

FEEDING BIOLOGY OF THE STARFISH

Coscinasterias calamaria (Gray), 1840

(Asteroidea : Asteriidae)

ROY STEWART BELL

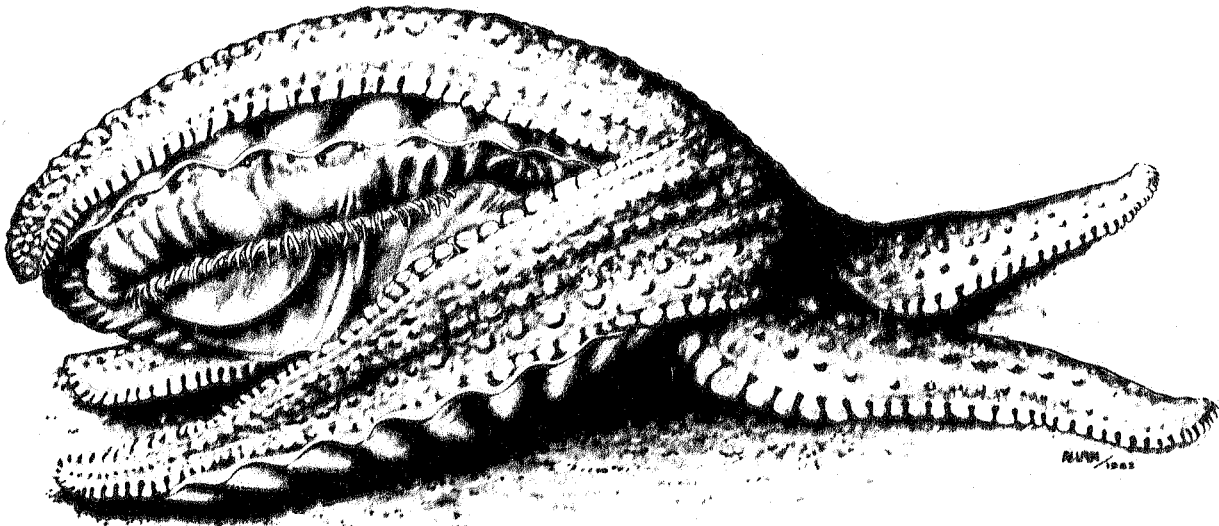
University of Tasmania

1977

A thesis submitted
toward the degree
of Bachelor of
Science with Honours.



DESTROY ALL STARFISH



**IT IS ESTIMATED THAT 1 STARFISH
CAN KILL 10 SCALLOPS PER DAY.**

**DO NOT CUT UP STARFISH
AND THROW LEGS INTO THE
WATER EACH LEG MAY
DEVELOP INTO ANOTHER
STARFISH.**

**STARFISH SHOULD BE KEPT
IN CASES AND BROUGHT
ASHORE TRY THEM AS
GARDEN MANURE AFTER
THEY HAVE DIED.**

**CLEANLINESS AND QUALITY
ARE ESSENTIAL!**

For Further information contact: Department of Agriculture, Fisheries Division, Morrison St., Hobart.

ACKNOWLEDGEMENTS

I would firstly like to thank all members of the Zoology department who assisted me during the course of this study. In particular, I am indebted to Dr. D. Ritz for the original suggestion which led to this study, for his assistance throughout the year and finally for his criticism of the manuscript. My thanks also to Dr. R. White who reviewed the final stages of the manuscript in Dr. D. Ritz's absence, and Mr. A. J. Dartnall whose advise during the year has been most helpful. To Dr. T. Dix of the Marine Fisheries Division of the Department of Agriculture, many thanks for guidance during the early stages of this study, and for the kind loan of scallop survey reports.

I am grateful for the assistance during scallop sampling of fisheries officers J. Woods, R. Parker and R. Green, and the many others who helped with field work. Diving safety and support was generously given by Messrs. R. Mawbey, P. Last, P. Jarvis, J. Pope, A. M^CGifford and especially Mr. D. Breeze. I would also like to thank Messrs. T. C. and D. Sward for allowing me to conduct experiments from their jetty at Kettering.

I did appreciate and benefit from the free flow of information and materials amongst my fellow honours students, especially Mr. G. Shaw and Mr. T. Fletcher who obligingly taught me photography. Thanks are also due to Dr. R. Gaymer for unselfishly lending me his photographic equipment, and Dr. A. M^CKee for producing some fine electroscanning micrographs.

I am grateful to Mrs. M. Drelich for typing this thesis so accurately and promptly, and to Mr. A. Wilson for his continual encouragement and help. Finally, I wish to express my appreciation to Miss V. Lanzlinger who was a great help both behind the typewriter and on field trips as a diver and data recorder.

CONTENTS

page

Summary

Chapter 1 GENERAL INTRODUCTION

1A	Introduction	1
1B	Study Areas & Sampling Sites	5
	i Starfish Sampling Sites	5
	ii Scallop Sampling Sites	7
	iii Study Areas	9
1C	Experimental Animals:Description and Habitats	10
	i Scallops	10
	ii Starfish	12

Chapter 2 FEEDING IN *Coscinasterias calamaria*

2A	Introduction	14
2B	Feeding Rates	17
	i Materials & Methods	17
	ii Results & Discussion	18
2C	Feeding Preferences	22
	i Materials & Methods	22
	ii Results & Discussion	24
2D	Food Preference Model	27
2E	Feeding on Broken Bivalves	30
	i Materials & Methods	30
	ii Results & Discussion	32
2F	Conditioned Feeding	34
	i Materials & Methods	34
	ii Results & Discussion	35
2G	Feeding in the Field	37
	i Materials & Methods	37
	ii Results & Discussion	38
2H	General Discussion	46

Chapter 3 SPONGE - SCALLOP - STARFISH INTERACTIONS

3A	Introduction	50
3B	Materials & Methods	51
	i Feeding Experiments	51
	ii Force Experiments	53

	page
3C Results	55
i Feeding Experiments	55
ii Force Experiments	57
3D Discussion	59
<u>Chapter 4 ESCAPE BEHAVIOUR OF PREY</u>	
4A Introduction	62
4B Responses to Live Starfish	66
i Materials & Methods	66
ii Results	68
4C Avoidance Responses to Starfish Extracts	74
i Materials & Methods	74
ii Results	76
4D Escape Responses in the Field	77
i Materials & Methods	77
ii Results	78
4E Discussion	80
<u>Chapter 5 GENERAL DISCUSSION</u>	85
<u>REFERENCES</u>	86
<u>APPENDIX</u>	94

SUMMARY

1. Aspects of the feeding biology of the large predatory starfish, Coscinasterias calamaria, were studied with an emphasis on three of its prey species, the scallops Pecten meridionalis, Equichlamys bifrons and Mimachlamys asperrimus. Where possible, experimental observations were supplemented with field data.
2. Feeding rates were calculated for C. calamaria to be:
0.50 commercial scallops (P. meridionalis)/starfish/day;
0.33 queen scallops (E. bifrons) /starfish/day;
0.36 doughboy scallops (M. asperrimus) /starfish/day;
0.25 mussels (Mytilus edulis planulatus) /starfish/day;
3. The feeding rate of C. calamaria expressed as a percentage of the body weight ranges from 3.9% to 5.1% per day.
4. Factors affecting feeding rates were examined. Differences in rates were attributed to:
 - i) different surface textures of scallops ;
 - ii) adductor muscle size ;
 - iii) calorific content of food types;
5. C. calamaria does not prefer any one scallop species to another. The apparent preference for commercial scallops probably reflects the differences in feeding rates.
6. A preference model is proposed to determine whether true preferences exist.

7. C. calamaria consumes significantly greater quantities of damaged bivalves than uninjured bivalves. As the feeding rate did not differ between damaged and undamaged scallops, it was concluded that a true preference for injured scallops exists.
8. C. calamaria becomes conditioned to eat one food type when only one food species is presented to it for a period of one month. When offered a choice of two food types, conditioned starfish chose that which they had previously been exposed to.
9. From measurements in the field it was found that adult C. calamaria select mussels from all size ranges whilst juvenile starfish eat small mussels.
10. C. calamaria consumes a diverse range of prey species in the field.
11. 41% of C. calamaria were feeding in the field during September.
12. An examination of Marine Fisheries Department data on scallop and starfish distributions in Oyster Bay, revealed that the main population of starfish was not feeding on scallop beds. Seasonal changes in position of scallop beds is not followed by corresponding changes in starfish movements.
13. The interactions between doughboy scallops (M. asperimus), their sponge cover and starfish was investigated. It

was found that sponge covering significantly reduces predation by altering the surface texture of the scallop shell. This increases the efficiency of the escape response by decreasing the adhesive ability of C. calamaria's tube feet.

14. In feeding experiments it was found that significantly fewer sponge-covered than clean shelled doughboy scallops were captured and eaten by C. calamaria.
15. Force experiments showed that C. calamaria can exert a significantly greater pull on scallops without sponge than on sponge-covered scallops.
16. It is suggested that the association of M. asperrimus with sponges is a mutualism with predation as one of the forces structuring it.
17. An investigation of the escape reactions of scallops to starfish was conducted. It was found that the strongest reactions were elicited by the large carnivorous asteroids C. calamaria and Astrostole scabra.
18. Only starfish of the order Forcipulatida elicited the swimming response in scallops. Asteroids of the orders Phanerozonida and Spinulosida provoked weak responses.
19. Avoidance responses to starfish extracts were generally weaker in intensity than responses to contact with living starfish. This difference may be due to lack of tactile stimulation with starfish extracts.

20. The doughboy scallop reacted less strongly to living starfish when attached to the substrate than when unattached.
21. The reaction of scallops to C. calamaria is considered to be true escape behaviour in response to a recognised predator. It is considered that biochemical similarities between C. calamaria and other asteroids which do not feed on scallops, cause these bivalves to react unnecessarily to contact with the latter.

1A INTRODUCTION

Among the most basic interspecific relationships of animals within a community are those between predator and prey species. In order to understand community structure and its trophic relationships, it is essential that predator - prey interactions be known. However, insufficient knowledge of the quantitative aspects of many such interactions exists. Although ecologists have long recognized the theoretical importance of predator - prey interactions to the understanding of community properties, knowledge of such natural components of the interactions as the role of food preference, the actual types of prey species consumed by a particular predator, and the relative efficacy of escape responses has lagged (Mauzey et al, 1969).

Because of economic implications, considerable attention has been attracted to the notorious ability of certain asteroids to capture and consume bivalves. Their depredation of beds of scallops, oysters, mussels and clams in many parts of the world has long caused concern to fisherman and biologists. For example, in 1958, starfish destroyed oyster beds in Connecticut, causing a monetary loss that year of between 10 and 15 million dollars (Loosanoff 1961). Carnivorous members of the Asteriidae and other asteroids with suckered type feet were the predators concerned. Similarly, Dickie and Medcof (1963) reported that mass mortalities of the scallop, Placopecten magellanicus, were associated with increased abundance of Asterias vulgaris, a starfish known to prey on scallops. A long drawn out controversy concerning the mechanism by which such starfish attack bivalves, has ensued

since 1892 when Bell correctly stated that "dividing its arms into two sets it will pull aside the valves of an oyster", (Feder and Christensen 1966). It is now generally accepted that a great number of asteroid species use force applied by the tube feet to open bivalves, their stomach is everted and the soft parts of the mollusc are digested extraorally.

In Tasmania, the most ubiquitous, large predatory asteroid is the eleven-armed spiny sea star Coscinasterias calamaria (Gray). This species is not endemic to Tasmania but is widely distributed in the Indo-Pacific Region (Fell, 1959). In fact H.L. Clark (1946), records it as undoubtedly the commonest littoral starfish of the southern coasts of Australia.

C. calamaria is a sub-tidal animal commonly found in shallow coastal waters, but has been recorded to a depth of 40 fathoms (Fell, 1962). Colour is variable ranging from tan through yellow, grey-brown to blue-grey. Arm number is very variable ranging from 7-13 in adult specimens, with eleven being most common (Crump, 1969). Adults attain a maximum size of about 35-40 cm in diameter (i.e. $R = 15-20$ cm).

The historical documentation of the association of C. calamaria with scallop beds dates back to the early 1900's when Flynn (1918, in Fairbridge 1952) tabled a report suggesting that a decline in density of scallop numbers in the Derwent Estuary beds may have been attributed to starfish predation. More conclusive evidence was presented by Olsen (1955), who reported an estimated 75-80% mortality on an extensive, densely populated scallop bed in the D'Entrecasteaux Channel over the 4 year period 1951-55. He attributed the reduction in scallop numbers primarily to predation by

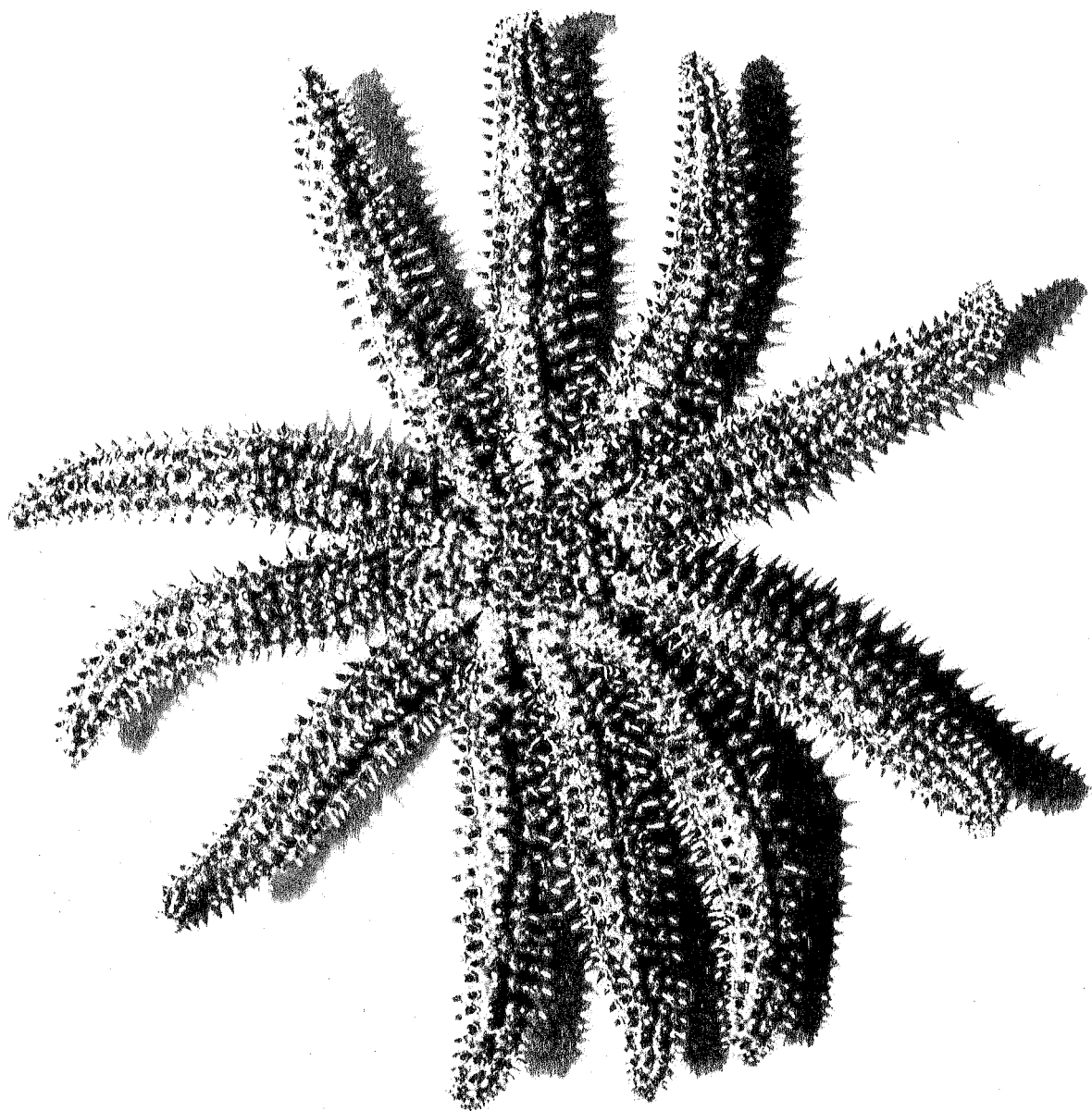
C. calamaria. During the past decade, officers of the Sea Fisheries Division of the Department of Agriculture have recorded numbers and distributions of starfish in Tasmanian waters whilst gathering information for scallop density reports. However, these data are not in a form which can be used specifically to shed more light on the feeding habits of C. calamaria. As recently as October, 1977, C. calamaria was reported to be depleting the reefs of Port Phillip Bay of mussels (Mytilus edulis planulatus) and juvenile abalone (Notohaliotis ruber, Leach).

Little quantitative study has been carried out on the general biology of C. calamaria, its feeding behaviour and prey relationships. Crump (1969) studied some aspects of the natural feeding habits of this species in New Zealand waters, but conducted only five laboratory experiments to determine feeding preferences. Dartnall (1972) writes, "No critical data have yet been published on the effect of C. calamaria on the scallop industry. Most evidence is inductive having been gleaned incidentally to studies on commercial scallops. It appears that there is an urgent need for a planned investigation into the biology of C. calamaria which has been implicated, on no critical evidence, as a danger to one of Tasmanian's fisheries".

The present study was designed to investigate certain aspects, of the feeding biology of C. calamaria, with an emphasis on three of its lamellibranch prey species, the commercial scallop, Pecten meridionalis (Tate), the queen scallop, Equichlamys bifrons (Lamarck), and the doughboy scallop, Mimachlamys asperimus (Lamarck). All three species occur

sympatrically in the D'Entrecasteaux Channel and were economically important before the closure of this fishery in 1965. Although fishable stocks in the channel have declined drastically (Harrison, 1965), C. calamaria is still the most common carnivorous asteroid found in association with scallops in this region (unpubl. fisheries data 1977).

Within the context of general feeding biology, experiments were planned to investigate feeding preferences and rates, and some of the factors influencing predation by C. calamaria. Such factors include escape responses of scallops to C. calamaria and other predatory starfish, the "attractiveness" of damaged tissue, the past feeding history, the interactions between sponge covered scallops and starfish and the effect of different shell textures on feeding rates.



Scale 1:2

Plate 1: 11 Armed Spiny Seastar

Coscinasterias calamaria

1B. STUDY AREAS AND SAMPLING SITES

1. STARFISH SAMPLING SITES

Large populations of C. calamaria were found throughout the year on sub-tidal mussel beds in the Derwent Estuary. Starfish were collected by diving at Blackman's Bay blowhole, site #1. Wave action in this area is strong and intertidal pools are few, restricting C. calamaria to sub-tidal habitats. Specimens were collected from a depth of 1 to 12 metres. The substratum comprises large mudstone ledges upon which the mussels M.e. planulatus live, with caves, crevices and cliffs dropping off onto a sandy bottom at 3 to 12 metres. Starfish, Uniophora sinusoida (Perrier), and Patirella calcar (Lamarck), used in escape response experiments, were also collected from this site.

C. calamaria were studied and collected at a second site, Flinder's Reef at Taroona. (Fig 1). This rocky outcrop is densely covered with mussels. Starfish were found feeding on them in extensive tidal pools at low water. Stars were also studied at this site from low water mark to a depth of 10 metres.

C. calamaria were occasionally sampled from other sites including; Gordon jetty and Port Arthur where they were feeding on oysters, Little Taylors Bay on Bruny Island where they were eating the cockle Katelysia rhytiphora (Lamy), and at Middleton where they were eating M.e. planulatus.

Of the three remaining asteroids used in behavioural work, two were collected from scallop beds in the

6

D'Entrecasteaux Channel, these being Tosia magnifica (Muller and Troschel) and Nectria ocellata (Perrier). The third, Astrostole Scabra (Hutton), Tasmania's largest asteroid, was collected from sub-tidal reefs at Spring Beach, Eagle Hawk Neck and Maydena on the East Coast.

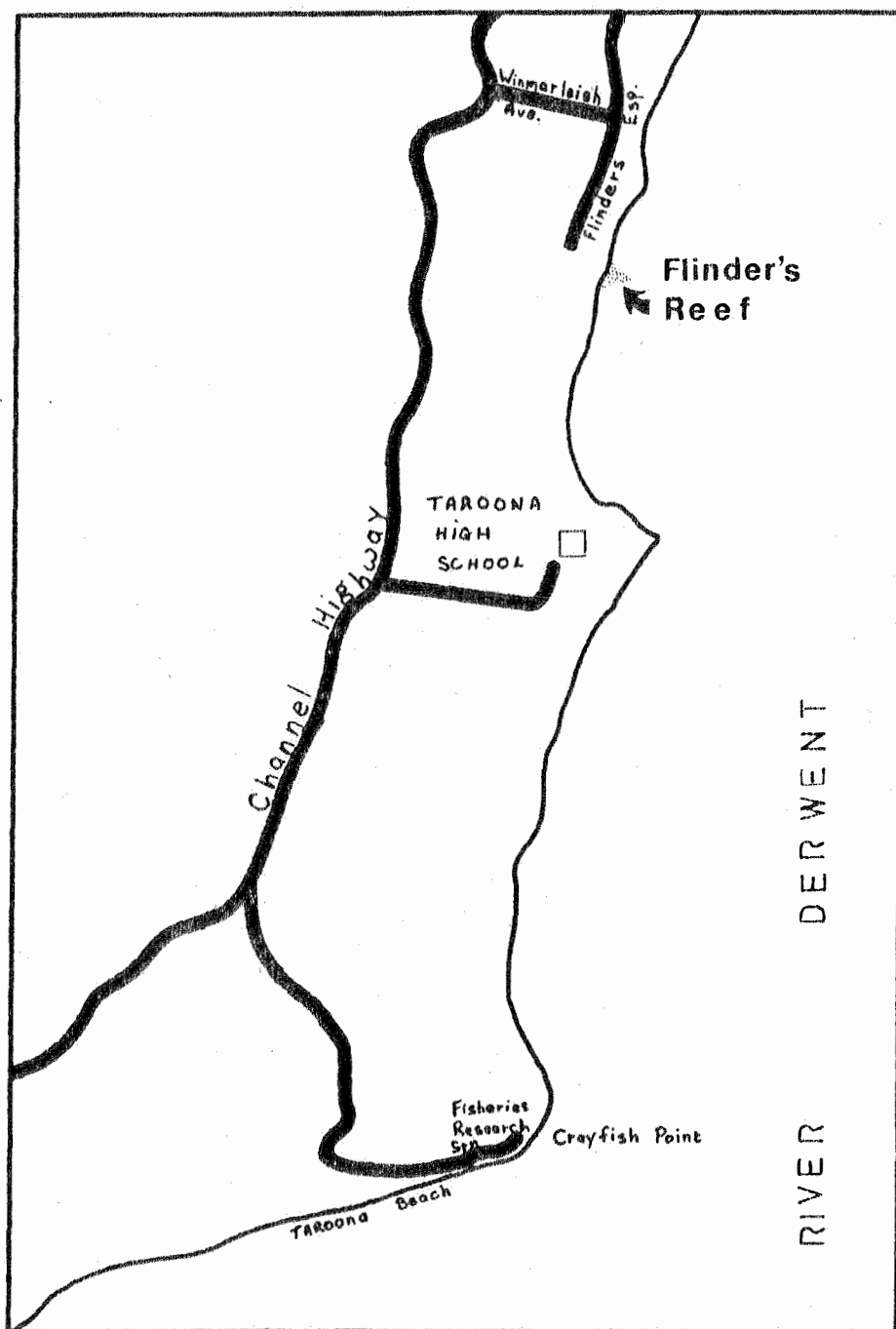


Fig 1: Sample site & Study Area- Flinder's Reef, Tarooma.

ii. SCALLOP SAMPLING SITES

Scallops were collected regularly from eleven sites along the D'Entrecasteaux Channel, and three sites on the East Coast using either S.C.U.B.A. gear or a compressor and hookah. This involved a total of 35 hours diving. Substrata vary with the conditions at each site. Thick mud, sand, bryozoan coral, gritty gravel and rubble reefs were among those encountered. Scallops from the Channel were collected from Huon Island, Great Taylors Bay, Little Taylors Bay, Mountain Creek, Gordon, Middleton, Woodbridge, Helliwells Point, Kettering and Tinderbox Bay (Fig 2). East Coast scallops were found in Schouten Passage, Windlass Bay and beneath the Triabunna woodchip jetty.

Part of the scallop sampling could not have been done without the help of Tasmanian fisheries officers who kindly allowed the author to participate in the scallop survey of the D'Entrecasteaux Channel from the F.R.V. Penghana during June 1977. Forty-two dredge hauls were made and numbers of each species of scallop were recorded from Dennes Point in the north to Partridge Island at the southern entrance to the channel. Scallop sampling on the east coast was also conducted from Fisheries Research Vessel Penghana.

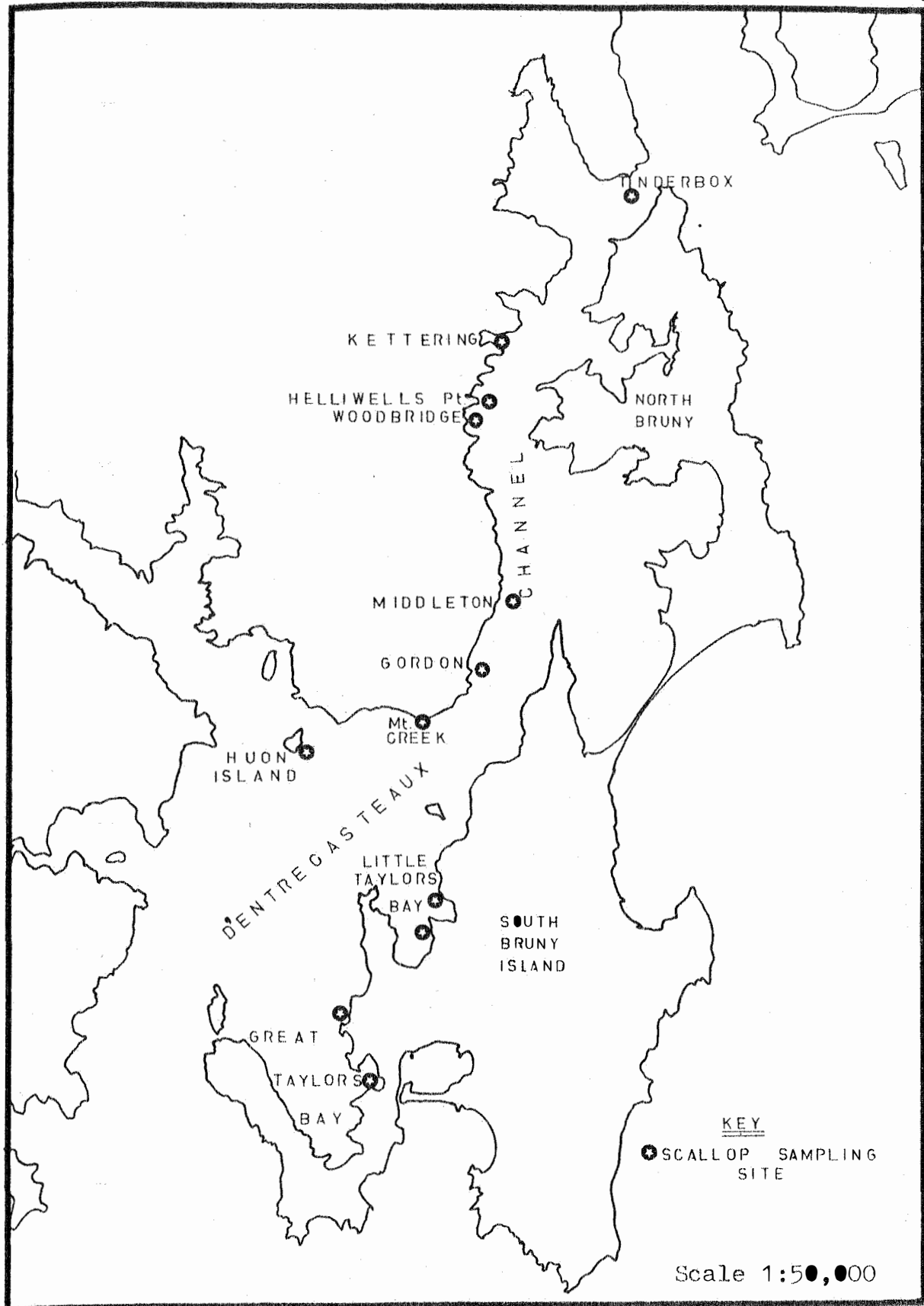


Fig 2: Scallop Sampling Sites in the D'Entrecasteaux Channel.

iii. STUDY AREAS

Underwater experimentation was carried out using S.C.U.B.A. at Blackman's Bay and Helliwell's Point.

Feeding preference experiments were conducted at Kettering where starfish and their food were placed in cages and suspended from a local fisherman's jetty.

Field surveys to study the natural feeding habits of C. calamaria were conducted at Flinder's Reef, Tarooma.

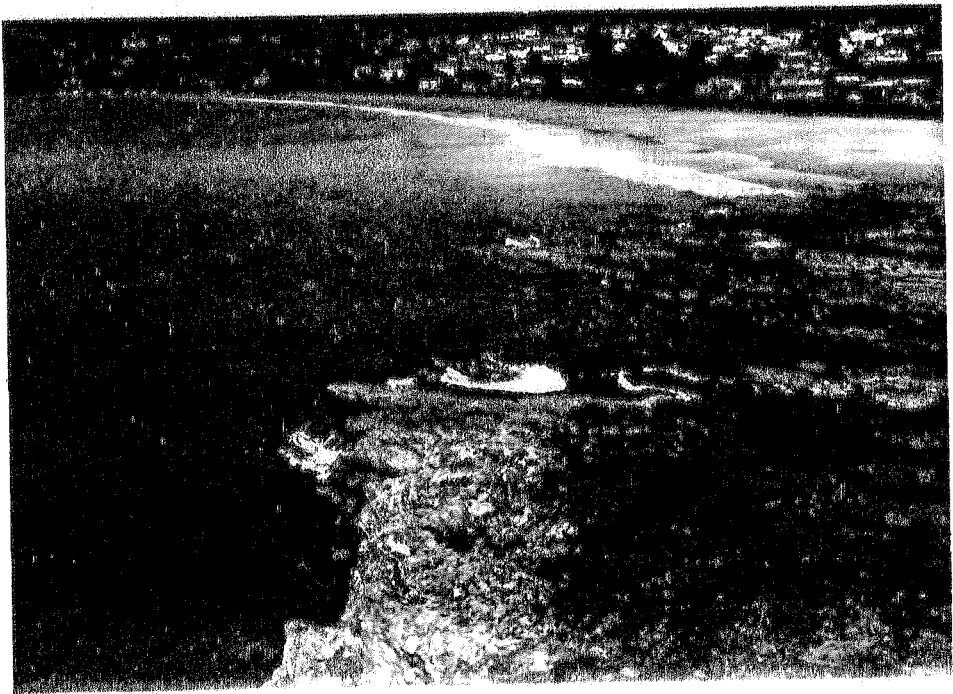


Plate 3. Blackman's Bay Study Area



Plate 4. Sward's Jetty, Kettering.

1C. EXPERIMENTAL ANIMALS; DESCRIPTION AND HABITATS

i. SCALLOPS

Of the four species of scallop living in the D'Entrecasteaux Channel, the doughboy is presently the most common, as was the case in the early years of the fishery. However numbers decreased dramatically during the period 1940 - '65 (Harrison 1961), when commercial scallops became more profuse. Now, fewer commercials than queens are present, whilst the least common species, Mesopeplum tasmanicum (Adams and Angas), is rarely encountered. (Only one specimen found by the author during eight months of sampling, including forty-two dredge hauls through the channel).

Doughboys, M. asperimus are found in nature attached by byssal threads to rocks, dead shell and bryozoan corals, although a small percentage are found lying on muddy or sandy substrata. Thus, attached doughboys usually live in a semi-upright position with the anterior margin some distance from the sea floor. In contrast, commercial and queen scallops lie horizontally on their right hand valves. The left hand valve of a commercial scallop is flat whilst that of a queen is concave and slightly larger, such that it overlaps the lower valve. The above two species are commonly found resting in saucer-shaped depressions which have been gradually excavated in the silt by the ejection of water during the course of normal feeding activity.

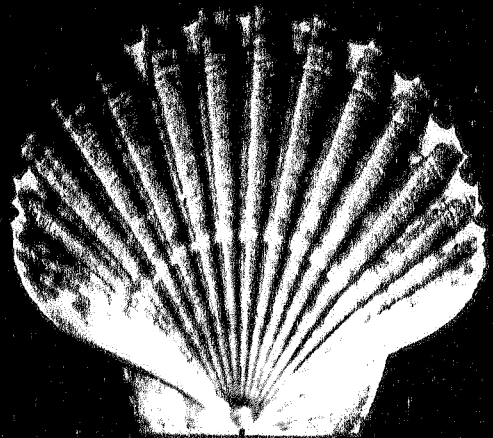
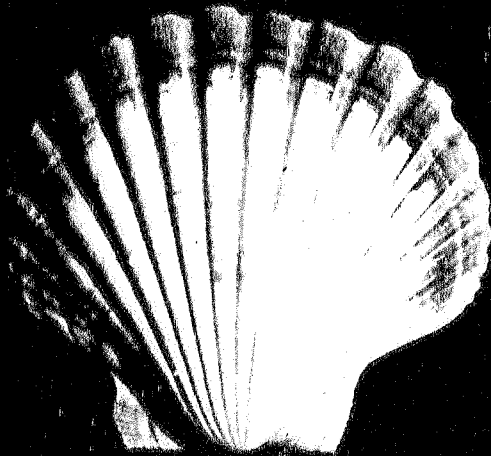
Doughboy and commercial scallops are mostly found in waters 7 to 20 metres in depth (Olsen 1955), whilst queen scallops prefer a depth range of 2 to 13 metres and are

frequently found close to, or actually on rocky reefs, as well as silty areas.

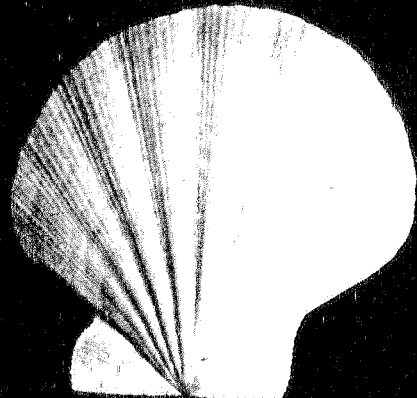
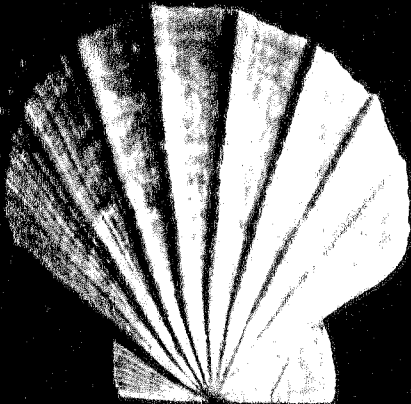
Compared to the doughboy scallop which has a rough spiky exterior, the valves of the queen and commercial are relatively smooth. The commercial's flat uppermost valve is commonly coated with a fine layer of sand and silt, whilst the queen occasionally carries a light covering of epizoic algae. However the great majority of doughboy scallops support sponge growth, many being completely enclosed in a thick layer (see plate 7, Ch. 3).

The swimming action of scallops is well documented (Dakin 1952, Thomas and Gruffydd 1971, Lansell 1969), and will not be described here, suffice to say that they swim forwards and upwards with a series of clapping movements which forceably eject water streams from either side of the hinge line.

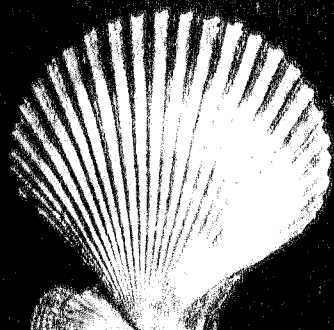
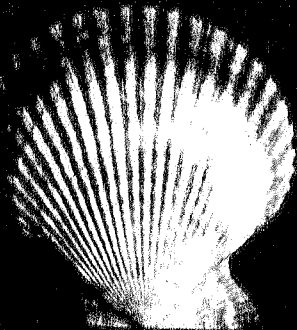
Perception of changes in a scallop's immediate environment is enhanced by virtue of numerous eyes and tentacles on its mantle edge. Thus, such stimuli as moving shadows, diffusing chemicals or actual contact provoke all three species of scallops found in the D'Entrecasteaux Channel to tightly close their valves or swim away.



Pecten meridionalis
(Commercial scallop)



Equichlamys bifrons
(Queen scallop)



Mimachlamys asperimus
(Doughboy scallop)

ii. STARFISH

C. calamaria commonly inhabits sub-tidal reefs and sandy, muddy or gravelly substrata, where it feeds on a variety of molluscs, crustaceans and flesh from dead animals. This species adopts a characteristic feeding posture (plate 6) in which it humps itself over its prey and either enshrouds it in folds of its extruded stomach, or inserts stomach lobes through openings in the shell or exoskeleton of its victim.

A further 5 starfish were used during the course of this study. Astrostole scabra which commonly grows to a diameter of 45 cm (18 inches) and has been recorded by Fell (1959) to 20 inches across, is a predator of gastropods, including the commercial abalone N. ruber, the triton Argobuccinium vexillum Sowerby and the elephant snail Scutus antipodes Montford, (Dartnall, 1969), whilst the author has observed this species feeding on the common thaid Dicathais textilosa Lamarck. Unconfirmed reports from local fishermen associate the presence of A. scabra with scallop beds on the East Coast. Little is known of the biology of this large 7 armed starfish which is described by Fell (1962) as the most voracious of New Zealand's asteroides.

Uniophora sinusoida lives on littoral reefs in the D'Entrecasteaux Channel but is not found on scallop beds. This species feeds on tunicates and to a lesser degree, small native oysters Ostrea angasi Sowerby and mussels M.e. planulatus. Adults have 5 arms and grow to a diameter of 16-20 cm.

Patiriella calcar, a common asteroid of the littoral zone,

is recorded by Shepherd (1968) as omnivorous, feeding on detritus, algae, gastropods, pelecypods and as scavenging moribund animals. It prefers the shallower waters of its range. This species has 8 short arms and adults are commonly 6 - 8 cm in diameter (Clark, 1946).

Asteroids Nectria ocellata and Tosia magnifica are both commonly found on scallop beds in the D'Entrecasteaux Channel. N. ocellata is an orange colour in the field, and attains an adult size similar to that of U. sinusoida. Shepherd (1967a) noted that this species feeds on sponge. T. magnifica, the biscuit star (Dakin, 1952), is a salmon pink to brown colour, has very short arms, is pentagonal in shape and rarely grows larger than 10 cm. No feeding data are available for T. magnifica. However, a related species T. australis Gray, feeds on detritus, molluscs, rock encrusting ascidians and bryozoa (Shepherd, 1968). T. magnifica is commonly found associated with bryozoan corals on scallop beds in the Channel, and has occasionally been observed naturally perched on top of doughboy scallops attached to the coral.

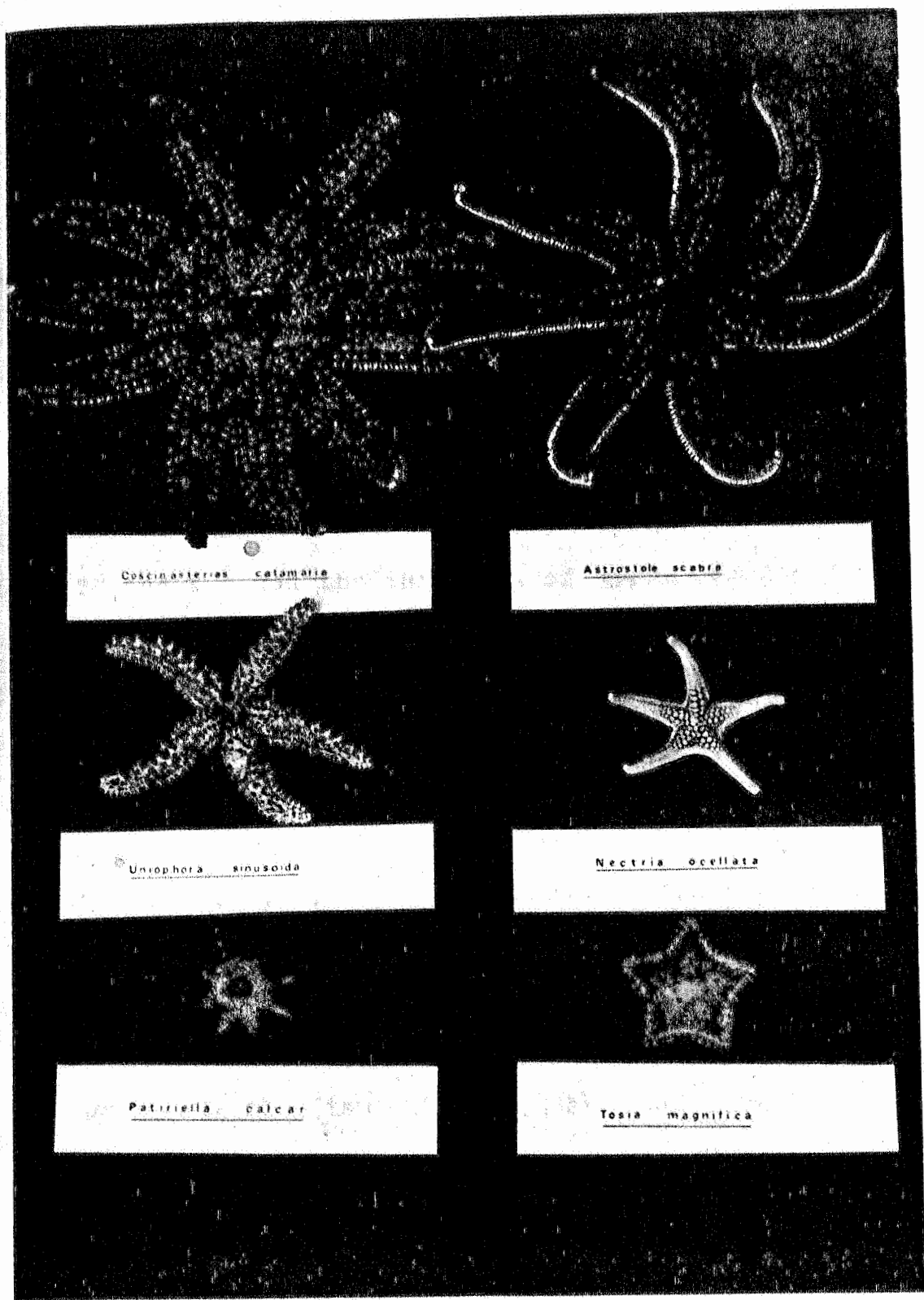


Plate 5. Starfish used for behaviour experiments.

Chapter 2

FEEDING IN *Coscinasterias calamaria*

2A INTRODUCTION

According to Anderson (1966) the typical asteroid is a predatory carnivore. Therefore, a knowledge of predator - prey interactions is important in assessing the feeding behaviour of starfish. A large body of work on asteroid feeding habits has been published, (reviewed by Feder and Christensen 1966) and many such publications deal with predator preferences and feeding rates, but the distinction between the two and the influence of one upon the other is often vague. Predation is usually selective in some sense : given a variety of prey, the pressure will be greater on certain species, age groups or size ranges.

A preferred prey species is measured as that which is consumed in the greatest quantities when the predator is given a choice of food types. The influence of preference acts before the predator has actually seized its prey, and is directed by the attractiveness of the food. In the case of a predatory starfish, the attraction may involve recognition of a certain type of prey behaviour, the influence of past history on the learning processes of the starfish or the recognition of a chemical stimulus coming from the prey. Experiments (Castilla, 1972, Zafiriou, Whittle and Blumer, 1972) and field observations have provided definite evidence that substances attractive to starfish are released from prey.

Mauzey et al (1968) found that some starfish in Puget

Sound were specialists preferring to feed exclusively on one prey type, whilst others were more generalized in their diet in the field, even though they exhibited preferences in laboratory studies. The practical implications of studying feeding preferences were clearly shown by Hancock (1955), when he found that the starfish, Asterias rubens, under certain conditions, may be beneficial to oyster culture because it prefers to feed on competitors (mussels and slipper limpets Crepidula fornicata) or enemies (Urosalpinx) of the oysters instead of the oysters themselves.

Feeding rates on the other hand, are influenced by preferences, but mainly governed by physical factors of the prey and the environment. These factors influence predation efficiency and thereby control the numbers eaten in a given time. The relationship between feeding rates and preferences may be confused if no preference is displayed. In this case, differences in numbers eaten are due purely to factors affecting the rate. For a predatory starfish these factors include predator size, prey size, changes in the surrounding water temperature, time spent searching for the prey, the efficiency of a prey's escape response, surface texture of the shell or exoskeleton, the quantity of edible tissue per food item, the amount of energy needed to overcome the captured prey's defensive mechanisms (i.e. bivalves clamping shut) and the actual food requirements of the predator.

Mauzey (1966) has shown that the latter varies with maturing of the sexual organs, whilst Mackenzie (1969) found that seasonal temperature changes in the sea reduced

the feeding rate of the starfish Asterias forbesi to one third the rate at optimal temperatures. The effect of prey size on feeding rates was demonstrated by Hancock (1958) who confined starfish with a large supply of mussel spat. He found that after an initial high feeding rate, the mussels gradually grew too large for the starfish to open. Hancock (1965) also suggested that a difference in feeding rates on the same mussel species collected from two different areas is a product of differences in size of the adductor muscle, and hence differences in their ability to resist the starfish's pull. The effect of differences in surface texture on the rate of feeding has not been sufficiently studied. Bloom (1957) found that sponge cover reduces starfish predation on scallops by interfering with tube feet attachment. However, reference to differences in feeding rates caused by differing shell textures could not be found in the literature.

In the present study, experiments were designed to quantify the feeding rates and preferences of C. calamaria. In order to determine the importance of certain factors influencing the results obtained from the above experiments, further experiments were conducted on (i) conditioned starfish, (ii) feeding on damaged bivalves and (iii) different scallop surface textures.

2B. FEEDING RATES

i. MATERIALS AND METHODS

Experiments to determine the rate of feeding of C. calamaria on bivalves were conducted in cages immersed in the sea at Kettering. Scallops, mussels and cockles were collected from the East Coast and the D'Entrecasteaux Channel, and placed in galvanized wire cages ranging in size from 30 x 13 x 16 cm to 120 x 80 x 80 cm. The number of C. calamaria depended on cage size and quantity of bivalves present. Juvenile starfish were not used in order to eliminate one of the variables, starfish size, which affects feeding rate. Only adults in the size range 20-35 cms in diameter were selected. Christensen (1970) found that adult starfish (Astropecten irregularis) consume a daily amount of food equal to 2% of their own living weight, whilst juveniles eat the equivalent of 18% of their body weight.

Feeding rates were calculated when single species of P. meridionalis, E. bifrons, M. asperimus and M.e. planulatus were presented to C. calamaria. Rates were also determined when all 3 scallop species were present at once.

In order to determine the feeding rate in terms of the percentage of the body weight of a starfish, a sample of bivalves and starfish were weighed and measured in the laboratory.

Experiment duration ranged from 3 to 17 days. Data recorded were the size and number of starfish and bivalves, date, and length of experiment. Surface water temperatures were recorded fortnightly.

ii. RESULTS AND DISCUSSION

Feeding rates for adult starfish, C. calamaria, were calculated from the data given in Appendix I, in terms of numbers of bivalves consumed per starfish per day. The data were averaged and are summarized in Table 1 below.

Table 1.
Feeding rates of C. calamaria on bivalves.

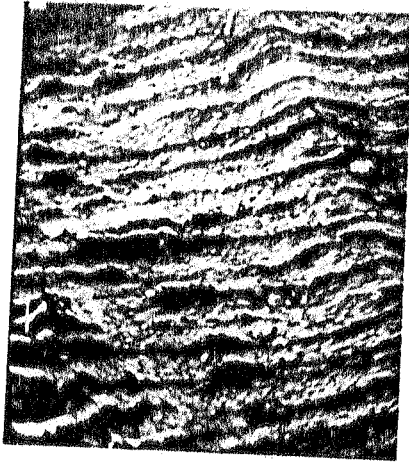
Bivalve	Rate = bivalves/star/day
<u>P. meridionalis</u>	0.50
<u>M. asperimus</u>	0.36
<u>E. bifrons</u>	0.33
<u>M.e. planulatus</u>	0.25
3 scallop species presented together	0.27

The rate of feeding on commercial scallops, P. meridionalis, is far greater than that on any other species of bivalve. The feeding rate on mussels is the lowest. Under experimental conditions and using these feeding data gathered during the winter months, it is calculated that it is possible for an adult C. calamaria to consume one commercial scallop every two days, or 180 scallops each year. This is far fewer than the claim of 3,650 presented in the frontispiece. Feder (1970) calculated that the starfish, P. ochraceus, consumes about 80 mussels (mean size 4.9 cm) each year in the field. C. calamaria, in caged conditions during winter, with unlimited prey, consumes about 90 mussels (ave. size 5.0 cm) annually. However, these experimental

feeding rates may not extrapolate to the field as access to food, prey density, ease of capture and other physical factors differ greatly in the natural environment.

The lower value obtained when the predator was confronted with three species of scallops (0.27 scallops/star/day) may be explained by several factors. Data for this result were gathered over the five month period, May-September, whilst data concerning feeding rates on individual species were collected during September only. Crump (1969) found that C. calamaria reduced its feeding rate during the winter months in New Zealand waters and this may well be the case here. Further studies over the summer months are necessary to quantify this prediction. Secondly, Crump (1969) records a burst in feeding activity during the spring, and relates this to maturing sexual organs. Again, it is probable that the high feeding rates recorded in September are associated with the sexual cycle.

Known factors affecting the varying feeding rates in different bivalve species are few in number. The "catchability" of prey was similar for each species. Therefore it is postulated that differing rates reflect differences in the ability of the starfish to consume various species. Prey size (i.e. surface area), surface texture and the ability to withstand the pull applied by the starfish (i.e. adductor muscle size) are probably the most important variables involved. The same size range of prey were used for all 3 series of experiments, thereby eliminating surface area variations. Adductor muscle sizes were not measured. However, the proportion by weight of the adductor muscle to other tissue in

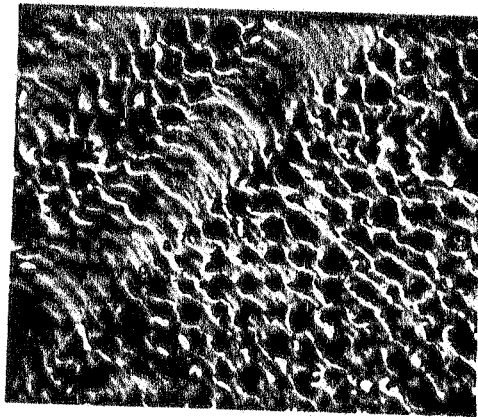


P. meridionalis
(commercial)



M. asperrimus
(doughboy)

outline of a tube-foot
at the same scale.



E. bifrons
(queen)

Plate 6A. Surface Texture of Scallop Shells

Scale 1:30

the scallop is high. An analysis of tissue weight per size class revealed that M. asperrimus is heavier than E. bifrons which is heavier still than P. meridionalis. This indicates that commercial scallops may be opened more easily and eaten more quickly.

Furthermore, an examination of surface textures illustrates some great differences between these three species. (see Plate 6A). P. meridionalis has a relatively smooth micro-surface, with low profile ridges. E. bifrons is covered in a "lattice"-like honeycomb structure, whilst M. asperrimus has a texture comprising long ridges and gutters covered with sharp spines. It is possible that the latter two surface textures hinder the attachment of the tube feet. The diameter of a tube foot from a small adult C. calamaria (22 cm) has been drawn to the same scale in plate 6A. More extensive areas are available for attachment on P. meridionalis than on the remaining two species. To continue this investigation, the force which a starfish was able to apply to each scallop was measured, using a technique described in chapter 3. Again the results indicate a further possible cause for the increased feeding rate on P. meridionalis. It was found that the greatest force could be applied to P. meridionalis and the least to the doughboy, M. asperrimus. (see table 2 below).

Table 2.
Starfish pull applied to scallop surface

Scallop	Starfish pull (gms per unit area)
<u>P. meridionalis</u>	235
<u>E. bifrons</u>	185
<u>M. asperrimus</u>	109

The average weight of adult C. calamaria in the 20-35 cm size class was calculated to be 424.5 g. Feeding rates expressed as percentages of starfish body weight are as follows:-

Feeding rate on:	<u>P. meridionalis</u>	5.1% per day
	<u>M. asperrimus</u>	4.5% per day
	<u>E. bifrons</u>	3.9% per day

C. calamaria was recorded to feed on a single queen scallop, E. bifrons, in the laboratory for 22 hours. Burnett (1960) records feeding Asterias forbesi in a humped position over clams from 8-48 hours, whilst Christensen (1957) found that the normal period of digestion of a clam for the starfish, Evasterias, was 7-15 hours. Considering the recorded feeding rate of 0.33, or one queen scallop every three days, and the actual period of digestion of 22 hours, it appears that C. calamaria spends a large amount of time not feeding between meals.

2C FEEDING PREFERENCES

1 MATERIALS AND METHODS

Preference experiments to determine the degree of selectivity of prey capture and feeding shown by C. calamaria, were conducted in the same cages and in a similar manner to feeding rate experiments already described.

Only adult starfish of diameter 20 to 35 cm were used as a literature survey revealed that feeding preferences vary with the size of this and other asteroid species. Crump (1969) found that juvenile C. calamaria tend to feed on gastropods, whilst adults of the species eat mainly bivalves. For these experiments, only those starfish which had been separated from their normal food source for 7 days or longer were used. This ensured that the effects of conditioning to one food type did not complicate preference results.

Bivalve numbers in each cage ranged from 6 to 60 with a mean of 20 animals. Throughout most of the experiments, starfish were presented with equal numbers of two bivalve species in each cage. Prey combinations were made from the three species of scallops, the mussel M.e. planulatus, and the cockle Katelaysia rhytiphora. Size ranges of both prey species were matched. In nature, it is usual that the starfish have several alternative prey rather than just two. All 3 species of scallops commonly occur together in the same beds in the D'Entrecasteaux Channel. To determine whether the results of the previous experiments on pairs of prey held generally, experiments were conducted to determine preferences when all three species of prey were present at

the same time. Of the 34 preference experiments, ten were conducted using the three scallop species together.

Cages were suspended in 2-3 metres of water from the side of a jetty in Little Oyster Cove, Kettering. Regular checks were made each week. The duration of experiments ranged from 5 to 17 days with a mean of 8 days.

Starfish preferences were determined from the relative numbers of each prey species eaten.

Three control experiments were conducted for 21 days each, to determine the percentage of natural mortalities and external predation. For these purposes, M. asperrimus, E. bifrons and M.e. planulatus were confined in small cages in the absence of starfish in densities far greater than those of the preference experiments.

ii RESULTS AND DISCUSSION

Preferred prey species are defined as those prey eaten when the predator is given a choice. Several factors which play a part in determining such preferences were either limited or manipulated in the choice experiments, to simplify the interpretation of results: (i) prey densities were maximized; (ii) foraging time was eliminated; (iii) equal numbers and size of different prey species were present and (iv) escape behaviour was limited by cage size. Under these circumstances, starfish had equal opportunity of detecting, capturing and consuming various prey species.

Natural mortalities in the control experiments were nil, and only one scallop was attacked and eaten through the wire of the cage by a starfish (C. calamaria).

For the results of preference experiments see Table 1 in Appendix I. It appears that C. calamaria does not make consistent prey choices when feeding on an abundance of bivalves.

When both mussels and scallops are offered together, either no choice is made, (i.e. same number of each are consumed) or the outcome of the experiment is random.

Similarly, the choices made between pairs of scallop species indicate the absence of a persistent trend for any one species to be preferred, although a weak preference for commercials appears to be present.

This weak trend is further displayed in the results of choices made between the three scallop species. See Table 3. Of ten experiments, P. meridionalis was preferred 7 times, E. bifrons twice and M. asperrimus once.

Table 3. C. calamaria feeding preferences when offered 3 species of scallops

Date	Total No. of Bivalves Offered	<u>M. asperrimus</u>	<u>E. bifrons</u>	<u>P. meridionalis</u>
11-6	24	0	5	7
11-6	24	2	7	7
5-8	30	3	2	6
12-8	33	2	0	3
29-8	24	0	2	5
8-9	24	1	0	2
16-9	48	3	0	3
16-9	30	3	3	7
25-9	30	1	3	0
2-10	30	0	1	2

The statistical analysis of the ten results showed that significantly more commercials were selected than either queens,

($t = 2.82$, d.f. = 9, $0.025 > P > 0.01$) or doughboys

($t = 3.36$, d.f. = 9, $0.01 > P > 0.005$). However there was not a significant difference between the numbers of queens and doughboys eaten. ($t = 0.92$, d.f. = 9, $0.4 > P > 0.2$) i.e. C. calamaria appears to discriminate P. meridionalis from the other scallop species, and may actively choose this bivalve. It does not however, make a choice between E. bifrons and M. asperrimus.

Food preferences of predatory starfish have been investigated by a number of authors. Feder (1959) found tha

the starfish, Pisaster ochraceus, prefers certain species when available, especially the mussel, Mytilus californianus, and certain barnacles. Christensen (1962) related preferences to feeding rates and noted that in the absence of "first class" or preferred prey species, food uptake is significantly reduced. He found that if only highly undesirable food species are present, the starfish, Astropecten irregularis, may almost stop feeding and lose weight.

From the findings of this and the previous section, it appears that feeding preferences are closely tied to feeding rates. Conclusions concerning the former should not be drawn without first considering the role feeding rates play in determining preferences. This interaction will be discussed in section 2D.

2D FOOD PREFERENCE MODEL

The relative numbers of prey captured by C. calamaria reflect their "catchability", which is controlled by such factors as efficiency of escape responses, surface texture, size and other variables which influence consumption rates. In order to determine whether true preferences exist the following model is proposed. Data used are the number and species of prey captured in single prey environments (See Appendix D) and also in multiple prey environments (Table 3). By comparing these two sources of data prey preferences may be quantified.

Let the observed feeding rate on commercial scallops be X_1 when only this one species is presented to the starfish. Similarly, let the feeding rates in the single prey environment be X_2 for doughboy scallops, and X_3 for queens. Now if all 3 species are presented to the predator at once, the expected feeding rate would be X . Assuming that no preferences are involved then

$$X = \frac{X_1}{3} + \frac{X_2}{3} + \frac{X_3}{3}$$

Under these circumstances the starfish would consume one third of its food requirements from each species. Inserting the data obtained from the feeding rate experiments on single prey species in section 1B, we find that

$$X = \begin{array}{ccccc} & \text{(commercial)} & & \text{(doughboys)} & & \text{(queens)} \\ X = & \frac{0.5}{3} & + & \frac{0.36}{3} & + & \frac{0.33}{3} \end{array}$$

when no preferences are shown.

$\therefore X = 0.40$ which is the mean feeding rate.

However, if preferences exist, then one or more species will be consumed, still at the same rate, but in greater quantities than the other species. To account for these preferences, the coefficients P_1 , P_2 and P_3 are added to the model such that

$$X = \frac{P_1 X_1}{3} + \frac{P_2 X_2}{3} + \frac{P_3 X_3}{3}$$

$$P_1 = P_2 = P_3 \quad \text{where no preference is shown.}$$

Using the feeding rate results from section 1B we find

$$X = \begin{array}{ccccc} & \text{commercial} & & \text{doughboys} & & \text{queens} \\ & P_1 & 0.5 & + & P_2 & 0.36 & + & P_3 & 0.33 \\ & & \underline{3} & & & \underline{3} & & & \underline{3} \end{array}$$

$$\therefore X = 0.17 P_1 + 0.12 P_2 + 0.11 P_3$$

Due to the influence of preference, the feeding rate X , observed when all three species are presented together, will not equal 0.40. Consider the case in which a strong preference is shown for commercial scallops. The value of X will rise to a point somewhere between 0.40 and 0.50. On the other hand, a strong preference for queen scallops will depress the value of X towards 0.33.

X can be measured experimentally by presenting the starfish with three scallop species together and calculating the rate of feeding. If X differs from 0.40, then a preference for one of the scallop species exists.

In the present study, the value of X obtained from 10 experiments in which *C. calamaria* was offered three scallop

species together, was found to be 0.27 scallops per starfish per day. (See Table 3, section 2C). Unfortunately, inferences regarding prey preferences cannot be drawn from this result as it is outside the range predicted by the model and the present data are not in an acceptable form for use in this model. As discussed earlier, this low feeding rate may be due to the effects of maturing sexual organs and water temperatures on feeding. A record of feeding rates over the calendar year would produce a complete set of useful data with the abovementioned factors naturally incorporated.

This model demonstrates the relationship between feeding rates and preferences. Its use in this study was restricted, but it has value in quantifying predator food preferences when acceptable data is at hand.

1 MATERIALS AND METHODS

A study of the attractiveness of damaged bivalve tissues to starfish was conducted by offering C. calamaria equal numbers of damaged and undamaged scallops, E. bifrons and M. asperimus, and mussels, M.e. planulatus. Experiments were carried out in cages at Kettering during September and October. Starfish were freshly collected from the field. Four adults were placed in each of four cages containing the bivalves. Two experiments were run using mussels only, whilst the remaining 2 experiments were conducted with scallops.

Bivalves were broken by using a pair of pliers to snap a small piece of shell away from the anterior margin. In this manner, no vital organs were injured, and death did not occur from handling procedures. A section of the exposed mantle was cut to allow the escape of tissue fluids into the water. In addition to releasing these fluids, this method of breaking the valves also produced a permanent opening which, it was considered, may have an effect on feeding efficiency.

Experiments were run for either 3 or 4 days. Feeding rates and preferences were recorded by noting the numbers of each food type eaten (broken and unbroken).

Further experimentation was carried out in the field using damaged and undamaged M.e. planulatus as attractants. Using S.C.U.B.A. gear, a 10 metre square of string was pegged

out in the sand at a depth of 6 metres. Two small cages, each containing 200 damaged mussels were tied to diagonally opposite corners of the square. Cages containing 200 unbroken mussels were fastened to the remaining two corners. Eighteen C. calamaria were collected from the nearby mussel bed and placed in strategic positions inside the square. The author intended to return after 24 hours to collect information on numbers of stars feeding on each cage. The fact that starfish are able to feed through a wire barrier was illustrated by Burnett (1960), who demonstrated that the starfish, Asterias forbesi, could digest clam flesh through a fine wire mesh.

ii RESULTS

A preference analysis of the results based on the numbers of each food type consumed, illustrates the presence of a trend to eat a greater proportion of damaged than undamaged bivalves.

Table 4. Feeding of C. calamaria on damaged bivalves

Date	Number of Starfish	Experiment duration	Numbers eaten		Feeding rate on damaged bivalves
			Undamaged	Damaged	
● 7-10	4	3 days	2	17	1.58
● 10-10	4	5 days	5	21	1.30
* 7-10	4	3 days	1	3	0.33
* 10-10	4	5 days	0	4	0.20

* Feeding on scallops : feeding rate = 0.27

● Feeding on mussels : feeding rate = 1.44

Similarly Chiasson (1952, in Dickie and Medcof 1963) found that the starfish, Asterias vulgaris, ate scallops with broken or injured shells before they ate uninjured scallops.

Two assumptions can be made from the data in Table 4. (i) that damaged bivalves are more attractive to C. calamaria and (ii) feeding efficiency is increased by the physical changes brought about by damaging the shell. Now feeding preference results may illustrate the trend, but feeding rates go further to explain the reasons for this trend.

The feeding rate of 0.27 on damaged scallops is the same as that recorded for undamaged scallops in section 2B.

Because the rate has not increased, some other factor is acting to cause C. calamaria to eat more damaged scallops. Therefore it appears that a true preference is exhibited here. The release of fluids from injured scallop tissue probably attracts C. calamaria to it. Further tests on this subject could be carried out in a Y-maze by placing scallop tissue in one arm, a living, undamaged scallop in the other and C. calamaria in the leg. With the water flow from the arms to the leg, the number of choices made by the starfish could be recorded to shed more light on the above hypothesis.

Feeding efficiency on broken mussels appears to have increased. The feeding^{rate} on uninjured mussels was found to be 0.25 in section 2B, where as damaged mussels were eaten at a rate of 1.44 mussels per starfish per day. This is almost 6 times the normal feeding rate. The time and effort involved in forcing the mussel valves apart would most certainly be reduced if the starfish extruded folds of its stomach through the opening in the fractured shell. Therefore the greater number of broken mussels consumed may not reflect the predator's preference, but merely a greater ease of feeding and a reduction in the digestive period.

Results were not obtained from the field experiments. All 18 starfish, being in an excitable state after capture, rapidly moved out of the square. However, all was not lost as the speed of escaping C. calamaria was measured to be about 60 cm. per minute.

2F CONDITIONED FEEDING

1 MATERIALS AND METHODS

To investigate the effects of conditioning (simple learning) on the feeding behaviour of C. calamaria starfish were transferred from a single prey situation, in which they had been feeding for one month or more, to a paired prey situation where equal numbers of the original prey species and one other prey species were offered as food. Starfish were conditioned to one food type in cages at Kettering. Only adult starfish were used. Numbers and size of each prey species eaten were recorded. Feeding rates were calculated as numbers of prey per starfish per day.

To supplement these experiments, starfish were collected from the mussel beds at Blackman's Bay, where it was assumed they had naturally become conditioned to mussels (M.e. planulatus). Only starfish feeding on mussels at the time of collection were used. These starfish were immediately placed in cages containing a selection of mussels from the same site, and an equal quantity of scallops.

On one occasion, starfish were collected from cockle beds (Katelysia rhytiphora) and offered a selection of cockles and juvenile queen scallops.

Seven experiments were conducted on cage-conditioned starfish, and five on those assumed to be conditioned in the field.

ii RESULTS AND DISCUSSION

C. calamaria were conditioned to feed on the mussel, M.e. planulatus, the doughboy scallop, M. asperrimus, and the queen scallop, E. bifrons in cages.

It was found that in 10 of the 12 conditioning experiments, starfish, when presented with a choice of two food types, continued to feed on the original prey species to which they had previously been exposed. See Table 5.

Table 5 Conditioned Feeding Response of
C. calamaria

<u>Cage conditioned</u>					
date	conditioned food species	additional species	numbers eaten c.d.s.a.s.	preference	
29-8	<u>M. asperrimus</u> (12)	<u>M. e. planulatus</u> (12)	1 4	a.s.	
8-9	<u>M. asperrimus</u> (10)	<u>M. e. planulatus</u> (10)	10 8	c.d.s.	
16-9	<u>M. asperrimus</u> (15)	<u>M. e. planulatus</u> (15)	8 3	c.d.s.	
25-9	<u>M. asperrimus</u> (11)	<u>M. e. planulatus</u> (11)	6 0	c.d.s.	
2-10	<u>M. e. planulatis</u> (10)	<u>E. bifrons</u> (10)	3 2	c.d.s.	
2-10	<u>M. asperrimus</u> (6)	<u>M. e. planulatus</u> (6)	1 0	c.d.s.	
2-10	<u>E. bifrons</u> (15)	<u>M. e. planulatus</u> (15)	4 0	c.d.s.	
<u>Field conditioned</u>					
5-4	<u>K. rhytiphora</u> (8)	<u>E. bifrons</u> (8)	8 0	c.d.s.	
30-5	<u>M. e. planulatus</u> (6)	<u>E. bifrons</u> (6)	0 2	a.s.	
30-5	<u>M. e. planulatus</u> (25)	<u>K. rhytiphora</u> (25)	12 5	c.d.s.	
5-8	<u>M. e. planulatus</u> (30)	<u>E. bifrons</u> (30)	15 4	c.d.s.	
29-8	<u>M. e. planulatus</u> (6)	<u>E. bifrons</u> (6)	5 0	c.d.s.	

note: numbers in brackets are numbers of prey offered.

These data were subjected to a students "t" test which showed that the conditioned response is significant. ($t = 2.97$, d.f. = 11, $0.025 > P > 0.01$). Christensen (1973) refers to this type of behaviour as ingestive conditioning. He found that flatworms, Stylochus ellipticus, gathered from barnacle beds, displayed a distinct preference for barnacles, whilst those known to feed on oysters alone continued to feed on oysters in the laboratory, even in the presence of barnacles. The presence of ingestive conditioning in a predatory starfish may have important ecological implications which will be discussed in section 2H.

Observational studies of the feeding habits of C. calamaria were conducted in the field to substantiate experimental findings. Records of prey captures were made throughout the study, usually as incidental notes taken whilst diving. An underwater writing pad was constructed from a white plastic disc (after Grace 1967). See Appendix I. Notes were written in pencil which was easily removed with steel wool when no longer required.

A more intensive survey was made at Flinder's Reef Tarooma, where C. calamaria were studied in intertidal pools at low water. To determine whether C. calamaria is size selective when capturing its prey, the relative lengths of starfish and their prey, the mussel, M. e. planulatus, were measured. Starfish were measured as a diameter across two opposing arms. Arm length varies considerably so two measurements were recorded and averaged. An anterior-posterior measurement was recorded for mussels.

Further notes were taken on other species of prey being consumed. The percentages of feeding and non-feeding starfish were recorded.

Finally, to tie in findings from the above field work and cage experiments on preferences, data on scallop and starfish distributions on the East Coast, on loan from the Fisheries Research Laboratory, Tarooma, were examined, interpreted and mapped.

ii RESULTS AND DISCUSSION

Prey species taken in the field are listed in Table 6 below .

Table 6: Food of C. calamaria in the field.

common name of prey	species
oyster	<u>Ostrea angasi</u> Sowerby
mussel	<u>Mytilus edulis planulatus</u> Lamarck
cockle	<u>Katelysia rhytiphora</u> Lamy
gastropod	<u>Maoricolpus roseus</u> (Quoy and Gaimard)
heart-urchin	<u>Echinocardium</u> sp.
chiton	<u>Ischnochiton elongatus</u> Blainville
gastropod	<u>Parcanassa pauperata</u> Lamarck
turban shell	<u>Subnivalia undulata</u> Solander
barnacle	<u>Chamaesipho columna</u>
thaid (gastropod)	<u>Dicathais textilosa</u> Lamarck
crustacean	<u>Paragrapsus</u> sp.
starfish	<u>Coscinasterias calamaria</u> Gray
fish	<u>Squalus</u> sp.

C. calamaria was most commonly observed eating mussels, oysters and barnacles. These three species were the most numerous prey animals in C. calamaria's environment. The above food list is quite diverse and it would appear that there are few large molluscs living in the same habitat that are not attacked by this starfish. Crump (1969) conducted an extensive study on the natural feeding habits of C. calamaria in Otago Harbour, New Zealand. He found that this starfish was a potential predator on most of the

organisms occurring in its habitats including worms, tunicates, crabs, nudibranchs, pipe fish, bivalves and gastropods.

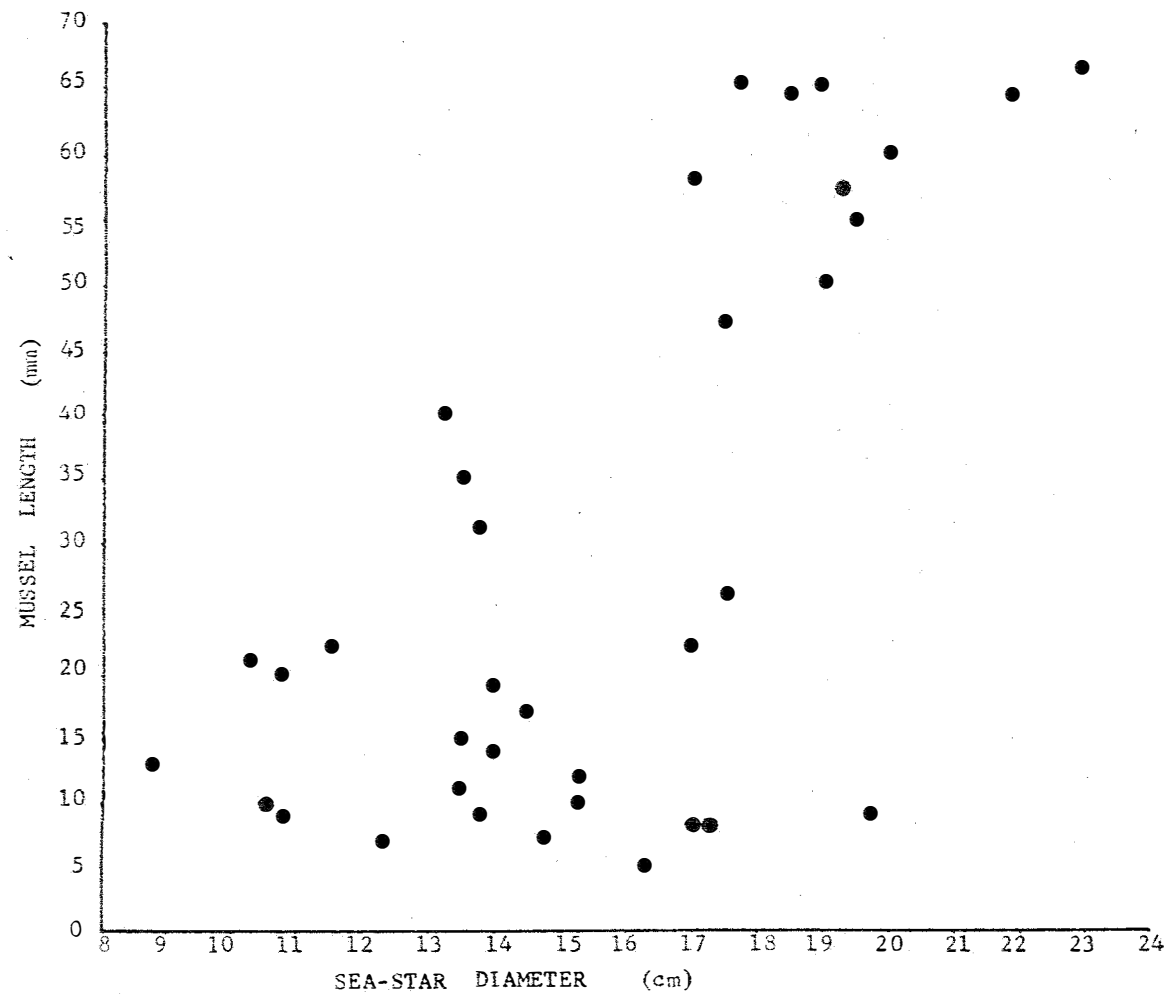
During a number of excursions into the field it was noted that C. calamaria congregated on areas densely populated with cockles, mussels and oysters. Grace (1967) made similar observations in 1965 and later, (1967) quantified these with an underwater population survey in New Zealand waters. She concluded that C. calamaria were most abundant where bivalves were densely populated, especially the cockle Amphidesma australe. Similarly, Crump (1969) found that C. calamaria feeds primarily on the most abundant and available mollusc in the environment.

Of a total of 85 starfish examined at Flinder's Reef, 41% were feeding. 60% of these were eating mussels which are the most abundant food source in the area. Crump (1969) recorded 1,800 field observations, 35% of which were feeding.

Data from the survey on prey size selectivity has been graphed in Fig. 3. The correlation of muscle length to starfish size is highly significant (corr. coef. = 0.641, d.f. = 34, $P < 0.001$). From this figure it can be seen that large starfish eat mussels of all sizes, but small starfish eat only small prey. These findings were incorporated in the caged feeding experiments in which only adult starfish were used.

An examination of the Fisheries Dept. data on starfish and scallop populations during 1973-'74 in Oyster Bay

Fig 3 . Predator / Prey Size Relationship Between Coscinasterias calamaria
and Mytilus edulis planulatus



Correlation Coef. 0.641

FIG 4 Starfish Population Density
Oyster Bay 1973 (May)

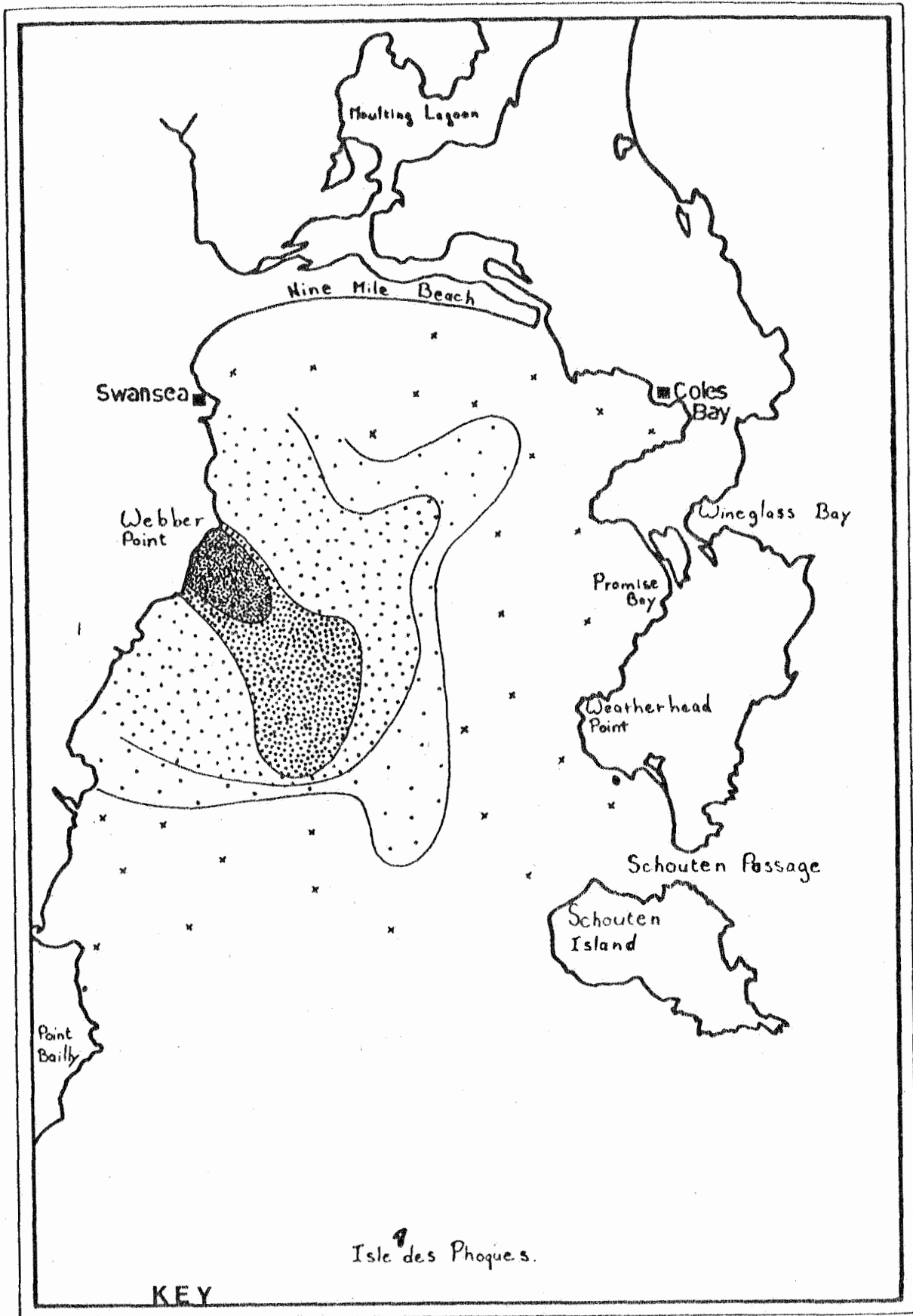


FIG 5 Scallop Population Density
Oyster Bay 1973(May)

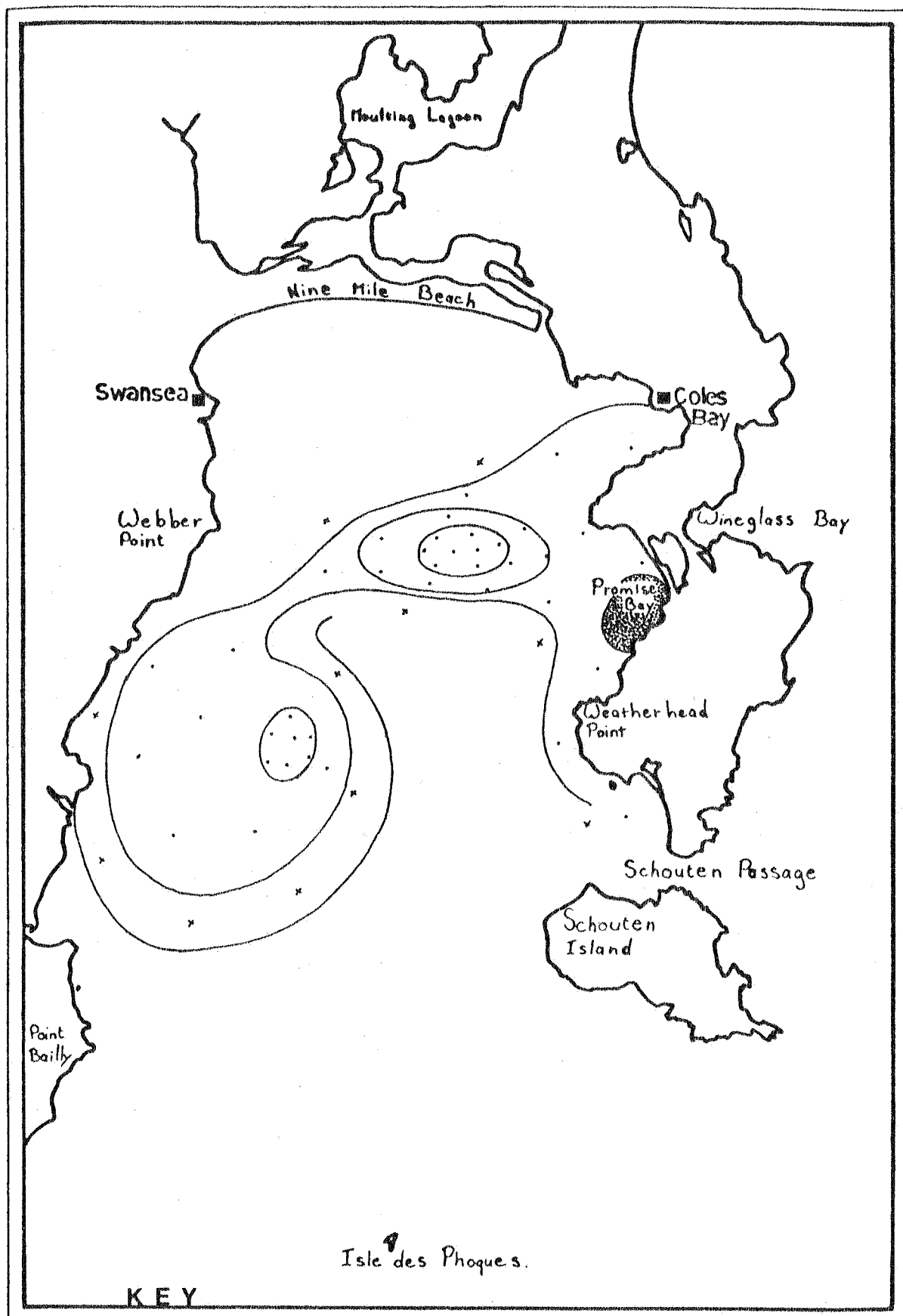
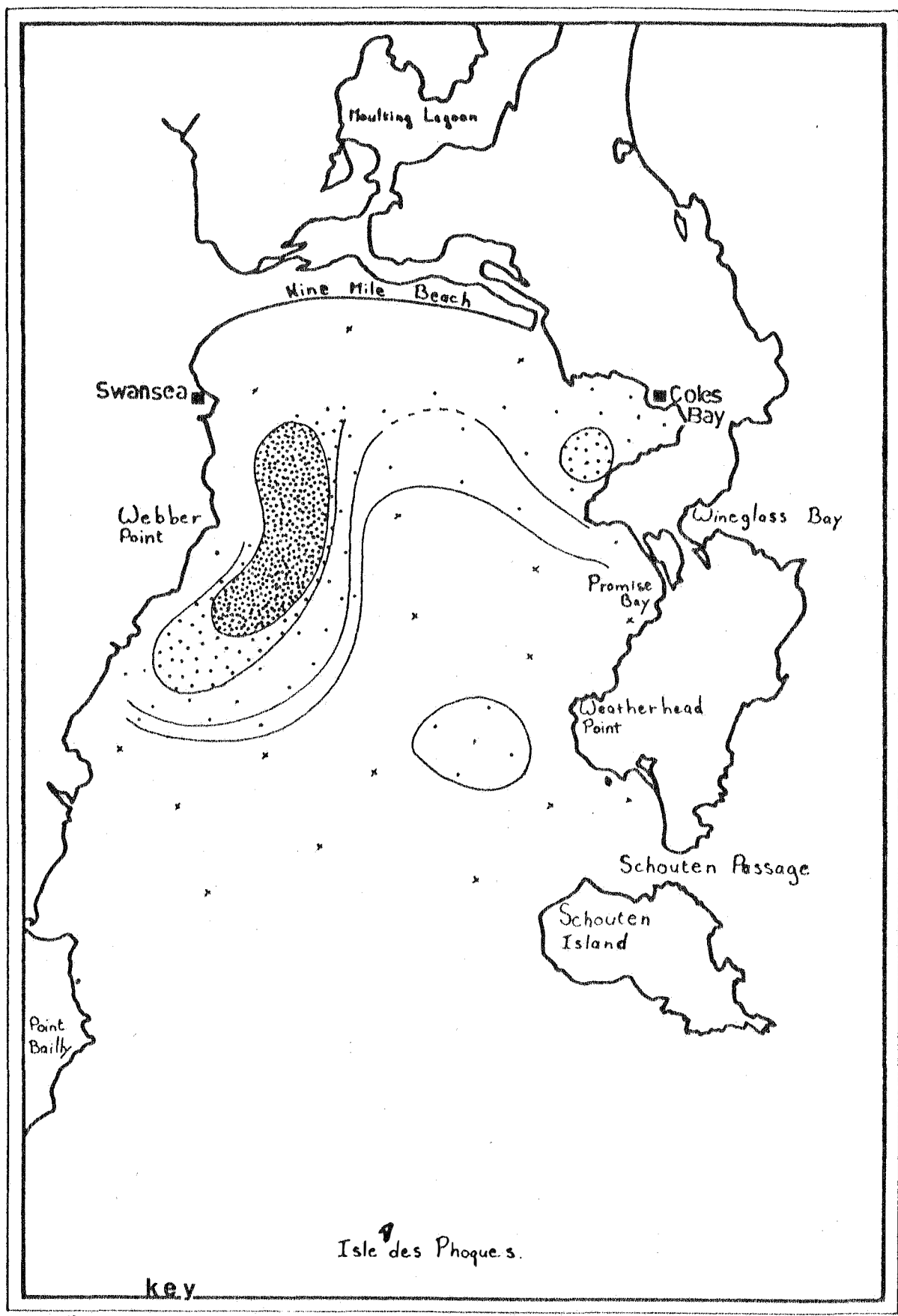
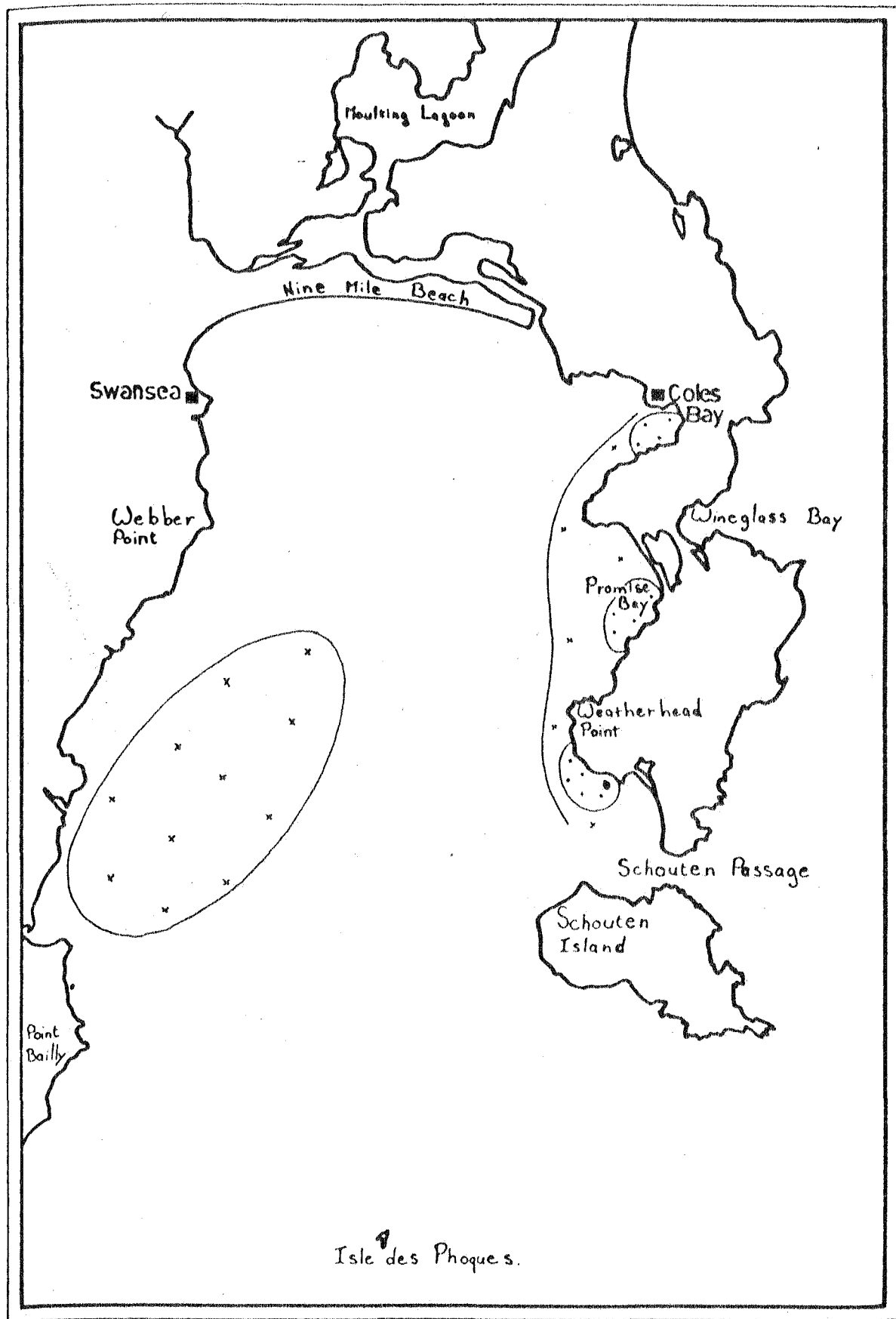


FIG 6 Starfish Population Density
Oyster Bay 1974 (May)



**KEY**• • 1 scallop/ 100-300 m²x 1 scallop/ 300-1200m²

2H GENERAL DISCUSSION

Experimental evidence and results from field work suggest that Coscinasterias calamaria has a generalised diet. An apparent preference for commercial scallops may in fact be due to the difference in feeding rates caused by surface texture and adductor muscle differences, and therefore may not involve an active choice. Further research incorporating a greater number of food species for this starfish is needed to establish the presence or absence of a distinct prey preference. This work may be enhanced by using gastropods in addition to bivalves. Crump (1969) conducted an extensive field survey on C. calamaria, and concluded that this starfish prefers bivalves to gastropods under natural conditions. However insufficient laboratory work has been done to supplement these findings. Behaviour in the field may be influenced by other factors apart from a true preference; i.e. abundance of different species, ingestive conditioning, competition and gastropod escape behaviour. These factors can be eliminated under experimental conditions to reveal prey preferences.

Feder and Christensen (1966) suggested that many forcipulate asteroids feed on the most abundant and readily available food in a particular environment. This view is supported to some extent by findings of this study, although more field work is needed. At Flinder's Reef, mussels are the most abundant food source, but barnacles thickly cover the majority of large mussels and rocks. 60% of feeding starfish were eating mussels whilst 20%

were feeding on barnacles. Crump (1969) also suggests that C. calamaria feeds primarily on the most abundant and available food in the environment.

The presence of ingestive conditioning may influence the dietary habits of a starfish. In section 2F it was shown that C. calamaria learns to eat one food type if only that food is present, and then exhibits a preference for that particular food when it is presented with a second choice. Under natural conditions in the field, a starfish would be advantaged in becoming conditioned to the most abundant food available. In this respect, time and energy would be conserved by not needing to search for dispersed prey. In addition to this, the greater the numbers of the more abundant food type, the more stable its population will be from season to season. By becoming conditioned to a food source such as mussels, C. calamaria has a food supply throughout the year and does not risk losing its prey through seasonal migrations or unpredictable spawning habits. Landenberger (1968) suggested that learning may play a part in aggregating starfish on an abundant food source. It is probable that once C. calamaria becomes conditioned to a prey species, this learning acts as a force to maintain the predator in close proximity to its prey population. A conditioned preference for mussels may act in such a way that C. calamaria would wander from one clump of bivalves to another, within the entire mussel bed, taking the non-preferred species as they were encountered between the mussels. (i.e. barnacles and oysters).

The calorific content of food types may also influence

the diet of a predatory starfish. The lower feeding rate on mussels, measured in section 2B, may be attributed to the energy requirements of C. calamaria. According to Altman and Dittmer (1968) a large mussel (Mytilus edulis) contains more calories (95 calories/100g) than a small scallop (81 calories/100g). Therefore, to gain the same amount of energy, C. calamaria would need to eat a greater number of scallops than mussels in a given time.

This energy budget may also figure in conditioning. Menge (1972) found that the starfish, Lepasterias hexactis, feeds on prey which is predictably abundant throughout the year. However this prey is poor in calories and L. hexactis gains most of its energy from the capture of few energy rich, but unpredictable species. Applying the conditioning hypothesis, it appears that L. hexactis has learnt to specialize on an energy poor but predictable energy source.

The attraction of starfish towards damaged scallops may be in response to different chemical stimuli than those produced by uninjured animals. Zafirion et al (1972) suggested that asteroids may all perceive living prey and injured tissue distinctly, and respond differently to each stimulus type. Intact bivalves may attract predators by erratically releasing metabolites, whilst damaged tissue may involve attraction in response to a number of biochemicals released from the tissue fluids in greater concentrations than natural excretory products. Apart from damage caused by dredging, the actual act of feeding on scallops may also release tissue fluids which could increase the attractiveness

of the scallop bed to nearby starfish. The concentration of attractants would be low after mixing with the surrounding sea water, but Whittle and Blumer (1970) have shown that chemotactic responses of predatory starfish are initiated by extremely low concentrations of certain amino acids of about two parts in 10^4 .

STARFISH-SCALLOP-SPONGE INTERACTIONS

3A INTRODUCTION

In Tasmanian waters the doughboy scallop, *M. asperimus*, is characteristically associated with sponges which frequently thickly cover both valves (plate 7). In the San Juan Archipelago, Washington, Bakus (1966) noted that certain scallop species have a sponge cover on one or both valves. Beau (1965) suggested that such an association is mutualistic, the sponge benefiting by having a rough, spiny substratum to grow on and possibly utilizing the scallop's excretory products as food, whilst the scallop may use the sponge's feeding current for respiration and "must also receive almost perfect protection when in the sponge". However, he makes no attempt to explain how this protection is gained, nor from which predators it is protected. Bloom (1975) found an association of sponges and scallops to be a mutualism, where the sponge was protected from predatory sponge-eating nudibranches by the scallop's motility, and the scallop was protected from predatory starfish by the presence of the sponge.

Bloom's (1975) observations raise questions concerning the efficiency of such an association on Tasmanian scallop beds. To investigate the possible benefit to the scallop, experiments were designed using a known scallop predator, the asteroid, *C. calamaria*, and the scallop, *M. asperimus*. The aim of this experimentation was to determine whether predation was affected by sponge cover and, if so, to investigate the most likely factor accounting for it, namely hindrance to tube foot adhesion.

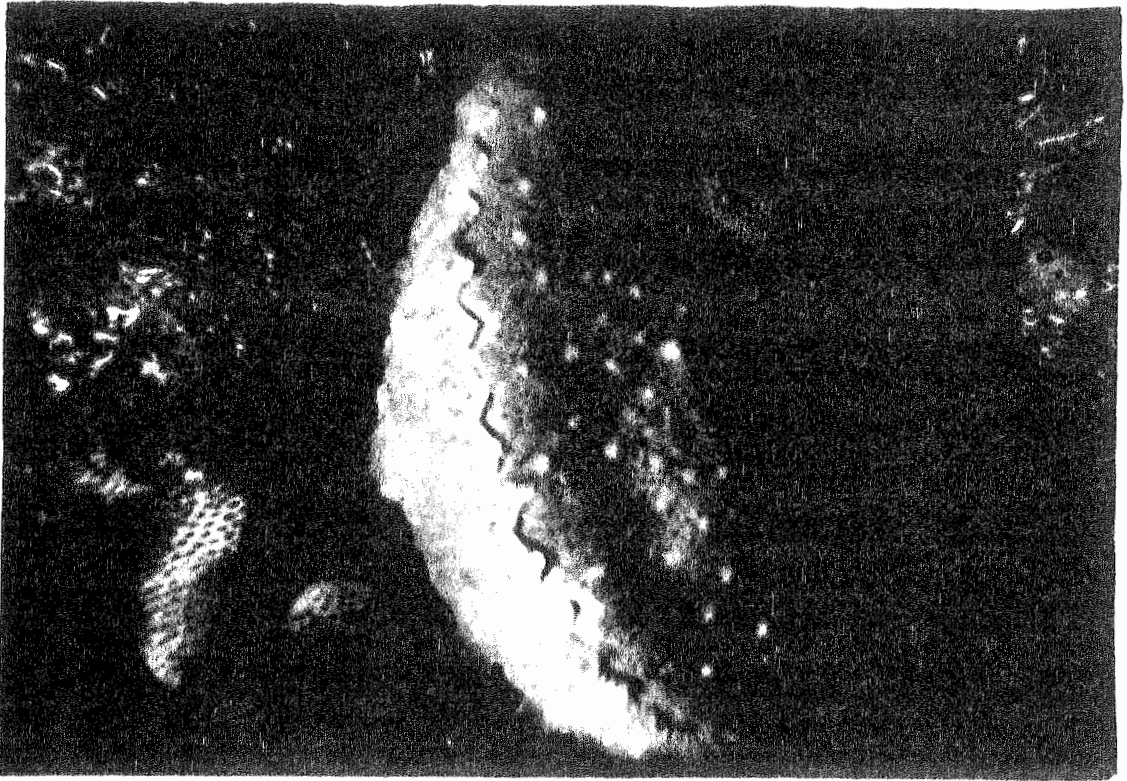


Plate 7. Sponge-covered doughboy scallop

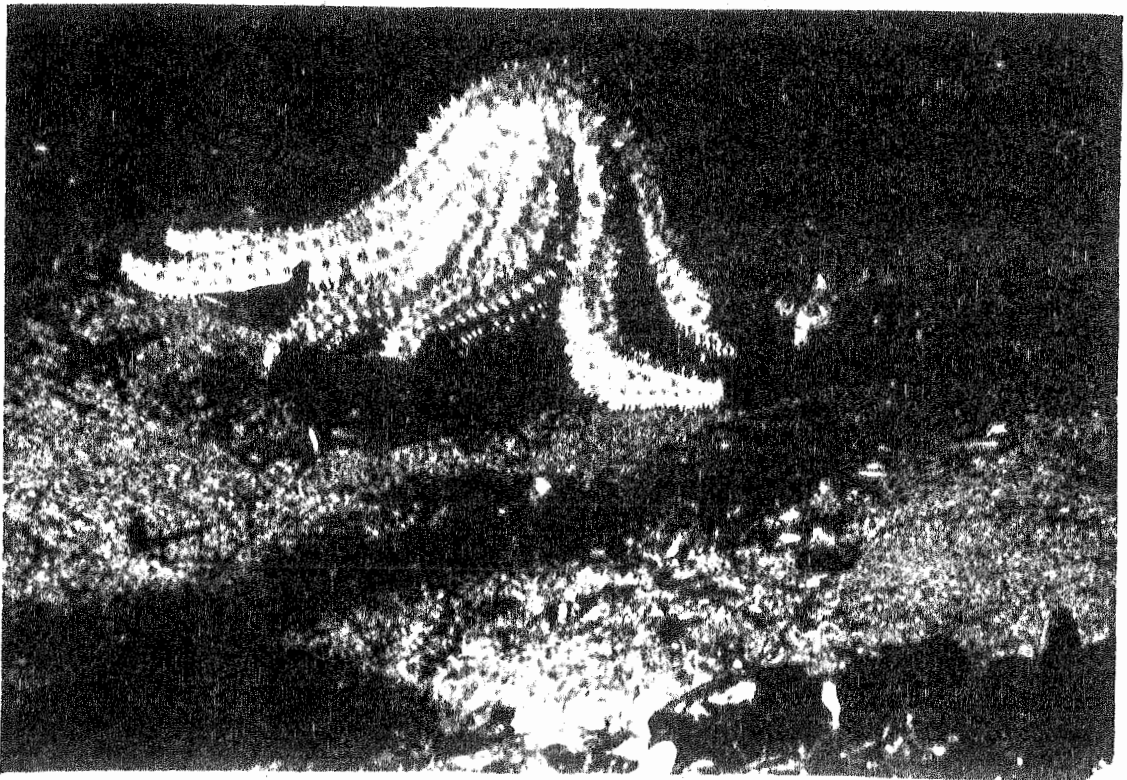


Plate 6. Humped feeding position of C. calamaria
in the field.

1. FEEDING EXPERIMENTS

Sponge covered doughboy scallops, M. asperrimus, were collected from scallop beds at Helliwell's Point in the D'Entrecasteaux Channel. Only those with a thick sponge covering on both valves were selected and transported to Kettering in several 6 gallon barrels, taking care not to damage the sponge. They were then placed in galvanized wire cages with equal numbers of doughboy scallops which had had all the sponge removed with a small scrubbing brush.

Depending on the size of the cage and the number of scallops present, a number of C. calamaria, varying from 2 to 5, was added to each cage. Where possible, fresh starfish were used for each new experiment.

Although cages of different sizes were used, each was large enough to allow scallops to escape from starfish by swimming freely. The size range of the 5 cages used varied from 120 x 80 x 80cm to 40 x 30 x 20cm. Cages were suspended from the side of T. Swards' jetty at Kettering in 6 to 8 feet of water.

Duration of experiments ranged from 3 to 11 days. Time was of little consequence as relative numbers of scallops eaten were the data required. Upon completion of each experiment, data recorded were the numbers of sponge-covered and clean shelled scallops eaten, number of starfish, size of stars, size of scallops, duration of experiment and the date.

Starfish size was measured as a diameter from tip to tip of 2 opposing, uncontorted arms. Two such measurements were made and the average, corrected to the nearest centimetre, was recorded.

Scallop size was measured as the length in millimetres from the hinge line to the anterior margin. Scallops were recorded as eaten when all the soft tissues had been digested. However, a scallop in the process of being devoured when the cage was examined was recorded as eaten, because the star had shown a preference for it and, it was assumed, would have continued until all the flesh was eaten.

A total of 15 experiments in cages were conducted in this manner.

A control experiment during which only M. asperrimus were present in the cage, was run for a period of 21 days in order to measure natural mortality and external predation.

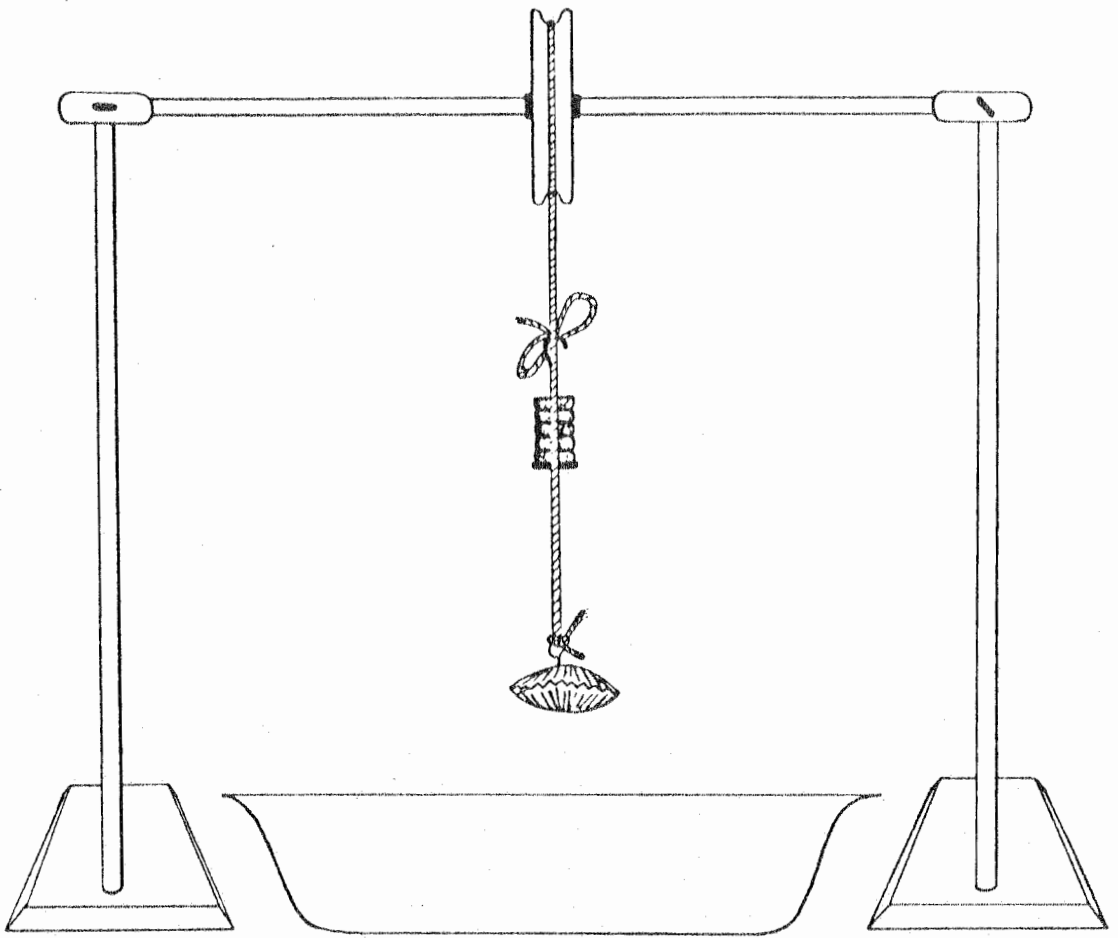
ii. FORCE EXPERIMENTS

To follow up work conducted at Kettering, a series of experiments were run in the laboratory of the zoology department in order to determine the relative forces C. calamaria is able to apply to sponge covered and clean shelled doughboy scallops in a given time.

Ten sponge covered, adult M. asperrimus were selected. All 10 were of similar size. This minimized differences in surface area presented to the starfish.

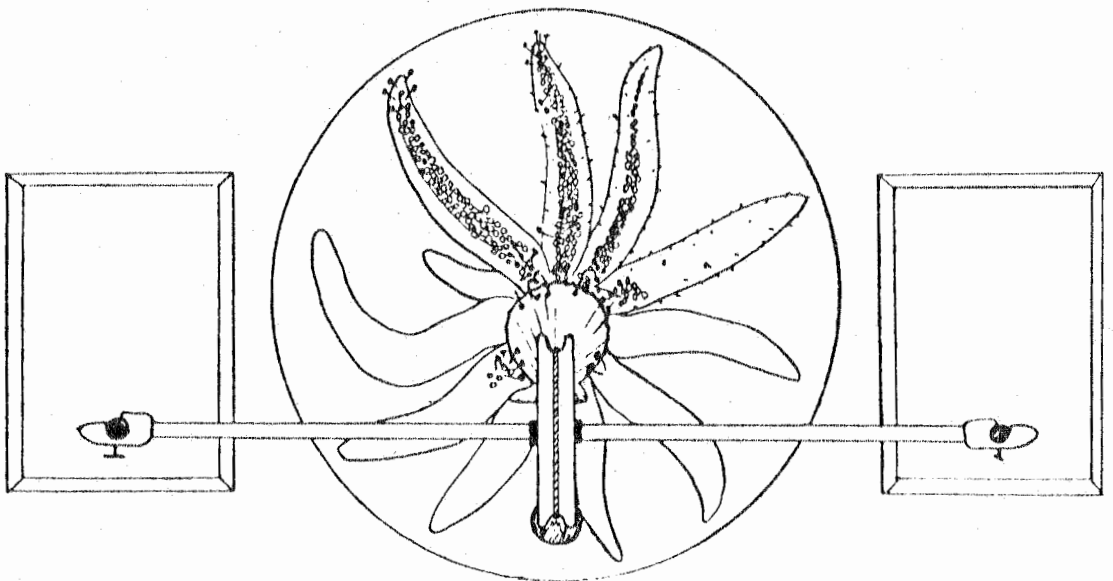
The sponge was scrubbed from one valve of each scallop, a small wire loop was glued to the centre of each clean shell and a 60 cm piece of string attached. A loop was tied in the free end of the string which was then strung across a pulley so that the attached scallop could be raised and lowered. Fresh sea water was transferred to a large enamel basin which was placed beneath the pulley. One freshly caught C. calamaria was immersed in the water with its tube feet facing the sponge covered scallop above it. (See fig 8). The scallop was then lowered to rest on the upturned star, and a period of 15 seconds allowed for its tube feet to attach to the sponge surface, after which weights were added to the loop in the string. The weight required to pull the scallop free from the star's tube feet was recorded.

Attachment time for the weights was minimized by conducting 3 preliminary runs to get an estimate of the weight required for subsequent trials. Each scallop was tested twice. Two stars, both 23cm in diameter, were used alternately



LATERAL VIEW

Scale 1:4



OVERHEAD VIEW

Fig 8 Apparatus Used in C. calamaria Force Experiments
on M. asperrimus

throughout the experimentation, being changed after each group of 5 trials. The water was changed as each star was replaced. After 24 trials, 3 of which were preliminary runs, the sponge cover was completely removed from the scallops, and the procedure repeated.

Finally, using the same starfish and methods, the force placed on E. bifrons and P. meridionalis was measured. Sixteen trials were carried out, 8 on one individual of each species. The starfish were presented with only the clean surface of both these scallops which were selected because they had a surface area similar in size to that of the doughboys.

1. FEEDING EXPERIMENTS

C. calamaria has not to the author's knowledge been recorded eating sponge. However, the sponge cover on a number of *M. asperrimus* had been reduced during the experiments with caged animals. This indicates vigorous escape behaviour, including swimming and bumping against the sides of the cage causing damage to the sponge. Marked differences in predation of the two food types are apparent in the data. Fewer sponge covered scallops than scallops without sponge cover were captured and eaten by the starfish in all but one of the 15 feeding experiments. These statistics were tested using a student's 't' test, and a highly significant difference between them was found. ($t = 6.135$, d.f. = 14, $P < 0.001$). These results indicate that there is a distinct difference in efficiency of predation. The presence or absence of sponge cover was the only major factor which may account for this difference. Time was unimportant as feeding rates were not required, and size differences were minimal as clean scallops were matched in size with sponge covered *M. asperrimus*.

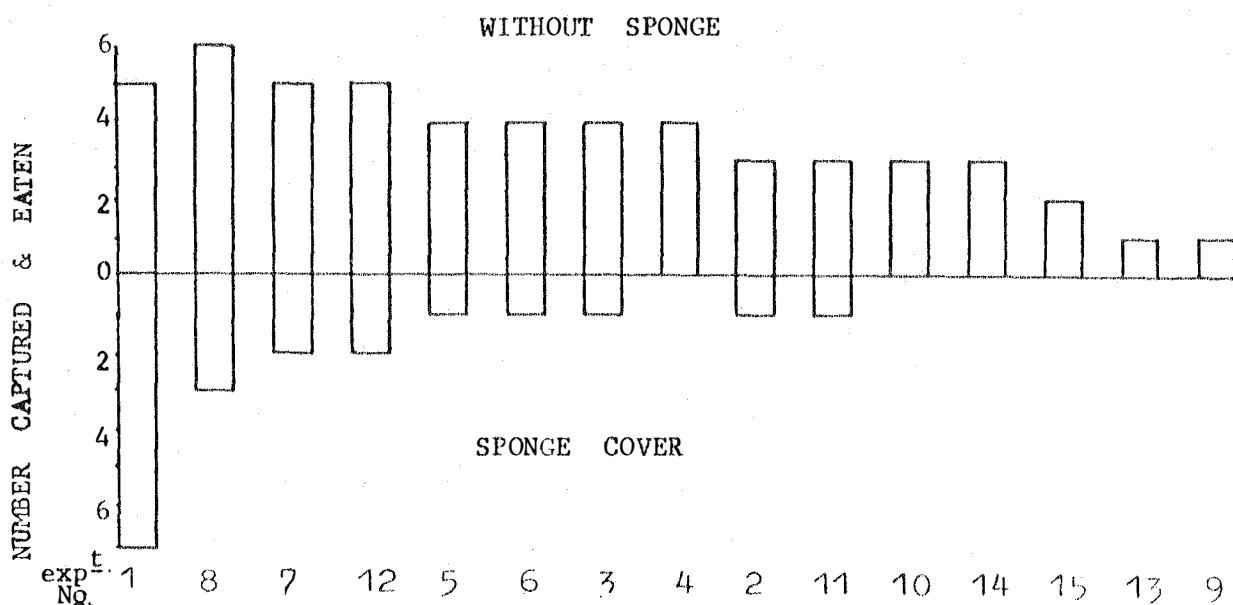


Fig 9 Predation by *C. calamaria* on *M. asperrimus*

With and without Sponge Cover

The data obtained are diagrammatically represented in fig. 9. Here it can be seen that in experiments 2 to 15, predation (measured as numbers captured and eaten) on scallops without sponge cover is between 100 - 300% higher than on sponge covered scallops.

From a total of 252 doughboy scallops offered during the course of feeding experiments, starfish captured and ate 72. Of these, 53 had been scrubbed clean whilst only 19 were sponge covered, the latter representing only 28% of the total number of scallops consumed.

3C. RESULTS

ii. FORCE EXPERIMENTS

The force (F) which a starfish was able to apply to either type of surface was measured as the weight required to pull the scallop free (W_1) minus the weight of the scallop submerged in sea water (W_2). The area upon which this force acted was taken as 1 unit, being the surface area of the lower valve of the scallop.

$$\therefore F \text{ (per unit area)} = W_1 - W_2$$

From the data gathered from force experiments it can be seen that C. calamaria is able to apply a far greater force to doughboy shells without sponge than to sponge covered scallops. In fact, when the figures are averaged, it is found that the force applied to a clean shell is 6 times greater than that applied to a sponge surface.

The forces applied to clean shells ranged from 47 grams to 205 grams per unit area, which were in all trials higher than the range 7-35gm/unit area applied to sponge covered scallops. These data were statistically analysed and the two samples were found to be highly significantly different ($t = 5.07$, d.f. = 9, $P < 0.001$). Results are illustrated in fig. 10.

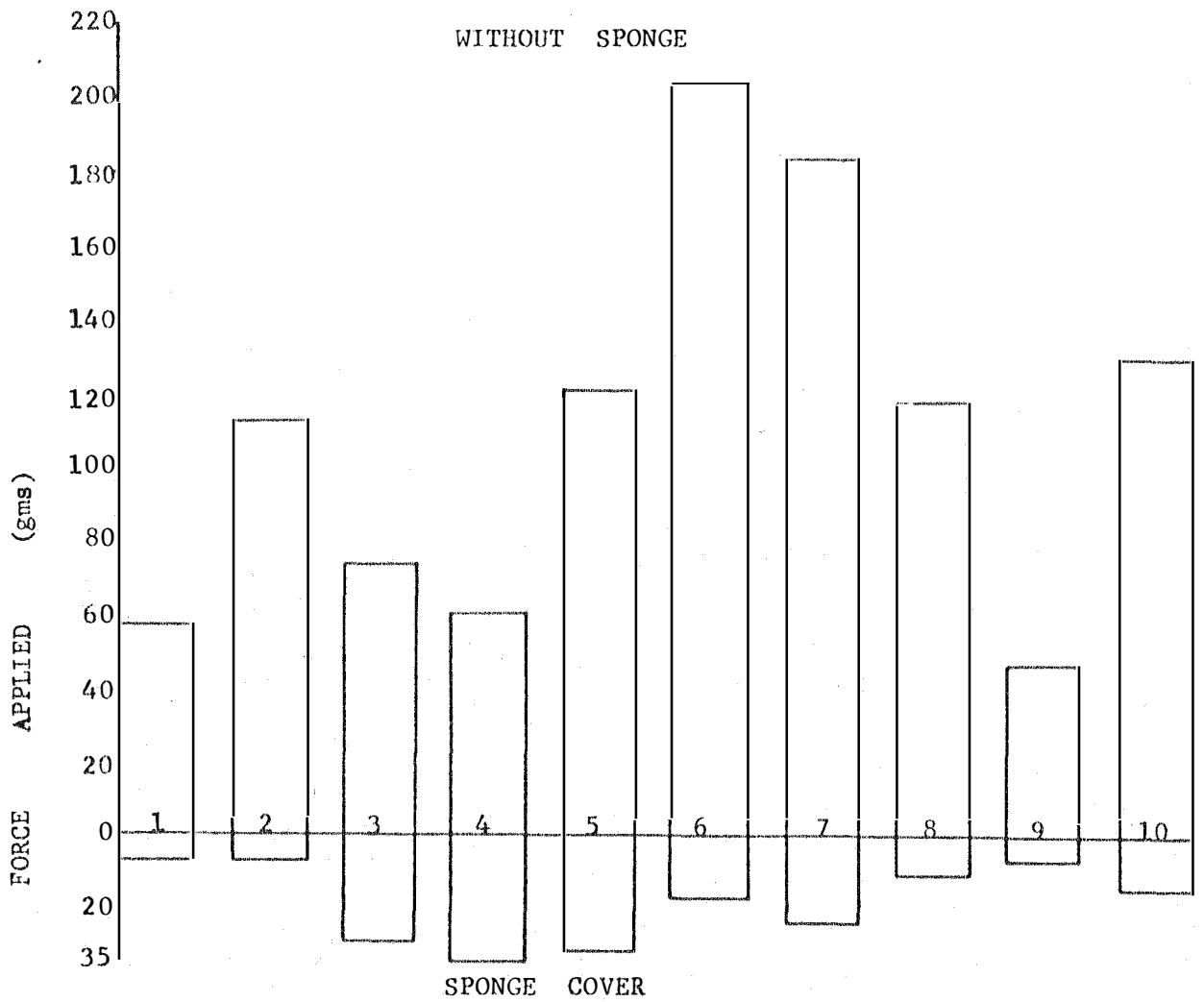


Fig 10. Force Applied by C. calamaria to M. asperimus

With and Without Sponge Cover

Note : Each block represents the mean force applied to one scallop during several trials.

Feeding experiments indicate that predation efficiency on M. asperimus by C. calamaria was lowered by the presence of sponge cover. Predation on clean surfaced shells was three times greater than on sponge covered scallops. Now sponges may protect scallops from intense starfish predation by emitting chemicals which either repel stars or camouflage the scallop scent, by tactile camouflage or hindrance to tube foot adhesion.

Of these possibilities, that with most potential appears to be the latter. Tactile camouflage may be of minor importance but cannot be assessed until the mechanism by which C. calamaria detects its food is established. Valentincic (1975) has demonstrated that chemoreception is important in food finding mechanisms of the starfish, Marthasterias glacialis (L), a close relative of C. calamaria, whilst Crump (1969) noted that the ability of C. calamaria to detect cockles, Chione stutchburyi (Gray), buried beneath the surface indicates that it has well developed powers of chemoreception. Under these circumstances it would appear that tactile camouflage would be of little impedance to predation by C. calamaria.

There is no evidence to support the hypothesis that these sponges chemically deceive or repel starfish predators. In fact this would appear most unlikely. The great majority of M. asperimus in the field have sponge cover to some degree, and yet in chapter 2 it was shown that feeding rates on them did not differ markedly from that on E. bifrons which does not carry any epizoic sponge.

Now the sponge cover on M. asperrimus changes the surface texture of the scallop shell. This alteration acts in such a way as to decrease the suction efficiency of the predator's tube feet. Six times more force is required to pull a clean shell away from the tube feet of a starfish than to free a sponge covered scallop of the same size. Therefore, once C. calamaria has come into contact with a scallop, it has an increased capacity to hang on to it if sponge cover is either sparse or lacking altogether. Similarly, the scallop which quickly responds to the contact of a predatory starfish by clapping vigorously in an attempt to swim away, will be more successful in escaping if tube foot adhesion is impaired by the presence of sponge.

The time factor becomes important when one considers escape reactions, their intensity, the interval between starfish contact and the scallop's response, and the relative increase in force a starfish can apply with time.

Feder (1955), in a study on feeding mechanisms, stated that a starfish, Pisaster ochraceus, 30cm in diameter, could exert a maximum pull of 4000 grams on a 10cm mussel. During the course of this experimentation it was noted that with increasing intervals of time, the force required to release a scallop from a star's grip also increased. This relationship was not quantified, but a general trend appears to show that by doubling the time of contact, the force increases by 20-200%, whilst tripling contact time allows the pull to increase 4 to 6 times. Further research should be conducted to determine the time required for C. calamaria to crawl far

enough across a doughboy scallop in order to capture it. Capture may prove to be a product of the size and number of tube feet in contact with the bivalve. Minchin (pers. com.), has recorded photographic evidence of a large starfish, Marthasterias glacialis, using only the tip of one arm to capture a juvenile commercial scallop in Irish waters. In this case, which would appear to be the usual method of contact, the starfish was able to grip the scallop strongly enough to hold it before the full escape reaction was elicited. His photographic series shows that this response was of little use once the starfish had a purchase on its prey.

To conclude, it has been shown that under experimental conditions in which M. asperrimus is confined with its natural predator, C. calamaria, the sponge covering significantly reduces predation by altering the surface texture of the shell and so increases the efficiency of the swimming escape response by decreasing the adhesive ability of the asteroid's tube feet. Hence, the concurrence of M. asperrimus and sponge appears to be a mutualism with predation as one of the major forces structuring the association.

Chapter 4

ESCAPE BEHAVIOUR OF SCALLOPS TO ASTEROIDS.

All organisms are sensitive to chemical changes in their environment. Many aspects of behaviour of marine organisms are elicited or controlled, partly or wholly, by specific chemical cues, usually at low concentrations. Whittle and Blumer (1970) found that the starfish, Asterias vulgaris, responded to concentrations of oyster tissue in the parts per billion range.

The detection of the presence of one species by a different species using chemical cues is termed interspecific chemoreception. Food finding, host detection by parasites and predator recognition by prey are some of the many instances in which interspecific chemoreception is involved. Many molluscs are able to detect predatory starfish using chemoreception and accordingly act in a defensive manner. The typical escape reaction moves the organism away from the predator, usually in a violent fashion.

Phillips (1976) divides such behaviour into avoidance responses which are elicited by water-borne chemicals diffusing from a distant predator, and escape responses which are elicited upon contact with the predator. Feder and Lasker (1964), in an attempt to extract the material from starfish which cause escape responses, showed that the active substance was concentrated on the epidermis of the tube feet. The exact chemical composition is still unknown, although several workers have isolated it as a saponin-like substance (Feder and Lasker, 1964; Mackie, 1970; Mackie and Grant, 1974).

Ansell (1969) suggested that consideration of the ecological consequences of escape behaviour is restricted by lack of information on natural feeding habits. However, since 1969, several informative studies have illustrated the value of avoidance responses (Phillips, 1976; 1977; Dayton et al, 1977; Menge, 1972). The fact that escape behaviour does have value was demonstrated by Feder and Christensen (1966), who reported a number of starfish which feed on responding organisms.

The recognition and avoidance of predators does have important ecological implications. Successful avoidance could effectively remove the prey organism from the predator's diet. However some marine organisms are unable to distinguish the unique biochemical factors of its predator from similar biochemical factors of other organisms which do not prey on them. Mausey et al (1968) recorded a "running" response of ophiuroids in the presence of the starfish, *Luidia foliolata*, although in the area of observation, these brittle-stars were not eaten by this starfish.

On the other hand, a particular mollusc may respond to a predatory starfish that it naturally encounters, but not to predators from foreign habitats. For instance, Edwards (1969, in Phillips 1976) recorded the neogastropod, *Olivella biplicata*, responding vigorously to escape from *Pisaster brevispinus* but not from the predaceous *Pisaster ochraceus*. Similarly Feder (1963) found that in tidal pools along the Californian coast, the limpet, *Acmea scabra*, which did not show an escape response to the starfish *Pisaster ochraceus*, was consumed by the latter in a proportion far

greater than that in which it occurred in nature.

Thus, for the mollusc involved, it would appear that the most beneficial behaviour is to be able to recognise and escape from its predators, whilst also being able to recognise the non-predatory organisms in its environment. Dayton et al (1977) have shown that most of the prey species of a large active asteroid, Meyenaster gelatinosus (Meyen), have extremely effective running escape behaviour in which they release their attachment to the substratum, to be swept safely away from their predator. They also suggest that these prey species can discriminate between foraging and non-foraging M. gelatinosus, which indicates something more than chemoreception is involved. Vibrations caused by moving starfish is offered as a possibility. Along the same lines, Dickie and Medcof (1963) observed the scallop, Placopecten magellanicus, to almost always react vigorously to contact by Asterias vulgaris a known scallop predator (Chiasson 1952, in Dickie and Medcof 1963), whilst it did not respond to Crossaster papposus which does not appear to feed on scallops.

An understanding of community structure and relationships may go far in explaining these complex predator-prey systems. Furthermore, a study of systematics may clarify some aspects of escape behaviour. Incorporating this approach in his study, Margolin (1964) found that limpets of the genus Acmaea responded only to starfish of the order Forcipulatida, whereas those belonging to the order Phanerozonida and Spinulosida did not evoke escape responses.

The present study was designed to quantify escape

reactions of 3 species of scallops to 6 species of Tasmanian starfish belonging to the 3 common orders mentioned above. Three of these asteroid species are frequently found on scallop beds, and a fourth is reportedly associated with them. The remaining 2 species do not live with scallops. Experiments were planned to investigate the reactions of scallops to live starfish in the laboratory and in the field, and to determine the effectiveness of starfish extracts in provoking avoidance responses. By taking into consideration the conclusions on feeding behaviour derived from chapter 2, the ecological implications of these escape and avoidance responses can be evaluated.

4B RESPONSES TO LIVE STARFISH

i MATERIALS AND METHODS

Pecten meridionalis, Equichlamys bifrons and Mimachlamys asperrimus all escape from potential predators by clapping movements of their valves. Attempts were made to induce escape reactions to 6 different species of asteroid, these being Coscinasterias calamaria, Astrostole scabra, Nectria ocellata, Uniophora sinusoida, Patiriella calcar and Tosia magnifica (Plate 9).

Behavioural observations were carried out in the laboratory with the animals in a glass aquarium of dimensions 60 x 35 x 40 cms. A gravel layer 2 cm deep, was added, and the tank was topped up with sea water which was changed regularly throughout the experimentation. Scallops were taken from the D'Entrecasteaux Channel and used within 48 hours of capture. Most starfish were freshly caught along with the scallops, but on several occasions stars which had been kept in holding tanks for up to 21 days were used, with no observable deterioration of response intensity.

Three to six scallops were placed in the tank each time. Starfish were placed on the gravel and allowed to crawl freely towards the scallops. Slowly moving species (i.e. U. sinusoida) were placed either adjacent to, or on top of the scallops. Responses were recorded descriptively in longhand. Scallops which reacted by clapping were allowed to recuperate in the holding tank for a period of 4 hours or longer. Fange (1963) found that the radula muscle of the gastropod Buccinum undatum required 1 - 1½ hours for complete relaxation

after stimulation with starfish extracts. Both juvenile and adult starfish and scallops were used.

A control experiment was conducted in which 2 individuals of each species of scallop were placed in the aquarium in the absence of starfish. Normal movements were recorded for a period of 45 minutes after which reactions to various mechanical stimuli were noted.

4B RESPONSES TO LIVE STARFISHii RESULTS

160 observations of escape behaviour were recorded. Each observation involved a number of reactions elicited by the presence of the starfish and actual contact with it. Contact occurred in every trial. Eleven types of reactions were noted. These were subjectively ranked in the order 0; (no reaction), to 10; (full swimming response). Refer to table 7 below.

Table 7 : Escape Response of Scallops to Sea-stars.

Graded value	Response
0	No reaction.
1	Tentacles extended.
2	Valves close slowly.
3	Valves remain partially closed.
4	Valves remain tightly closed.
5	Weak clap without raising valve.
6	Weak clap from raised valve position (no locomotion).
7	Series of weak claps with no locomotion.
8	Single jump = 1 sharp clap.
9	Series of jumps = series of sharp claps.
10	Swimming = consecutive claps

The strongest response resulting from each individual contact was tabulated. (Appendix I, table 7b). The data were then grouped into 2 categories, these being "weak" and "strong" reactions. The latter were those involving

movement of the scallop away from its potential predator, whilst weak responses did not involve displacement. (Appendix I, table 8). Where no reaction occurred after continuous contact of several minutes, a negative response was recorded. The relationships between the strength of the response and the 6 starfish species are illustrated in figures 11 to 13.

The numbers of trials conducted on each starfish species differed. This was a reflection of the availability of fresh specimens to work with and the number present at the time of experimentation. Therefore, the data are presented not as numbers of responses, but as the percentage of trials responding either weakly or strongly.

Figures 11 to 13 show that the greatest percentage of strong escape responses to live starfish are evoked by the first 3 species, C. calamaria, A. scabra and U. sinusoida. These three species consistently evoked some form of response, whilst the remaining 3 species P. calcar, T. magnifica and N. ocellata all gave negative responses in 3 trials or more. The latter 3 produced a greater percentage of weak responses than strong in all scallop species tested. However P. calcar produced a 43% strong reaction in the doughboy scallop M. asperimus. This was 4 times greater than either the commercial or queen's response to P. calcar. Furthermore, M. asperimus reacted more strongly to U. sinusoida than did the other 2 species of scallop.

Swimming, the most violent escape reaction, was displayed by all scallop species on contact with C. calamaria and A. scabra whilst U. sinusoida provoked several swimming

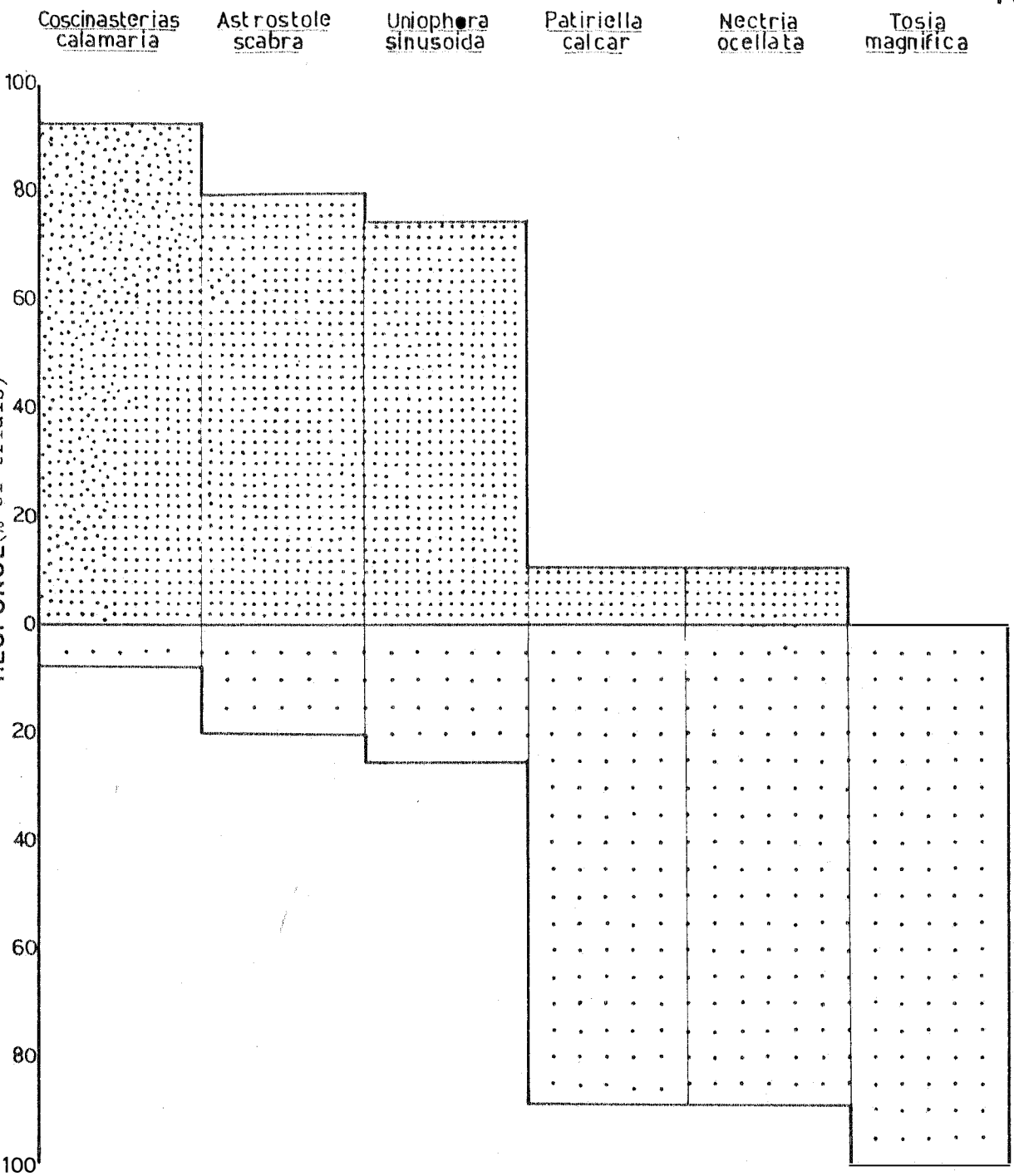


Fig 11 **Escape Response of P. meridionalis to Asteroids.**

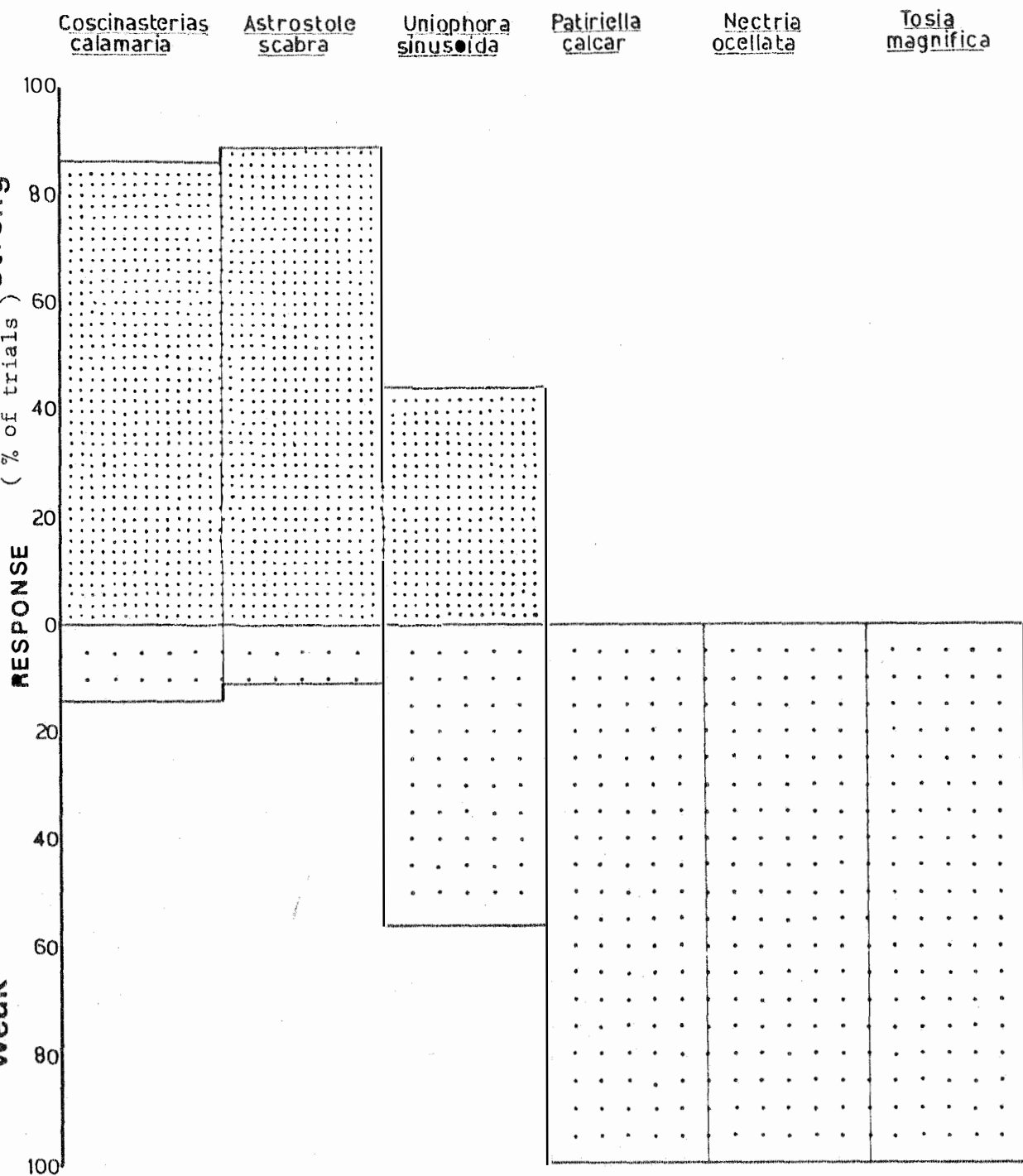


Fig 12 Escape Response of E. bifrons to Asteroids

<u>Coscinasterias</u> <u>calamaria</u>	<u>Astrostole</u> <u>scabra</u>	<u>Uniophora</u> <u>sinusoida</u>	<u>Patiriella</u> <u>calcar</u>	<u>Nectria</u> <u>ocellata</u>	<u>Tosia</u> <u>magnifica</u>
---	------------------------------------	--------------------------------------	------------------------------------	-----------------------------------	----------------------------------

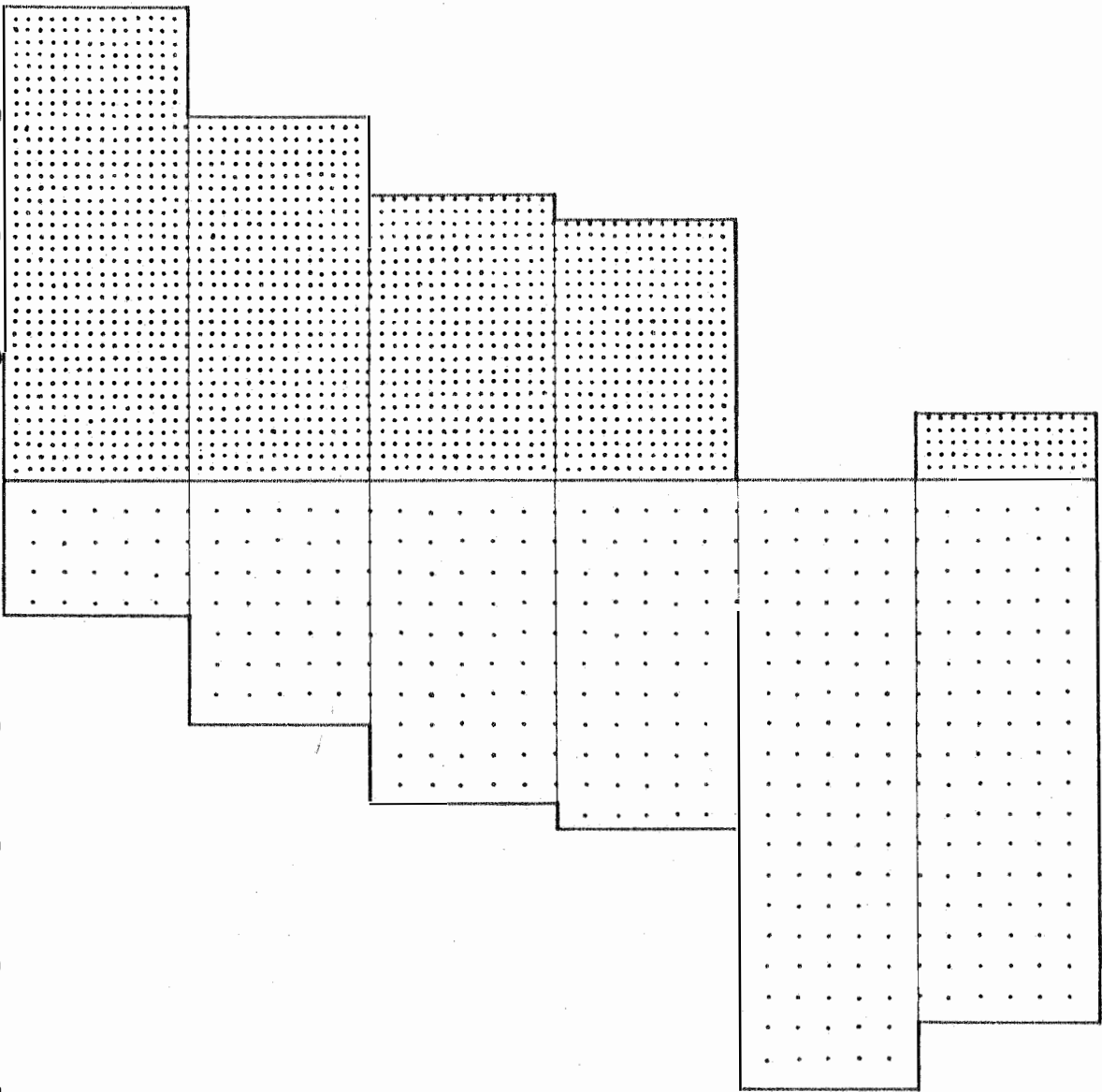


Fig 13 Escape Response of M. asperimus
to Asteroids.

reactions, but only in the doughboy scallop M. asperrimus.

A general trend of decreasing response is apparent from C. calamaria through to those species on the R.H.S. of the diagrams. Lecomte recorded a similar relationship in 1953 when he found that the scallops, Pecten jacobaeus and Chlamys opercularis, responded violently to Marthasterias glacialis, and much less strongly to other starfish tested.

There was no relationship found between intensity of response and size of either starfish or scallops.

The control experiment supplied data on non-escape movements recorded in the absence of starfish. Stimuli used included moving shadows, fast movement, lighted flash bulbs, loud conversation and slamming doors. All responses were weak, consisting of gradual valve closures. Delayed slow closure (5-15 secs) resulted from flash illumination. Several weak claps were recorded from queen scallops when mechanical stimuli were not being applied. Owen (1966, in Thomas et al 1971) associates these movements with the removal of pseudo faeces from the pallial cavity of the scallop.

4C AVOIDANCE RESPONSES TO STARFISH EXTRACTS

1 MATERIALS AND METHODS

Avoidance responses to extracts of 3 asteroid species were recorded in aquaria in the laboratory. Crude extracts were made from starfish tube feet by crushing 20 ml of them in a mortar. This was then diluted to 250 ml with deionized water. The mixture was shaken vigorously and allowed to settle. 200 ml of fluid was decanted for experimental purposes. When not in use, the extracts were stored at 0°C for a maximum period of 30 days. Feder and Lasker (1964) found that excised tube feet maintained their ability to evoke strong responses for at least one year after storage at - 15°C.

For each experiment, three scallops were placed in an aquarium with freshly collected sea water. 0.1 ml of extract, diluted to 0.5 ml with sea water, was directed towards the mantle of each scallop through a 1 ml syringe fitted with a 15 ml extension tube. In this manner, extracts could be administered with little mechanical disturbance to adjacent scallops. Extracts were ejected at a slow, constant rate from a distance of 5-10 mm from the mantle edge.

The aquarium water was drained and replaced after each third trial. Approximately 13-15 litres were used each time.

Tube feet extracts were made from C. calamaria, A. scabra and U. sinusoida. Aboral extracts were made by crushing and diluting the calcareous body wall and the

epidermis from sections of the upper surface of C. calamaria,
and U. sinusoida.

As a control, a number of trials were run using 0.5 ml
of sea water in the syringe in place of the extracts.

4C AVOIDANCE RESPONSES TO STARFISH EXTRACTS

ii RESULTS

95 individual observations of responses to starfish extracts were made. The most noticeable trend is that generally, these responses are less intense than those evoked by live starfish. Only 1 of the 95 responses ($\approx 1\%$) involved swimming (E. bifrons), compared to 16% swimming responses to contact by living starfish. Thomas and Gruffyd (1971) came to a similar conclusion that crude extracts did not produce such marked differences in escaped responses as the live asteroids from which they were prepared.

There is no significant difference between reactions to tube feet and aboral surface extracts ($t = 0.915$, d.f. = 2, $0.50 > P > 0.30$). This finding supports the work of Montgomery (1967) who found that responses of several species of abalone were of equal strength when stimulated with tube feet and aboral epidermis.

Results from the control experiments were all negative, indicating that the mechanical stimulation of a stream of sea water does not provoke a reaction.

4D ESCAPE RESPONSES IN THE FIELD

1 MATERIALS AND METHODS

Experiments with C. calamaria and scallops were conducted in the field at Helliwell's point in the D'Entrecasteaux Channel. One specimen of C. calamaria 15 cm. in diameter, was collected from shallow water and taken out to the scallop bed at a depth of 15 metres to induce escape responses in the 3 species of scallop found there. This work was carried out using S.C.U.B.A. gear.

The star was held at arms length and gradually moved towards each scallop in order not to alarm it. It was then carefully placed on top of the scallop such that the tube feet were overhanging the gape between the two valves. Most scallops closed up as the diver approached, but left enough gape for their tentacles to be partially extended. Only one (queen) in 50 scallops approached actually swam away. The starfish was allowed to remain on each scallop for 90 seconds. This arbitrary time was restricted by the permissible diving time at this depth, but structured around a reaction time of 1-30 seconds contact time observed in the laboratory. One starfish was used for all 15 experiments. 5 observations were made on each species of scallop. All M. asperimus were attached to bryozoan coral by byssal threads; all P. meridionalis were seated in shallow depressions and all E. bifrons were openly sitting on the muddy surface.

4D FIELD RESPONSES

ii RESULTS

The number of trials conducted (15) was limited by time, 10 minutes only at a depth of 15 metres. However, despite this paucity of results, responses for each species of scallop were surprisingly consistent. All 5 P. meridionalis swam away from the starfish after a contact period of 5 - 30 seconds. Each scallop clapped vigorously between 18 - 40 times, swam up off the sea floor and settled on average 90 cm (3ft) away.

Queens on the other hand, responded by swimming during three trials, and twice with a series of jumps resulting from violent, intermittent claps.

Escape responses from doughboy scallops were all of low intensity, the strongest being a single clap. This greatly contrasts with reactions elicited in the laboratory.

The data from table 11 are illustrated in fig 14. Here the 'strong' response has been subdivided into (a); full swimming, and (b); 'strong', the latter being either one or a series of jumps away from C. calamaria. This figure clearly illustrates the gradation of responses.

Table 11 : Escape Response of Scallops to
C. calamaria in the Field (% of trials)

	<u>P. meridionalis</u>	<u>E. bifrons</u>	<u>M. asperimus</u>
Strong	100%	60%	0
Weak	0	40%	100%

Fig Escape Response of Scallops to *C. calamaria*
in the Field.

Plate 9 : a, b, c.

Escape reaction of the commercial scallop,
Pecten meridionalis, to the starfish,
Coscinasterias calamaria.

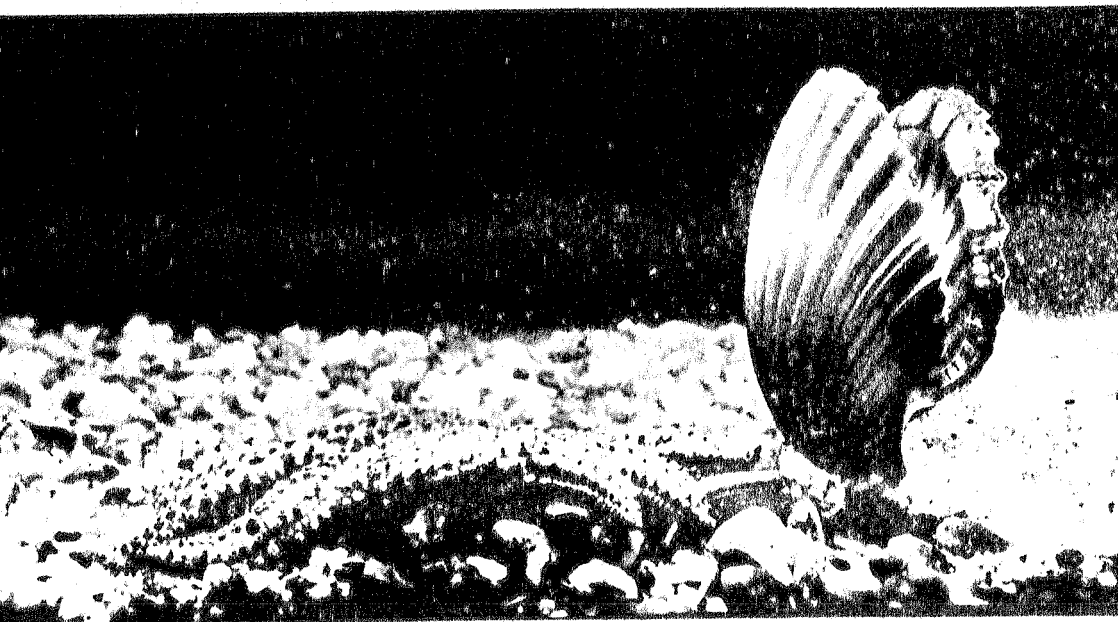
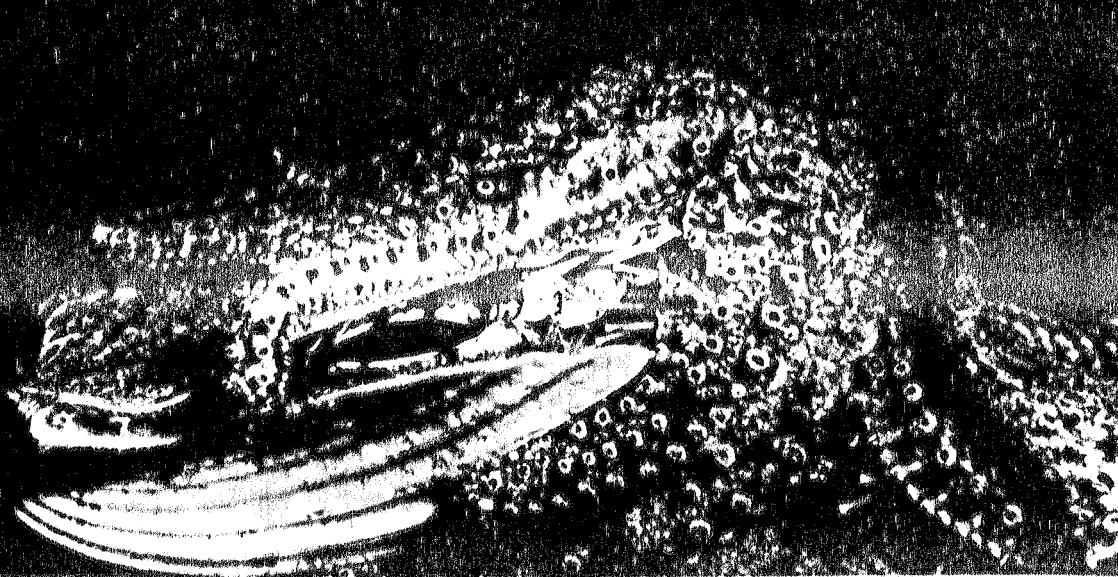


Plate 10 : a, b, c.

Escape reaction of the queen scallop,
Equichlamys bifrons, to the starfish,
Coscinasterias calamaria.

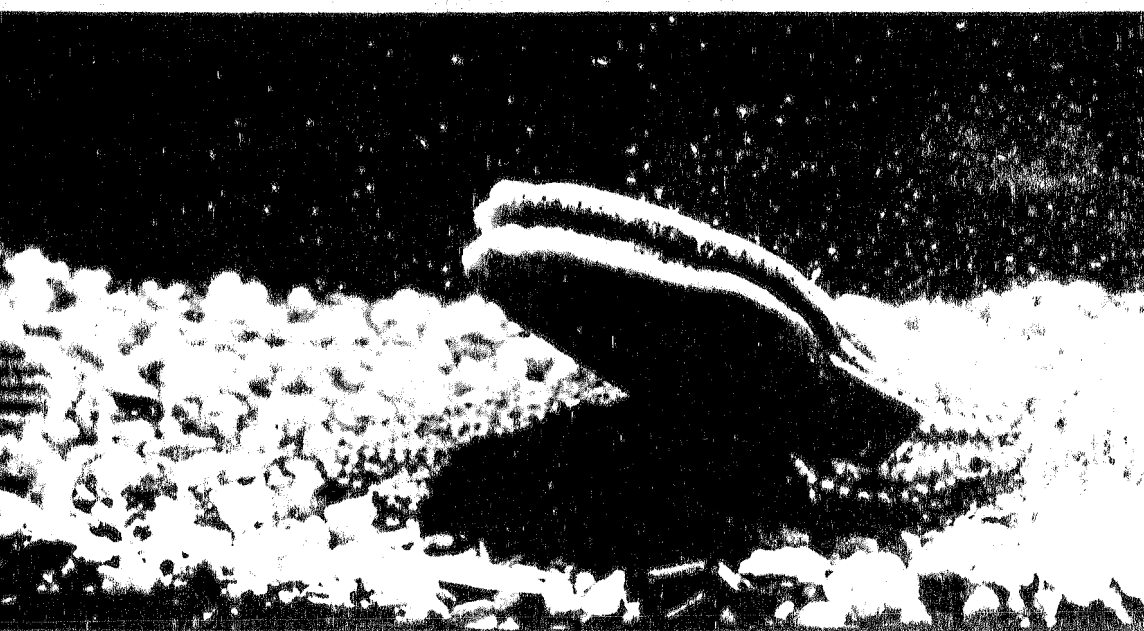
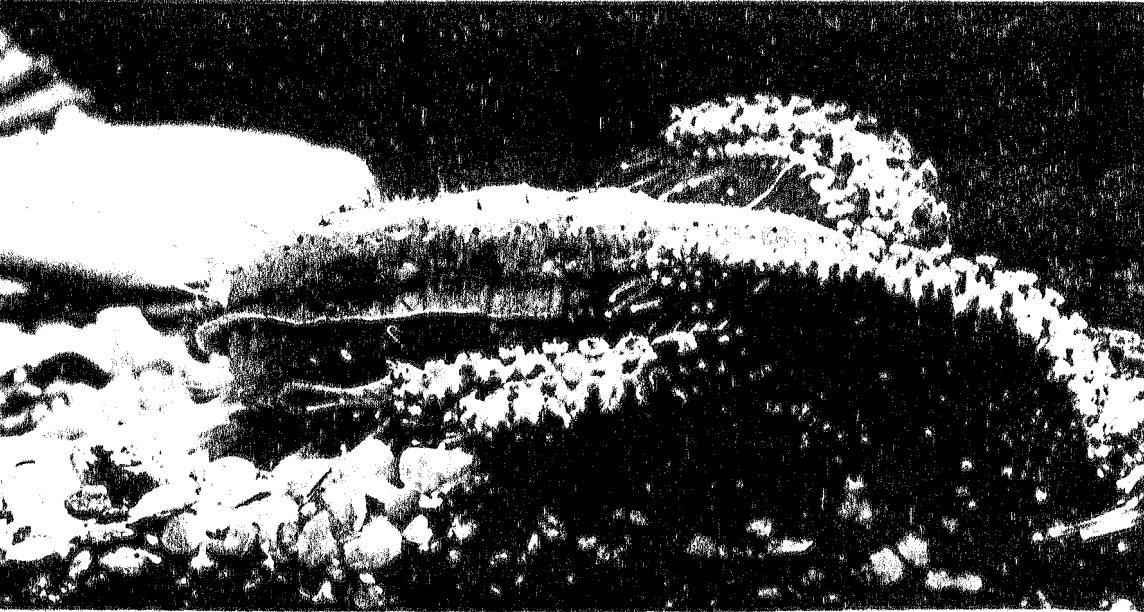
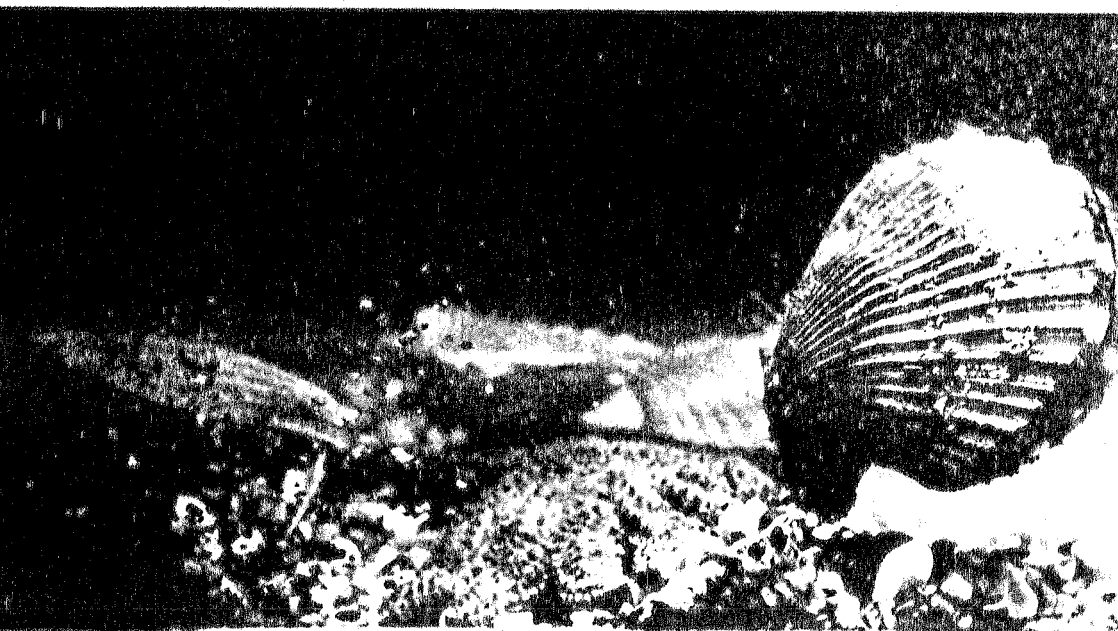
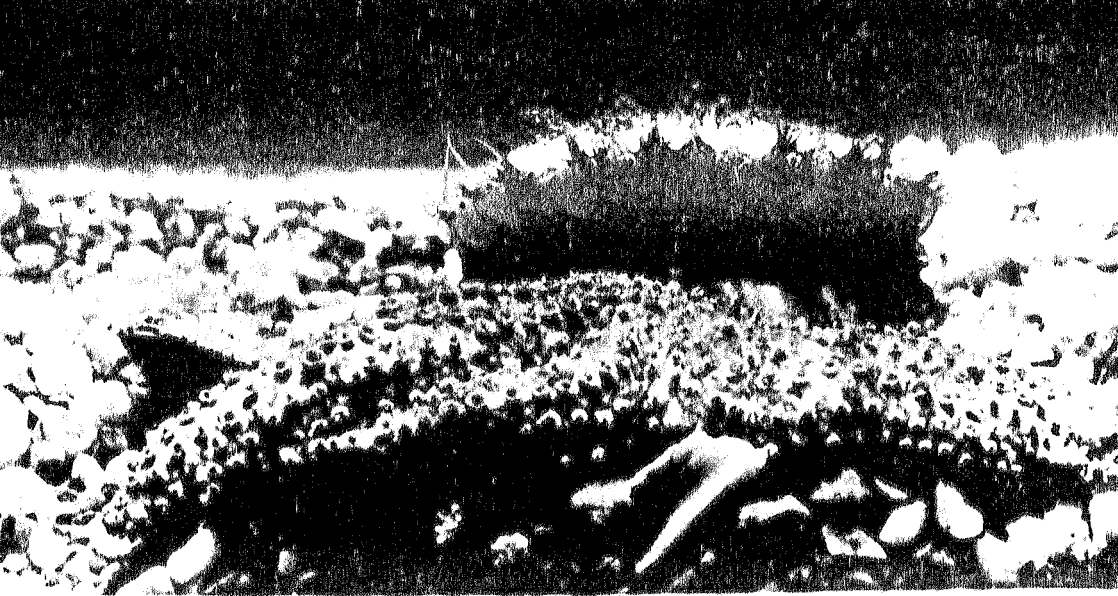


Plate 11 : a, b, c.

Escape reaction of the doughboy scallop,
Mimachlamys asperrimus, to the starfish,
Coscinasterias calamaria.



4E DISCUSSION

The ability of scallops to respond differentially in their intensity of reaction to starfish would appear to have considerable ecological importance. Clearly, a great deal of energy is conserved by not reacting violently to harmless species. Pecten meridionalis, which is characteristically found in shallow depressions, and almost completely camouflaged with sand and silt, would certainly be more vulnerable to predators if it is forced to leave this depression and sit openly on the sea floor. In this exposed situation, it is also more likely to be captured by dredges and nets. Equichlamys bifrons, which, according to Olsen (1955), forms larger depressions than commercial scallops, would be disadvantaged in the same manner. However, the statement of Thomas and Gruffydd (1971), that "it [Pecten maximus], has to expend energy and time preparing another depression", is questionable since it implies that this species purposefully buries itself. More realistically, the scallop gradually excavates a hollow in a presumably unintentional manner, by ejecting water from all around its gape. The diameter and depth would be a result of the length of time it is left undisturbed.

Hartnoll (1967) found that the scallop, Pecten maximus, once recessed, will remain in the same position for a period averaging nearly a month. He suggested that this species will remain recessed until disturbed by predators such as the whelk, Buccinum undatum, the starfish, Asterias rubens, the crab, Cancer, and the lesser octopus, Eledone.

On the other hand, Mimachlamys asperimus would be forced to detach itself from the substratum if disturbed by predators, and subsequently secrete more byssal threads for re-attachment. Although M. asperimus did not detach when touched by C. calamaria in field experiments, Bloom (1975) has recorded a similar species, Chlamys rubida, to detach and swim away within 3-10 seconds of contact by a predatory starfish.

Differences in degree and intensity of a scallop's escape reaction to various species of predators may be due to two factors ; differences in the chemical nature of the active substances secreted, or differences in the quantity liberated. Most of the evidence in the literature supports the latter hypothesis, and initial work by a number of researchers suggests that steroid saponins are involved. (Mackie, 1970; Feder, 1972; Mackie and Grant, 1974). Feder (1972) points out that these active, saponin-like substances are found in most tissues of a starfish, but are concentrated in the epithelial covering of the tube feet and body. This view is supported by the findings using starfish extract in this study. The intensity of reactions to tube feet and aboral surface extracts were not significantly different.

Conversely, variations in the response of different scallops to the same asteroid species must be due to differences in ability to detect the same active substance. Therefore, it can be concluded that both in the field and in the laboratory, P. meridionalis is the scallop most sensitive to the starfish, C. calamaria, whilst M. asperimus is the least active, and hence the least sensitive of the 3

species. Similarly, Montgomery (1967) found differences in responsiveness of two abalone species to a single species of asteroid, and suggested that the most vigorous abalone had a more highly developed sensory epithelium.

Whilst M. asperimus may be the least sensitive scallop to C. calamaria, strong reactions are evoked by the starfish, U. sinusoida and P. calcar. This sensitivity to "weaker" starfish may be a reflection of the state of the byssal threads. The percentage of strong responses of unattached doughboy scallops in aquaria was 5 times greater than that of attached scallops in the field. It appears that M. asperimus becomes more sensitive to starfish when it is unattached. Further research is required in this area.

The higher intensity of response of scallops to live starfish than to tissue extracts, is a product of chemical as well as tactile stimulation. The added stimulus of contact with the tentacles, and perception of movement by the scallop's numerous eyes (plate 8), were absent during the tissue extract experiments.

Now, C. calamaria readily eats scallops under experimental conditions and is found in nature on scallop beds. Fisheries officers have reported dredging up scallops tightly held by feeding starfish. Thus the reaction of scallops to C. calamaria appears to be true escape behaviour. Reactions to the remaining 5 species are less intense and appear to be in response to an "active substance" that does not necessarily involve specific predator recognition.

Low intensity responses were made by all three species of scallop to the non-predatory starfish, *T. magnifica* and *N. ocellata*, whilst the larger carnivorous species, *C. calamaria* and *A. scabra*, consistently evoked strong responses. Reviewing these two groups of responses with a systematic approach, one finds that *C. calamaria*, *A. scabra* and *U. sinusoida* belong to the Forcipulatida order of asteroids, whilst *P. calcar*, which produced a response intermediate between the two extremes, belongs to the order Spinulosida. (See Fig. 15). *T. magnifica* and *N. ocellata* belong to the Phanerozonida order. Of these three orders, only the forcipulates elicited full swimming responses.

Clark (1958) recorded similar results while studying the behaviour of New Zealand starfish. He found that although forcipulate species elicited escape responses in the gastropod, *Melagraphia aethiops* (Gmelin), *Patiriella regularis* Verrill, a spinulosan, did not. Similarly Crump (1968) reported that the flight response of the gastropod, *Struthiolaria papulosa gigas* Sowerby, did not occur in species of the orders Phanerozonida and Spinulosida but was violently displayed on contact with forcipulate asteroids. According to Fell and Pawson (1966), the Spinulosida and Forcipulatida represent two distinct lines of asteroid evolution that arose from the basal phanerozone condition. Few spinulosan, and even fewer phanerozone asteroids are reported in the literature to open bivalves by force. In contrast, studies reporting the bivalve feeding habits of forcipulate asteroids are well documented. The evolution of four rows of suckered tube feet on the long narrow arms of forcipulates may have occurred in response to the mechanical requirements of opening bivalves.

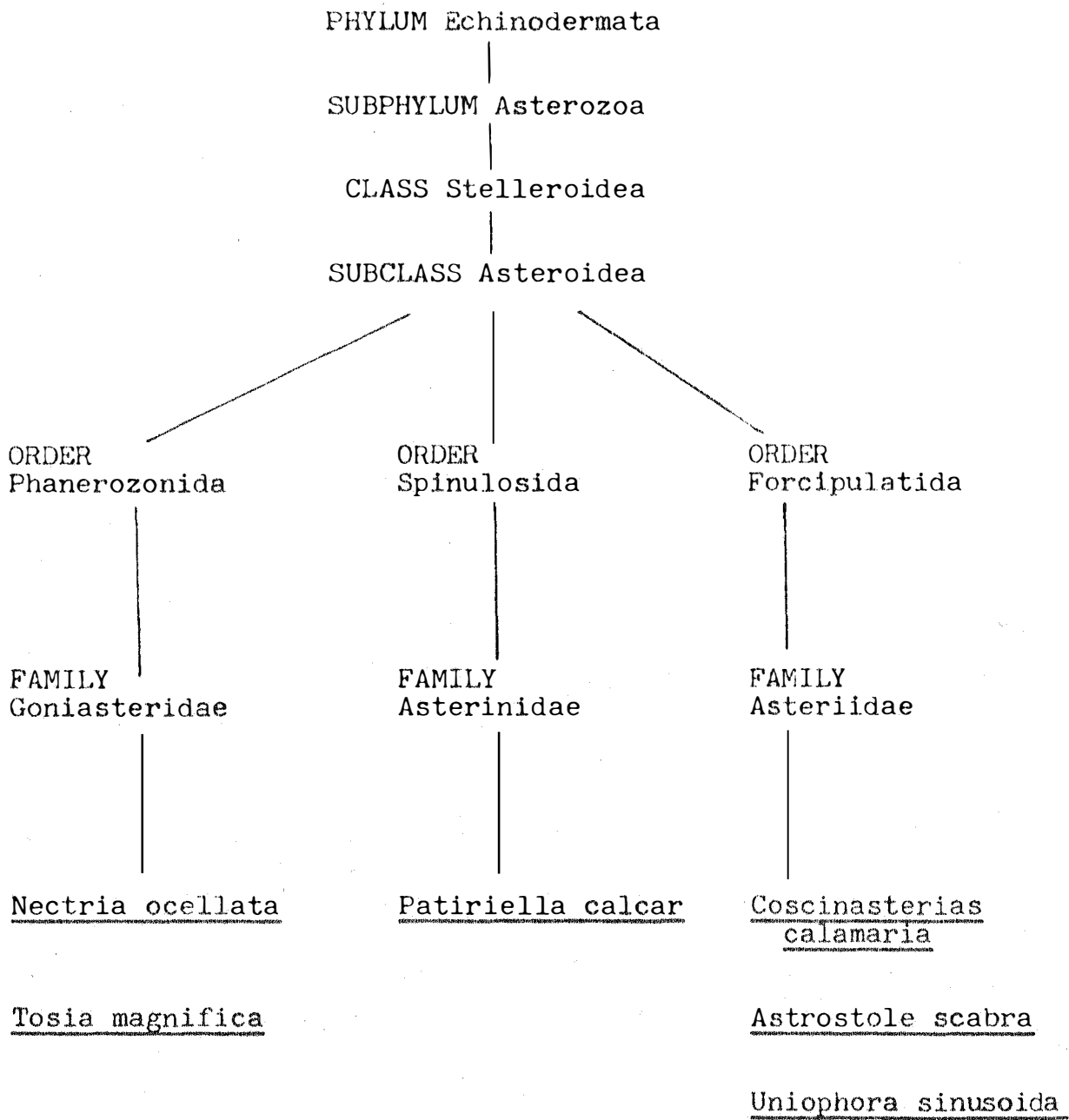


Fig 15: SYSTEMATIC RELATIONSHIPS BETWEEN SOME TASMANIAN ASTEROIDS

GENERAL CONCLUSION

Many of the experiments in this study were designed to explain observations made in the field. Because Coscinasterias calamaria is not a specialized feeder in the laboratory, experimental findings can not be extended directly to the field. However, experimental observations can be used to provide a more detailed understanding of field observations.

According to Clark (1946), C. calamaria is the most common littoral starfish of the southern coasts of Australia. The success of this starfish may be due to its generalised diet which appears to be controlled by the abundance and availability of food organisms in its habitat. Adult C. calamaria do not appear to display a distinct preference for any of the bivalve species used in this study, although Crump (1969) found that adults of this species prefer bivalves to gastropods.

C. calamaria is infrequently recorded feeding on uninjured scallops, although reports associating this starfish with scallop beds are numerous. This may be attributed to the success of the scallop's escape response which may effectively remove it from the starfish's diet. It was shown that this response was more effective when the scallop's valves were enveloped in sponge. However, damage to scallops caused by commercial fishing gear may attract starfish to the scallop beds. Injury reduces the efficiency of the scallop's escape reaction and thereby increases predation upon it.

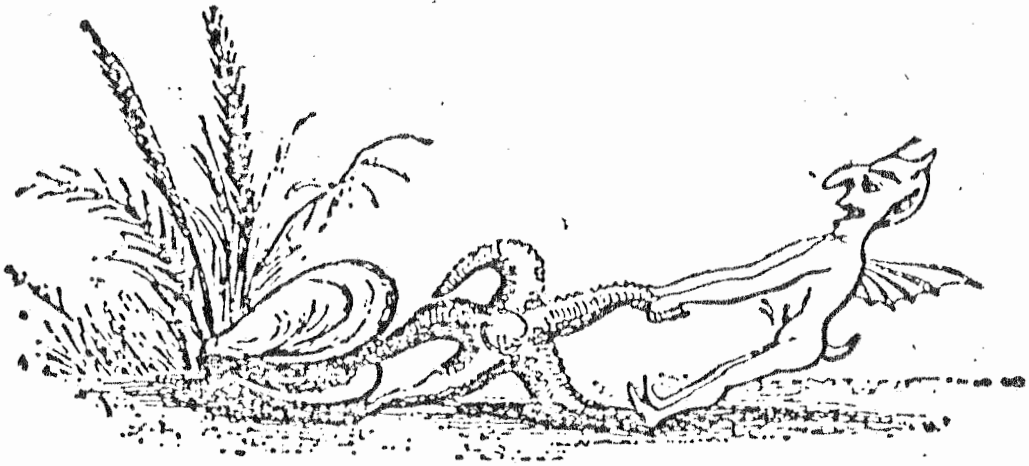


FIG. 16 —Tailpiece. From Forbes, *History of British Stat-fishes*

REFERENCES

REFERENCES

- ALTMAN, P.L. and D.S. DITTMER, 1968 : Metabolism, Biological handbook. Fed. Am. Soc. Exp. Biol.
- ANDERSON, J.M., 1960 : Histological studies on the digestive system of a starfish, Henricia, with notes on Tiedemann's pouches in starfishes. Biol. Bull., 119: 371-398.
- ANON., 1967 : Scallop Research in D'Entrecasteaux Channel. Tas. Fish. Res., 1(1): 7-10.
- ANSELL, A.D., 1969 : Defensive Adaptations to Predation in the Mollusca. Symposium on Mollusca. Part II. Mar. Biol. Ass. India., 487-507.
- BAKUS, G., 1966 : Marine Poeciloscleridan sponges of the San Juan Archipelago, Washington. J. Zool. Lond., 149: 415-531.
- BEAU, A.G., 1965 : Ecological Variation of Chlamys dieffenbachii (Reeve) (Mollusca, Lamellibranchiata). Trans. R. Soc. N.Z., 7(5): 93-96.
- BINYON, J., 1972 : Physiology of Echinoderms. Pergamon Press, New York.
- BLOOM, S.A., 1975 : The motile escape response of a sessile prey: A sponge-scallop mutualism. J. Exp. Mar. Biol. Ecol., 17: 311-321.
- BOURNE, N., 1964 : Scallops and the offshore fishery of the maritimes. Fish. Res. Bd. Canada. Bull. No. 145.
- CASTILLA, J.C., 1972 : Responses of Asterias rubens to bivalve prey in a Y-maze. Mar. Biol., 12: 222-228.
- CHRISTENSEN, A.M., 1957 : The feeding behaviour of the seastar Evasterias troschelii Stimpson. Limnol. Oceanogr., 2: 180-197.

- CHRISTENSEN, A.M., 1970 : Feeding biology of the sea star
Astropecten irregularis. Ophelia 8: 1-135.
- CHRISTENSEN, D.J., 1973 : Prey Preferences of Stylochus
ellipticus in Chesapeake Bay. Proc. Natl. Shell-
fish Assoc., 63: 35-38.
- CLARK, A.M., 1966 : Port Phillip survey. 1957-'63.
Echinodermata. Mem. Nat. Mus. Vict., 27: 289-384.
- CLARK, H.L., 1946 : The echinoderm fauna of Australia, its
composition and origin. Publs. Carnegie Inst.,
566: 1-568. Lord Baltimore Press, Baltimore.
- CLARK, W.C., 1958 : Escape responses of herbivorous gastropods
when stimulated by carnivorous gastropods.
Nature., 181(1): 137-138.
- CRISP, D.J. and P.S. Meadows, 1963 : Absorbed layers: the
stimulus to settlement in barnacles. Proc. Roy.
Soc. B., 158: 364-387.
- CRUMP, R.G., 1968 : The flight response in Struthiolaria
papulosa gigas Sowerby. N.Z. J. Mar. Freshwat.
Res., 2: 390-397.
- CRUMP, R.G., 1969 : Aspects of the biology of some New Zealand
echinoderms: Feeding growth and reproduction in the
asteroids, Patiriella regularis (Verill, 1867) and
Coscinasterias calamaria (Gray, 1840) Unpubl.
Doctoral Dissertation, Otago University.
- DAKIN, W.J., 1952 : Australian Seashores. Halstead Press,
Sydney.
- DARTNALL, A.J., 1969(a) : A field key to Tasmanian sea stars.
Tas. Fish. Res., Jan. 1969.
- DARTNALL, A.J., 1969(b) : New Zealand sea stars in Tasmania.
Pap. Proc. Roy. Soc. Tas., 103: 53-55.

DARTNALL, A.J., 1972 : Sea stars of Tasmania. Tas. Year Book.
1972. 72-79.

DAYTON, P.K., R.J. ROSENTHAL, L.C. MAHEN and T. ANTEZANA, 1977
: Population structure and foraging biology of the
predaceous Chilean asteroid, Meyenaster gelatinosus
and the escape biology of its prey. Mar. Biol.,
39(4): 361-370.

DEBEVOISE, A.E., 1975 : Predation on the chiton, Cyanoplax
hartwegii, Veliger 18 (supp.): 47-50.

DICKIE, L.M. and J.C. MEDCOF, 1963 : Causes of mass mortalities
of scallops (Placopecten magellanicus) in the south
western gulf of St. Lawrence. J. Fish. Res. Bd. Can.,
20: 451-482.

DIX, T.G. and M.J. SJARDIN, 1975 : Larvae of the commercial
scallop, Pecten meridionalis from Tasmania,
Australia. Aust. J. Mar. Freshw. Res., 26(10):
109-112.

DOEZEMA, P., 1969 : Carbohydrates and carbohydrate metabolism
of echinoderms. In Florkin M. and B.T. Scheer
(editors) Chemical Zoology III. Academic Press,
New York.

EMLLEN, J.M., 1966 : The role of time and energy in food
preference. Amer. Natur., 100: 611-617.

FAGER, E.W., A.O. FLECHSIG, R.F. FORD, R.I. CLUTTER and R.J.
GHELARDI, : Equipment for use in ecological studies
using S.C.U.B.A. Limnol. and Oceanogr., 11(4):
503-509.

FAIRBRIDGE, W.S., 1953 : Tasmanian commercial scallop. Aust.
J. Mar. and Freshw. Res., 4(1): 1-39.

FANGE, R., 1963 : Toxic factors in starfishes., Sarsia 10:
19-21.

- FEDER, H.M., 1955 : On the methods used by the starfish, Pisaster Ochraceus, in opening three types of bivalve molluscs. Ecology., 36: 764-767.
- FEDER, H.M., 1959 : The food of the starfish, Pisaster Ochraceus, along the California coast. Ecology., 40: 721-724.
- FEDER, H.M., 1963 : Gastropod defensive responses and their effectiveness in reducing predation by starfishes. Ecology., 44: 505-512.
- FEDER, H.M., 1967 : Organisms responsive to predatory sea stars. SARSIA., 29: 371-394.
- FEDER, H.M., 1970 : Growth and predation by the ochre star, Pisaster Ochraceus in Monterey Bay, California. Ophelia., 8: 161-185.
- FEDER, H.M., 1972 : Escape response in marine invertebrates. Sci. Am., 227(1): 93-100.
- FEDER, H.M. and R. LASKER, 1964 : Partial Purification of a substance from starfish tube feet which elicits escape responses in gastropod molluscs. Life Sciences., 3: 1047-1051.
- FEDER, H.M. and A.M. CHRISTENSEN, 1966 : Aspects of asteroid biology, in Boolootian, R.M., (editor). Physiology of Echinodermata. Interscience, New York.
- FELL, H.B., 1959 : Starfishes of New Zealand. Tuatara., 7(3): 127-142.
- FELL, H.B., 1962 : Native Sea Stars. A.H. and A.W. Reed, Wellington.
- FELL, H.B. and D.L. PAWSON, 1966 : General biology of echinoderms. In Boolootian R.A., (editor) Physiology of Echinodermata. Interscience publishers, New York.

- FERGUSON, J.C., 1969 : Feeding, digestion and nutrition in echinodermata. In Florkin M. and B.T. Scheer (editors), Chemical Zoology III. Academic Press, New York.
- GRACE, R.V., 1967 : An underwater survey of two starfish species in the entrance to the Whangateau Harbour. Tane., 13: 13-19.
- GRANT, J.F., 1971 : Scallop Survey - D'Entrecasteaux Channel, Tasmania. Tas. Fish. Res., 5(2): 21-24.
- HAMNER, P. and W.M. HAMNER, 1977 : Chemosensory tracking of scent trails by the planktonic shrimp, Acetes sibogae australis. Science., 195: 886-888.
- HARRISON, A.J., 1961 : Annual reproduction cycles in the Tasmanian commercial scallop Notovola meridionalis. Hons. Thesis., Tas. Uni.
- HARRISON, A.J., 1965 : Tasmanian scallop fishery and its future. Aust. Fish. Newsl. June, 1965.
- HARTNOLL, R.G., 1967 : An investigation of the movement of the scallop, Pecten maximus. Helgolander wiss Meeresunters., 15:(1-4) 523-533.
- LANDENBERGER, D.E., 1968 : Studies on selective feeding in the pacific starfish, Pisaster in Sth. Calif. Ecology 49(6): 1062-1075.
- LECOMTE, J., 1953 : Réactions de fuite des pectens en présence des Astérides. Vie et Milieu., 3(1): 57-60.
- LENHOFF, H.M. and K.J. LINDSTEDT, 1974 : Chemoreception in aquatic invertebrates. In Grant P.T. and A.M. Mackie (editors), Chemoreception in Marine Organisms. Academic Press, London and New York.

LOOSANOFF, V.L., 1961 : Biology and methods of controlling the starfish, Asterias forbesi. U.S. Fish and Wildlife Service, Fishery Leaflet., 520: 1-11.

MACKENZIE, C.L., 1969 : Feeding rates of starfish, Asterias forbesi (Desor), at controlled water temperatures and during different seasons of the year. U.S. Fish and Wildlife Service, Fishery Bulletin., 68(1): 67-72.

MACKIE, A.M., 1970 : Avoidance reactions of marine invertebrates to either steroid glycosides of starfish or synthetic surface active agents. J. Expt. Mar. Biol. Ecol., 5(1): 63-69.

MACKIE, A.M., R. LASKER and P.T. GRANT : Avoidance reactions of the mollusc, Buccinum undatum to saponin like surface active substances in extracts of the starfish, Asterias rubens and Marthasterias glacialis. Comp. Biochem. Physiol., 26: 415-428.

MACKIE, A.M. and P.T. GRANT, 1974 : Interspecies and intraspecies chemoreception by marine invertebrates. In Grant P.T. and A.M. Mackie (editors), Chemoreception in Marine Organisms. Academic Press, London and New York.

MACPHERSON, J.H. and C.J. GABRIEL, 1962 : Marine molluscs of Victoria. Handbook No. 2; Nat. Mus. Vic. Melb. Uni. Press.

MARGOLIN, A.S., 1964 : A running response of Acmaea to sea stars. Ecology., 45: 191-193.

MAUZEY, K.P., 1966 : Feeding behaviour and reproductive cycles in Pisaster ochraceus. Biol. Bull., 131: 127-144.

MAUZEY, K.P., C. BIRKELAND and P.K. DAYTON, 1968 : Feeding behaviour of asteroides and escape responses of their prey in the Puget sound region. Ecology., 49: 603-619.

MAY, W.L. and J.H. MACPHERSON, 1958 : An Illustrated Index of Tasmanian Shells. Tas. Govt. Press.

MENGE, B.A., 1972 : Foraging strategy of a starfish in relation to actual prey availability and environmental predictability. Ecological Monographs., 42: 25-50.

MONTGOMERY, D.H., 1967 : Responses of two haliotid gastropods (Mollusca), Haliotils assimilis and Haliotis rufescens, to the forcipulate asteroids (echinodermata), Pycnopodia helianthoides and Pisaster ochraceus. Veliger., 9(4): 359-368.

OLSEN, A.M., 1953 : Diving investigations on scallops. Fish. News Lett. Aust., 12(7): 5-7.

OLSEN, A.M., 1955 : Underwater studies on the Tasmanian commercial scallop, Notovola meridionalis. Aust. J. Mar. and Freshw. Res., 6: 392-409

PHILIPS, D.W., 1976 : The effect of a species-specific avoidance response to predatory starfish on the intertidal distribution of two gastropods. Oecologia., 23: 83-94.

PHILIPS, D.W., 1977 : Avoidance and escape responses of the gastropod mollusc, Olivella biplicata (Sowerby) to predatory asteroids. J. Exp. Mar. Biol. and Ecol., 28(1): 77-86.

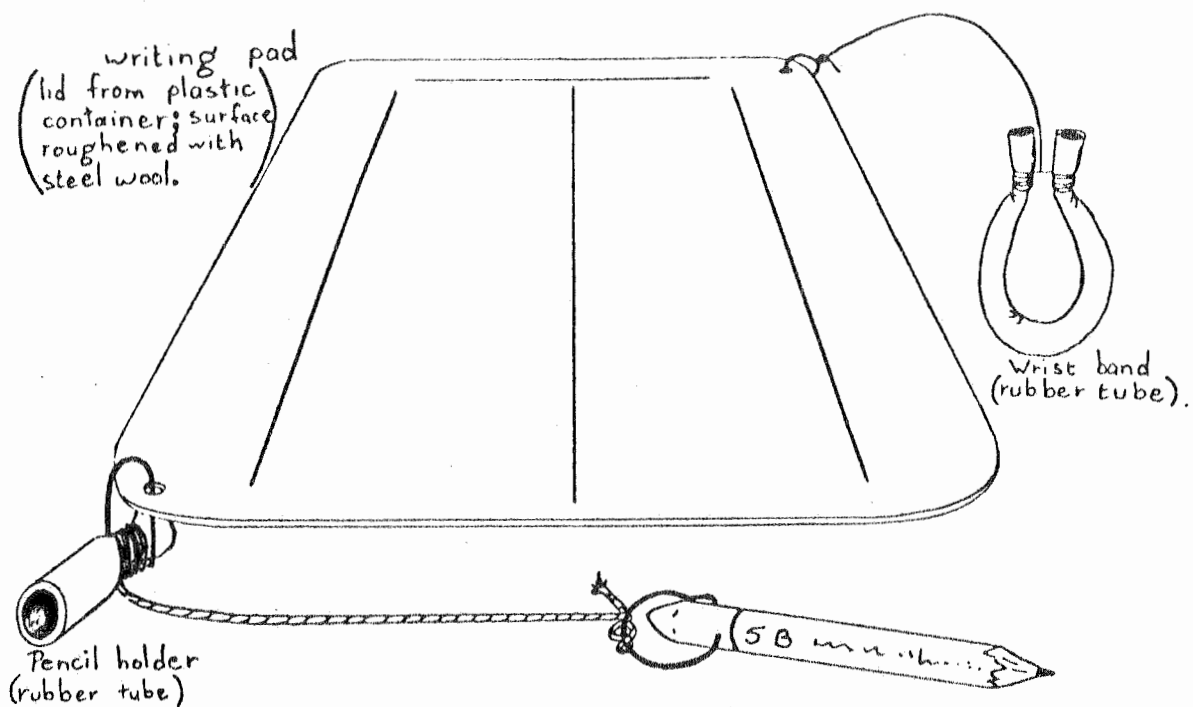
RAPPORT, D.J. and J.E. TURNER, 1970 : Determination of predator food preferences. J. Theor. Biol., 26: 365-372.

SANDERS, M.J., 1970 : The Australian scallop industry. Aust. Fish., 29(5): 2-11.

SHEPHERD, S.A., 1968 : The shallow water echinoderm fauna of South Australia. Part I: The Asteroids. Rec. Sth. Aust. Mus., 15(4): 729-756.

- SHEPHERD, S.A., 1967 (a) : Review of the starfish, Nectria,
(Asteroidea; Goniasteridae). Rec. Sth. Aust.
Mus., 15(3): 463-482.
- SHEPHERD, S.A., 1967 (b) : A revision of the starfish
Uniophora, (Asteroidea asteridae). Roy. Soc. Sth.
Aust., 91: 1-15.
- SNEDECOR, G.W. and W.G. COCHRAN, 1969 : Statistical Methods.
Iowa State Uni. Press.
- THOMAS, G.E. and L.D. GRUFFYDD, 1971 : The type of escape
reactions elicited in the scallop, Pecten maximus,
by selected sea-star species. Mar. Biol., 10(1):
87-93.
- VALENTINCIC, T., 1975 : Amino acid chemoreception and other
releasing factors in the feeding response of the
sea star, Marthasterias glacialis. Proc. 9th Europ.
Mar. Biol. Symp.,: 693-705. Harold Barnes (editor).
Aberdeen Uni. Press.
- WELLS, H.W., M.J. WELLS and I.E. GRAY, 1961 : Food of the sea
star Astropecten articulatus. Biol. Bull. Mar.
Biol. Lab. Woods Hole., 120: 265-271.
- WHITTLE, K.J. and M. BLUMER, 1970 : Interactions between
organisms and dissolved organic substances in the
sea: Chemical attraction of the starfish, Asterias
vulgaris, to oysters. 495-507. In Hood, D.W., (Ed.).
Symposium on organic matter in natural waters. Uni.
of Alaska. Sept. 2-4, 1968.
- WOLFE, D.C., 1969 : Starfish meal for poultry. Tas. Fish.
Res., 1(2): 13-14.
- ZAFIRIOU, O., K.J. WHITTLE and M. BLUMER, 1972 : Response of
Asterias vulgaris to bivalves and bivalve tissue
extract. Mar. Biol., 13: 137-145.

APPENDIX



scale 1:2

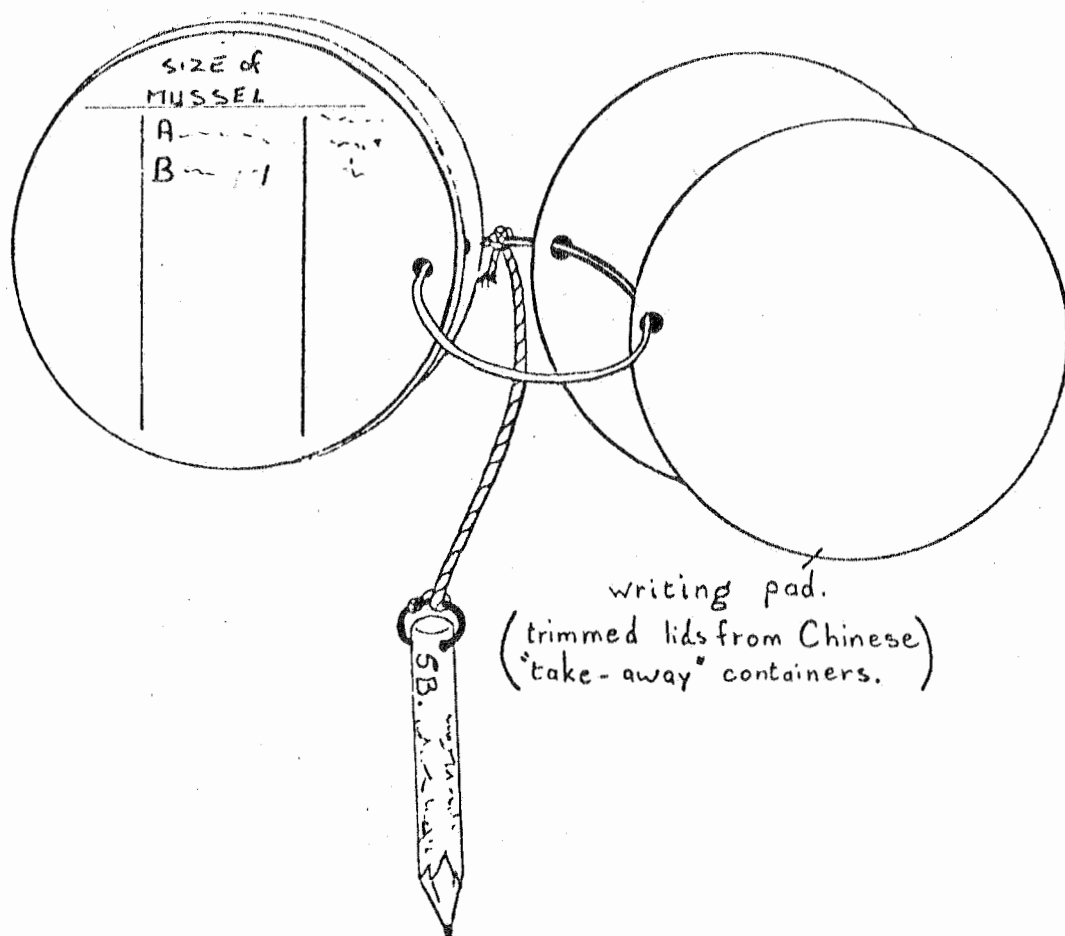


Fig 1 :
Under-water Recording Equipment used Throughout the Study

Table 1 : Prey selection experiments with unconditioned
Coscinasterias calamaria.

date	total # bivalves offered	<i>M. asperrimus</i>	<i>E. bifrons</i>	<i>P. meridionalis</i>	<i>M. e. planulatus</i>
15-4	30	1	1	-	8
20-4	24	3	4	-	3
27-4	12	3	-	-	0
27-4	12	-	4	2	-
2-5	6	1	-	-	0
12-5	8	-	●	2	-
12-5	10	-	3	-	0
19-5	10	-	2	-	0
19-5	4	-	2	1	-
24-5	10	-	1	-	0
5-6	26	-	-	-	2+1 <i>Katelaysia</i> <i>trigonella</i>
11-6	24	0	5	7	-
11-6	24	2	7	7	-
11-6	20	0	5	-	-
17-6	10	-	0	1	-
17-6	12	0	1	-	-
24-6	8	-	0	3	-
24-6	8	2	2	-	-
9-7	14	-	0	2	-
12-7	10	-	3	5	-
26-7	10	0	3	-	-
5-8	30	3	2	6	-
12-8	33	2	0	3	-
12-8	12	-	1	-	0
22-8	48	0	6	-	12
22-8	20	5	7	-	-
22-8	12	-	0	-	2
29-8	24	0	2	5	-
8-9	24	1	0	2	-
8-9	60	7	6	-	6
16-9	48	3	0	3	-
16-9	30	3	3	7	-
25-9	30	1	3	0	-
2-10	30	0	1	2	-

Table 2 : Results of preference feeding experiment in which
3 species of scallop were offered to C. calamaria.

date	total # scallops offered	No stars	<u>M. asperimus</u>	<u>E. bifrons</u>	<u>P. meridionalis</u>
11-6	24	4	0	5	7
11-6	24	3	2	7	7
5-8	30	5	3	2	6
12-8	33	3	2	0	3
29-8	24	5	0	2	5
8-9	24	4	1	0	2
16-9	48	3	3	0	3
16-9	30	3	3	3	7
25-9	30	4	1	3	0
2-10	30	5	0	1	2

Table 3 : Feeding rate of C. calamaria when only
commercial scallops were present.

date	duration of expt. (days)	number of stars	number of scallops eaten	rate = scallops/star/day
16-9	9	1	6	0.67
25-9	7	2	6	0.43
2-10	5	1	2	0.40
				$\bar{x}=0.50$

Table 4 : Feeding rate of C. calamaria when only
queen scallops were present.

date	duration of expt. (days)	number of stars	number of scallops eaten	rate = scallops/star/day
16-9	9	3	9	0.33
25-9	7	3	7	0.33
				$\bar{x}=0.33$

Table 5 : Predation by C. calamaria on M. asperimus in cages.

Expt. #	Date	Total # scallops in cage	# Captured & Eaten		# of Scallops Remaining
			Sponge Covered	clean	
1	29-6	20	7	5	8
2	9-7	32	1	3	28
3	18-7	20	1	4	15
4	5-8	26	0	4	22
5	12-8	26	1	4	21
6	18-8	26	2	5	19
7	22-8	10	1	4	5
8	29-8	20	3	6	11
9	29-8	8	0	1	7
10	5-9	14	0	3	11
11	5-9	12	1	3	8
12	8-9	16	2	5	9
13	8-9	8	0	1	7
14	16-9	10	0	3	7
15	2-10	14	0	2	12
			$\Sigma=19$	$\Sigma=53$	$\Sigma=180$

Table 6 : C. calamaria pull on scallop surface

Scallop Number	Force applied in grams per unit area.	
	sponge covered	clean
1	7	57
2	7	112
3	29	74
4	35	60
5	31	121
6	15	205
7	24	184
8	11	118
9	7	47
10	15	130
$\bar{x}=18\text{gms}$		$\bar{x}=109\text{gms}$

Note: data are averages of 2 trials on each scallop.

Table 7 :
Graded Values of Scallop Escape Response to Six Asteroid Species

<u>Coscinasterias</u> <u>calamaria</u>	<u>Astrostole</u> <u>scabra</u>	<u>Pateriella</u> <u>calcar</u>	<u>Uniophora</u> <u>sinusoida</u>	<u>Tosis</u> <u>magnifica</u>	<u>Nectria</u> <u>ocellata</u>
COMMERCIAL (<u>Pecten meridionalis</u>)					
4	9	1	5	1	9
10	9	1	6	2	5
9	9	6	9	2	0
10	8	9	6	1	0
10	2	0	8	0	0
10		0	7		1
8		2	4		0
8		1	6		5
9		2			5
8					
10					
10					
8					
10					
10					
10					
10					
DOUGHBOY (<u>Mimachlamys asperrimus</u>)					
10	10	5	1	6	6
10	10	8	6	5	0
9	10	8	9	1	6
9	4	1	6	5	5
10	4	8	7	5	
10		5	8	3	
10		5	10	1	
6			6	8	
7			2	0	
			10		
			6		
			1		
			9		
			8		
			8		
QUEEN (<u>Equichlamys bifrons</u>)					
8	10	2	8	1	0
8	9	1	8	5	5
8	8	1	6	2	2
8	4	2	1	0	2
9	9	1	5	0	1
10	8	0	8	3	1
10	9	2	8	5	0
10	9	1	2	0	2
4	9	3	1	1	
4					
10					
9					
10					
9					
9					

Table 7b: Escape Response of Scallops to Sea-stars.

Graded value	Response
0	No reaction.
1	Tentacles extended.
2	Valves close slowly.
3	Valves remain partially closed.
4	Valves remain tightly closed.
5	Weak clap without raising valve.
6	Weak clap from raised valve position (no locomotion).
7	Series of weak claps with no locomotion.
8	Single jump = 1 sharp clap.
9	Series of jumps = series of sharp claps.
10	Swimming = consecutive claps

Table 8 : Percentage Response of 3 Species of Scallops to 6 Species of Sea-stars.

Response	Sea-stars						Scallops
	<u>Coscinasterias calamaria</u>	<u>Astrostole scabra</u>	<u>Uniophora sinusoida</u>	<u>Patiriella calcar</u>	<u>Nectria ocellata</u>	<u>Tosia magnifica</u>	
0-7 (weak)	7%	20%	75%	89%	89%	100%	<u>Pecten meridionalis</u>
8-10 (strong)	93%	80%	25%	11%	11%	0	(Commercial)
0-7	14%	11%	56%	100%	100%	100%	<u>Equichlamys bifrons</u>
8-10	86%	89%	44%	0	0	0	(Queen)
0-7	22%	40%	53%	57%	100%	89%	<u>Mimachlamys asperrimus</u>
8-10	78%	60%	47%	43%	0	11%	(Doughboy)

TABLE. 9 : Response of Scallops to Starfish Tube Feet Extracts. (% of trials)

	<u>C. calamaria</u>		<u>A. scabra</u>		<u>U. sinusoida</u>	
	Strong	Weak	Strong	Weak	Strong	Weak
<u>Pecten meridionalis</u> (commercial)	67%	33%	0%	100%	33%	67%
<u>Equichlamys bifrons</u> (queen)	71%	29%	18%	82%	0%	100%
<u>Mimachlamys asperimus</u> (doughboy)	50%	50%	50%	50%	57%	43%

TABLE 10 : Response of Scallops to Starfish Aboral Surface Extracts. (% of Trials)

	<u>C. calamaria</u>		<u>U. sinusoida</u>	
	Strong	Weak	Strong	Weak
<u>Pecten meridionalis</u> (commercial)	20%	80%	17%	83%
<u>Equichlamys bifrons</u> (queen)	50%	50%	14%	86%
<u>Mimachlamys asperimus</u> (doughboy)	67%	33%	67%	33%

Table 11. Feeding rate of C. calamaria when only doughboy scallops were present.

date	duration of expt. (days)	number of stars	number of scallops eaten	rate = scallops/star/day
29-6	10	5	12	0.60
9-7	9	3	4	0.15
18-7	8	4	5	0.63
5-8	7	4	4	0.29
12-8	6	4	5	0.42
18-8	11	5	7	0.32
29-8	7	6	9	0.32
5-9	3	3	3	0.33
5-9	3	3	4	0.44
8-9	8	5	7	0.29
2-10	5	2	2	0.20
				Ave = 0.36

Table 12. Surface water temperatures
North West Bay, D'Entrecasteaux Channel.

date	temp. °C
17-5	12.7
24-5	12.7
4-6	11.5
11-6	10.3
6-7	10.2
19-7	9.1
30-7	8.5
2-8	9.2
9-8	8.7
22-8	10.2
19-9	11.7

revealed that concentrations of starfish do not co-incide with scallop beds. The most densely populated starfish zone situated near Webber Point, was stable over the year May '73 - May '74. Scallops are sparsely populated in this area. Therefore it is probable that they are feeding on a food source other than scallops. (See Figs. 4-7).

To test the findings in section 2C on scallop preferences, starfish numbers were correlated with numbers of the three species of scallops in Oyster Bay and Promise Bay. None of the associations correlated significantly.

As scallop populations changed due to fishing pressure and recruitment, there was no corresponding movement of starfish numbers. These findings are supported by Feder and Christensen's review (1966) in which they suggested that although the ability to sense food at a distance definitely plays a role for starfish, the direction of movement in the field is not controlled by food except over short distances. This distance would depend on current conditions and the intensity and concentration of perceptible food matter in the water. The common reports from fishermen of starfish "moving in" on scallop beds soon after dredging commences, and the findings in this study of feeding on broken bivalves, lends support to the hypothesis that dredging damages scallops and releases concentrated tissue fluids which attract nearby starfish to the dredging area. This greater intensity of food stimulation effectively increases the distance of attraction, thereby concentrating starfish in the scallop bed which is being fished at the time.