavily infected with *Diogenes*. However, the alga eventually dissolves the skeletal ossicles and will kill the seastar. The *Solaster* infected with *Diogenes* that were observed over a two year period all decreased in size (N=3). Infection by *Diogenes* will eventually kill those *S. stimpsoni* that have attained an essentially complete refuge in size from predators (fig. 2), thereby preventing a buildup in numbers in the size refuge, although this process may take a very long time. Infection by *Diogenes* could also increase the probability of mortality through predation by weakening the escape response.

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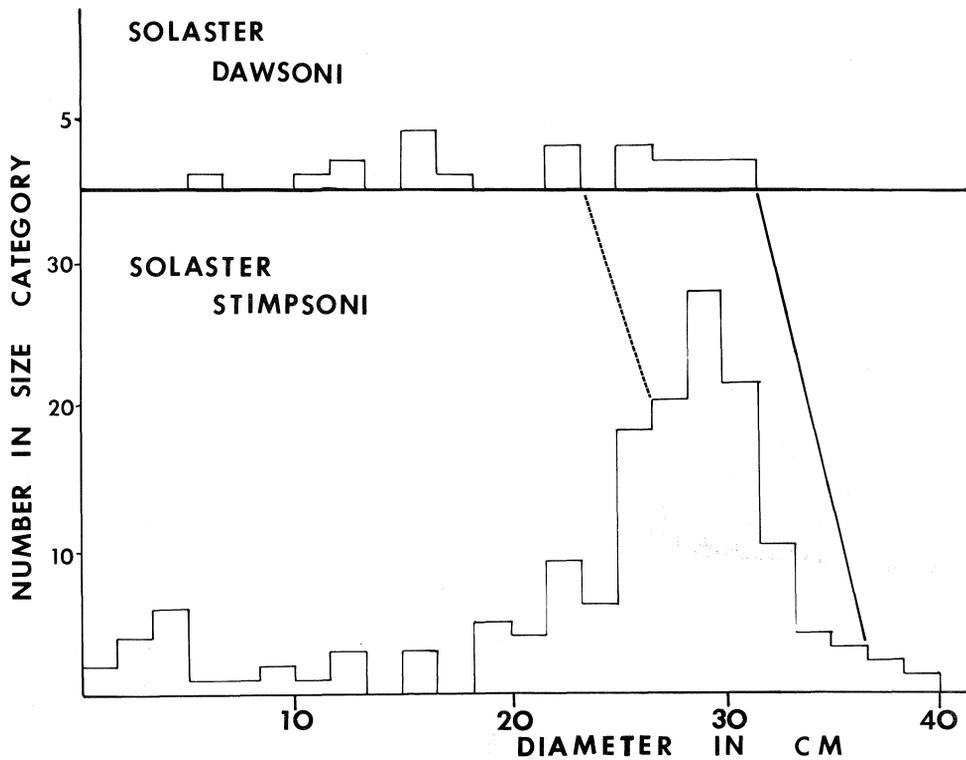
Fig. 2. Size distributions of *Solaster dawsoni* and *Solaster stimpsoni* at Eagle Point. Those *Solaster stimpsoni* larger than the size at the intersection with the broken line are safe from 50% of the *S. dawsoni* population by a refuge in size. Those to the right of the solid line have attained an essentially complete refuge in size from predation.

In contrast to *S. stimpsoni*, *S. endeca* does not have a defence response to predation by *S. dawsoni* (cf. fig. 2 in Mauzey, Birkeland and Dayton 1968 and fig. 3 in this paper). Probably due to this in part, *S. endeca* is the rarest member of the association (Table 5); *S. stimpsoni* is about 250 times as abundant. Similarly, *Leptasterias* is too small to escape *S. dawsoni* once attacked, although its small size may allow it to forage into crevices or cavities under cobble that *S. dawsoni* would pass over. The *Leptasterias* in the subtidal *C. lubrica* meadows have probably strayed from the intertidal part of their range where *S. dawsoni* very rarely wanders. *Dermasterias* has no behavioural defence or escape mechanism, but it can eventually grow too large to be consumed by *S. dawsoni*. With the lack of a behavioural mechanism that increases the effectiveness of the refuge in predator-prey size ratio, *Dermasterias* is only about 7% as abundant as *S. stimpsoni*. Once attaining the refuge in size, *Dermasterias* is susceptible to eventual mortality from infection by *Diogenes*. When attacked by *S. dawsoni*, *Pycnopodia* will autotomize one of its rays, which the *S. dawsoni* eats as *Pycnopodia* leaves the area.

The most remarkable aspect of this food-web association is its relative constancy in abundance from year to year at all trophic levels. The *C. lubrica* population maintained an abundance of 4.4×10^3 m^{-2} from 1968 to 1972. Our observations indicated no major differences
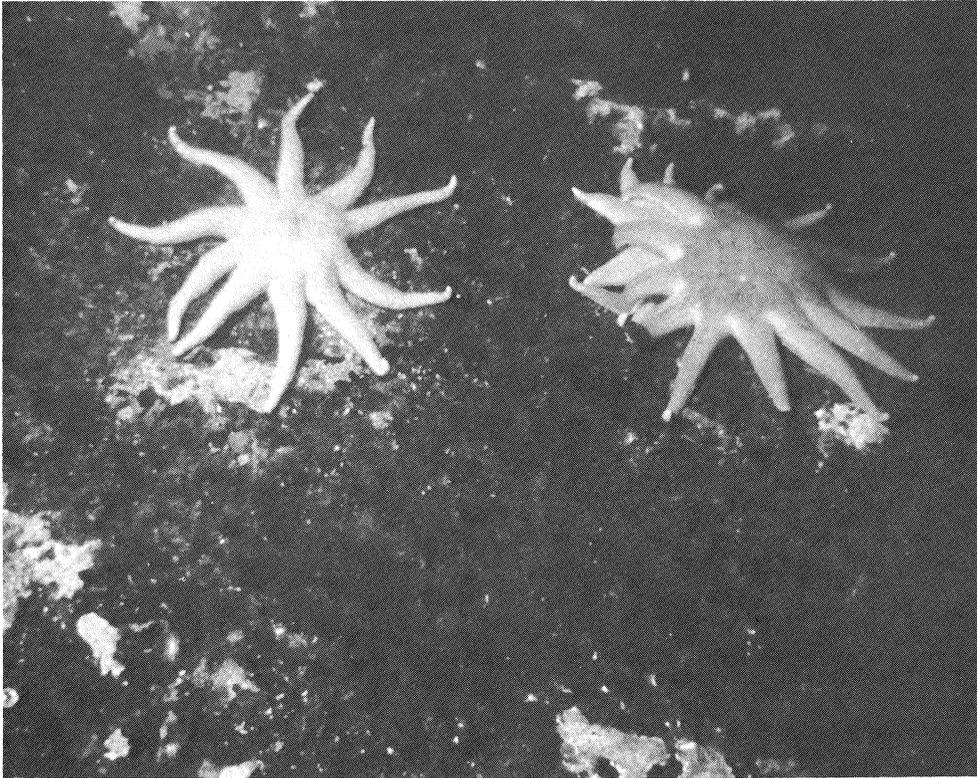
Fig. 3. *Solaster dawsoni* preying upon a *Solaster endeca* with a *Solaster stimpsoni* about 20 cm away. Note the lack of a behavioural escape or defence response by *S. endeca*. The dark tufts are tentacles of *C. lubrica*. *Cucumaria lubria* covers a major portion of the substratum.

from 1965 to 1974. Its most common predator species, *Solaster stimpsoni*, did not significantly differ in abundance through a nine year period (Table 4). The top predator, *S. dawsoni*, averaged 0.7/100 m^2 (2087 m^2 sampled) in 1968-1969 and 0.7/100 m^2 (648 m^2 sampled) in 1972. The interactions controlling the populations of these species differ with trophic level. A large portion of the individuals or available biomass of the *C. lubrica* population is left by predators (Table 3).

The prevention of overexploitation of *C. lubrica* might be explained as follows: *Solaster endeca*, *Leptasterias*, *Dermasterias* and *Pycnopodia* are all rare in the areas of *C. lubrica* under study because of predation by *S. dawsoni*. *Solaster endeca* and *Leptasterias* do not maintain a reproductive stock in the area. The few individuals present had strayed in from outside areas or wandered down from the intertidal and were temporarily missed by *S. dawsoni*. *Pycnopodia* is rarely killed by *S. dawsoni*, but leaves the area (often losing a ray) when attacked. *Dermasterias* does maintain a reproductive stock in the area, but recruitment to this stock may be limited by *S. dawsoni*.

Recruitment to the *S. stimpsoni* population is seriously impaired by predation, but the

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reproductive stock remains consistently common because of a behavioural defence mechanism that becomes increasingly effective with size and works especially effectively on vertical substrata that serve as spatial refuges.

Predation by *Solaster dawsoni* keeps *S. endeca*, *Leptasterias* and *Pycnopodia* from establishing populations in meadows of *C. lubrica*. *Solaster stimpsoni* and *Dermasterias* can maintain a reproductive stock in the area with a refuge in size, but with severe predation on the recruitment to these populations, *S. dawsoni* can prevent *S. stimpsoni* and *Dermasterias* from increasing to population sizes capable of overexploiting their food resource. The slow buildup of populations of seastars having reached this size refuge is most likely prevented by infection from the parasitic green alga *Diogenes* sp. These processes together contribute to the maintenance of a remarkable constancy in numbers of this association at three trophic levels.

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