Marine Biology 24, 131—136 (1974)


# Effects of Algal Grazing and Aggressive Behaviour of the Fishes *Pomacentrus lividus* and *Acanthurus sohal* on Coral-Reef Ecology

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## Abstract

Aggressive behaviour of the fishes *Pomacentrus lividus* Bl. Schn. and *Acanthurus sohal* Forskal from the Red Sea is briefly described, and its effect on intensity of algal grazing by herbivorous fish is demonstrated by settlement experiments. Green filamentous alga settles and grows at shallow depths over large areas of coral reefs, but is cropped by fishes to such an extent that it forms only a thin patchy matting on dead corals. Within pomacentrid territories, the alga forms a thicker matting on loosely cemented coralline rubble. Optimum depth range for growth occurs at less than 20 m. Rich growths of green filamentous alga, such as those which occur within pomacentrid territories or on settlement plates protected by wire netting cages, inhibit settlement of "lithothamnion" and invertebrates. While rasping and grazing fish feeders such as parrot fish and surgeon fish limit the distribution of certain invertebrates such as spirorbids, in shallow water it is also true that, were it not for such active removal of green filamentous alga, "lithothamnion" and many invertebrates would find fewer surfaces suitable for settlement.

## Introduction

The important role played by herbivorous fish and echinoids in limiting growth of green filamentous alga in shallow zones of coral reefs has been discussed by a number of authors (e.g. Stephenson and Searles 1960; Randall, 1961; Bakus, 1969; Dart, 1972). It has been suggested that browsing activities of herbivores are significant in restricting survival of many invertebrates which settle in the shallow algal zone, and also that green alga may inhibit settlement of invertebrates. Friedrich (1969) emphasised the need for more studies involving exclusion of fish from coralline substrates. I am not aware of any previous study which has demonstrated the correlation which exists between growth of green filamentous alga, cementation of coral rubble, settlement of invertebrates, and aggressiveness of a pomacentrid.

The investigations described in this paper were instigated as a result of a chance observation made while snorkel-diving on one of the patch reefs in the Towartit reef complex south of Port Sudan, in the Sudanese Red Sea. The author had been taking underwater photographs of fish feeding, and had found that one way of encouraging parrot fish and surgeon fish to feed was to remove loose pieces of algal-covered coral rubble from the reef and to place them on sand. Each time this was done many fish (mainly Acanthuridae, Siganidae, Chaetodontidae, and Balistidae) commenced browsing on the displaced rock and, within about 30 min the green matting of filamentous alga previously covering the rock had been consumed by fish, leaving it to merge inconspicuously with the colour of the lagoon sand. The question arose: why do these herbivorous fish not eat the green alga growing on the rocks *in-situ*? The intensity of their browsing on displaced rocks was so great as to suggest that the *in-situ* rocks would not have such a thick matting of green filamentous alga if they were grazed by surgeon and parrot fishes.

At this stage, it was observed that each time a fish approached the green algal-covered rocks it was chased off by the aggressive displays of dark grey pomacentrids, later identified as *Pomacentrus lividus* Bl. Schn. Similar aggressive defence of territory was exhibited if a snorkel diver approached pomacentrid-inhabited coral rubble. Following this observation, it became apparent to the author that rocks within pomacentrid territories may be covered with green filamentous alga as a result of reduced grazing by larger herbivorous fishes.

Several other characteristics of pomacentrid territories were observed at the beginning of the investigation. Fragments of dead coral were often poorly cemented (and, therefore, easy to remove for the photographic purposes mentioned above); there was little live coral growing among algal covered rocks but, around the edge of their territories, encrusting corals contained high densities of embedded serpulid tube worms (*Spirobranchus* sp.). A hypothesis was developed to explain how aggressive territorial behaviour of *Pomacentrus lividus* could be responsible for producing these ecological effects.

Settlement plates protected by wire netting cages were used to measure growth of green filamentous alga, and unprotected plates alongside these provided an estimate of the effect of fish grazing. Later experiments showed that the green filamentous alga is capable of settling and growing over most of the shallow reef-top, but that herbivorous fish are largely responsible for controlling the extent of its growth. Rasping and browsing activities of these fish expose new surfaces suitable for settlement of encrusting coralline algae (hereafter called "lithothamnion") and invertebrates. Defence of territory by *Pomacentrus lividus* allows the green alga to grow, forming a thick matting over loose rocks, and this inhibits settlement of "lithothamnion" and invertebrates such as Spirorbinae.

## Material and Methods

Experiments were carried out on a patch reef (Harvey Reef) among the Towartit reef complex south of Port Sudan. There are no diurnal tides in this region of the Red Sea and the sea level, which is affected by weather conditions, fluctuated by approximately 0.3 m about mean level during the period of investigations (January-March, 1973). Settlement plates, consisting of white porcelain bathroom tiles, glazed on one side, (surface area 225 $cm^2$) were held in place, matt side up, by screws. Care was taken to avoid fixing plates in shaded situations. Holes were made in the coral with a masonry punch and hammer, and fibrous "rawplugs" were inserted to retain the screws. Fish and echinoids were excluded from some plates by wire netting cages (mesh diameter 1.5 cm), with each side approximately 17 cm long.

Plates thus protected were fixed adjacent to unprotected plates. In Experiment 1 (see below), pairs of protected and unprotected plates were fixed at 0.5 m depth in 3 areas on top of the reef, and were left *in situ* for 15 days. In Experiments 2, 3, and 4, pairs of plates were fixed at different depths on the west side of Harvey Reef; they remained underwater for 30 days. Following removal of settlement plates, flora, fauna and sediment was scraped off. Green alga was separated from calcareous sediment by dissolving in dilute hydrochloric acid and filtering or centrifuging. The alga was dried in an oven (at approximately 100 °C), and dry weights were obtained by weighing on a chemical balance. Spirorbids were counted, and growth of "lithothamnion" was noted after the green alga had been scraped off the plates.

## Results

### *Observations on Two Species of Reef Fishes Demonstrating Aggressive Territorial Defence*

#### *Pomacentrus lividus* Bl. Schn.

*Pomacentrus lividus* is a small pomacentrid, approximately 10 cm long, usually dark brown in colour, but sometimes with a lighter vertical band on its flanks. Living specimens have an iridescent blue edge to their anal fin, and the tips of their rounded caudal fin lobes are light in colour. *P. lividus* is commonly found in shallow water, on top of patch reefs in the Sudanese Red Sea (and also in many areas of the Indo-Pacific Ocean). Small groups often inhabit crevices among dead coral, and colonies of up to a 1,000 or more fish (approximately 20 fish $\cdot$ $m^{-2}$) may occupy large areas of predominantly dead coral rubble, which is usually covered with a matting of green filamentous alga.

Encrusting corals often border colonial territories of *Pomacentrus lividus*, and these may be characterised by large numbers of embedded serpulid tube worms with conspicuous brightly coloured brachial crowns. Underwater observations and analysis of stomach contents indicates that *P. lividus* feeds on the green filamentous alga which grows within its territories. Intraspecific aggression is not readily observable underwater, but the equidistant spacing of individuals suggests that this does occur. *P. lividus* is, however, extremely aggressive towards most other fish which intrude into its territories. The author has observed large parrot fishes, about 70 cm in length being chased away by the aggressive display of these small pomacentrids. Indeed, on several occasions while working inside their territories, I have been forced to control an instinct to back away from their excited and somewhat frightening advances. Any fish which enters the territory to feed on green alga or to browse over the rocks invariably flees within seconds in response to aggressive displays of *P. lividus*.

*Effects of Aggressive Behaviour.* As a result of the virtual exclusion from their territories of other herbivorous fish, the following effects have been demonstrated (see experiments described below): (a) green filamentous alga flourishes on rocks protected by *Pomacentrus lividus*, whereas it is rapidly grazed by herbivorous fish outside territories of this pomacentrid; (b) few corals or other invertebrates settle on algal covered rocks within *P. lividus* territories; (c) coralline rubble inhabited by *P. lividus* is often loosely packed and poorly cemented, whereas rocks in similar zones outside its territories are more firmly cemented; (d) diversity of fish fauna is reduced in areas where *P. lividus* establishes large territories.

#### *Acanthurus sohal* Forskal

One of the most abundant surgeon fishes in shallow water on coral reefs in the Red Sea is *Acanthurus sohal*, a species endemic to the Red Sea and closely related to the Indo-Pacific species *A. lineatus* Linn. Adults are approximately 30 cm in length, and have a horizontal pattern of narrow stripes with an orange patch on each side, behind the operculum. The scalpel-shaped markings in the caudal region are also bright orange in colour.

*Acanthurus sohal* are usually found swimming as individuals around small coral knolls situated on sandy areas, or swimming together in loosely formed schools when they range over large areas of reef. They are herbivorous fish, and the author has observed groups of about 30 *A. sohal* invade rich algal areas defended by *Pomacentrus lividus*. The rapidity with which surgeon fish peck at the alga and retreat to undefended sandy areas is a measure of the effectiveness of the aggressive displays by *P. lividus*. Solitary *A. sohal* which attempt to feed within territories of *P. lividus* are usually less successful than members of larger groups, since sheer numbers are sufficient to stretch the defensive resources of *P. lividus* to the point where not all fish are immediately chased off.

When *Acanthurus sohal* is swimming close to its "home knolls", it is aggressive towards other members of its species and towards larger fish such as parrot fish. *A. sohal* displays aggression by swimming rapidly towards the intruder, turning at the last moment, so that its caudal region comes close to, or brushes alongside the other fish. At such times, prominent white patches are frequently displayed on the sides of the head, where there is normally a pattern of undulating narrow stripes. *A. sohal*'s aggression is often pronounced enough to make a snorkel diver move away from their "territories". It is somewhat surprising, therefore, that at other times *A. sohal* leave their "home knolls" and swim over large areas of the reef.

*Effects of Aggressive Behaviour.* The aggressive behaviour of *Acanthurus sohal* is of a different nature to that of *Pomacentrus lividus*. It results in the spacing-out of individual surgeon fish so that each has a territory centred around coral knolls. Intraspecific aggression such as this sets a limit to the population density of *A. sohal*, and this may be related to the amount of available food (i.e., green filamentous alga) on the reef. Like *P. lividus*, *A. sohal* is herbivorous, but food requirements of individual fish are much greater than those of the small pomacentrid. Intermittently guarded territorial knolls usually have a moderate covering of green and brown algae, but algal settlement-plate experiments (see Fig. 1) did not indicate the same degree of algal protection as that which occurs within territories of *P. lividus*. This is perhaps because, when defending their coralline knolls, surgeon fish were often observed to repulse the larger rasping feeders such as parrot fish, but did not prevent many smaller fishes from feeding on the rocks, from which they themselves grazed algae.

### *Settlement of Alga and Invertebrates*

#### Settlement of Green Filamentous Alga and Effects of Aggressive Behaviour by *Pomacentrus lividus* and *Acanthurus sohal*

Fig. 1 shows the different dry weights of green filamentous alga obtained from pairs of protected and unprotected plates placed at 0.5 m depth on the top of Harvey Reef. One pair of plates was situated within a territory guarded by a colony of *Pomacentrus lividus*, one pair was on a "home-range coral knoll" intermittently guarded by an individual surgeon fish, *Acanthurus sohal*, and the third pair was fixed to coral close to the others, but on a rock not protected by pomacentrids or surgeon fish.

Green filamentous alga grew on all settlement plates. The pair of plates within the territory of *Pomacentrus lividus* had approximately equivalent dry weights of alga, whereas there was a marked difference between weights of alga on protected and unprotected settlement plates outside the pomacentrid territory. This is explained by the aggressive defence of algal-covered rocks by *P. lividus* and the intensive grazing by fish on green filamentous alga outside territories thus protected. No echinoids were seen feeding on the plates, although many observations were made during day and night. The experiment also demonstrates that the green alga settles and grows rapidly in areas where coral rubble is not naturally covered by a thick algal mat.

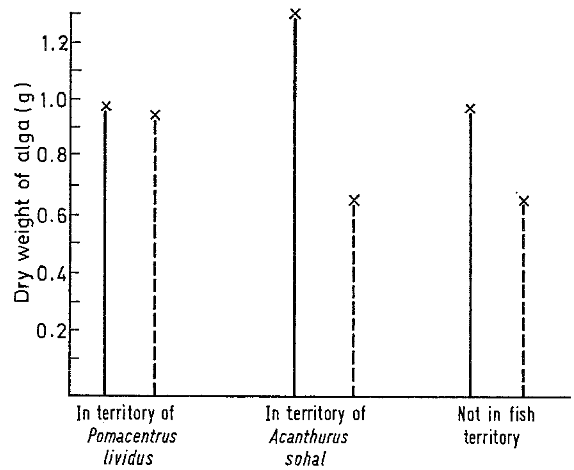


Fig. 1. Growth of green filamentous alga on protected (continuous lines) and unprotected (broken lines) settlement plates, each placed at 0.5 m depth for period of 15 days

#### Growth Rates of Green Filamentous Alga at Different Depths and Relationship to Intensity of Algal Grazing

Fig. 2 presents the dry weights of alga obtained from protected and unprotected settlement plates at different depths. Algal biomass from protected plates decreases with depth; that from unprotected plates does not.

The experiment indicates that fastest growth rates of green filamentous alga occur at the shallowest depths, and that there is a rapid decrease in the growth rate with increasing depth, until virtually no growth occurs at 20 m. Comparison of protected and unprotected plates provides a measure of the effect of fish grazing at different depths. As one might expect, algal grazing fish are concentrated in the shallowest regions, where the effect of their feeding is to remove most green alga from rocks. Dart (1972) has commented that the same is true for echinoids and, while the present author agrees with this, it should be mentioned that no echinoids were observed feeding on the settlement plates used in this experiment, although many fish were seen browsing on the plates in shallow water. The upper 10 m is the favoured depth zone for most of these herbivorous fish. The extreme difference in dry weights of alga obtained from protected and unprotected plates at similar depths in shallow zones indicates the importance of utilising protected settlement plates for all estimations of algal growth rates on coral reefs.

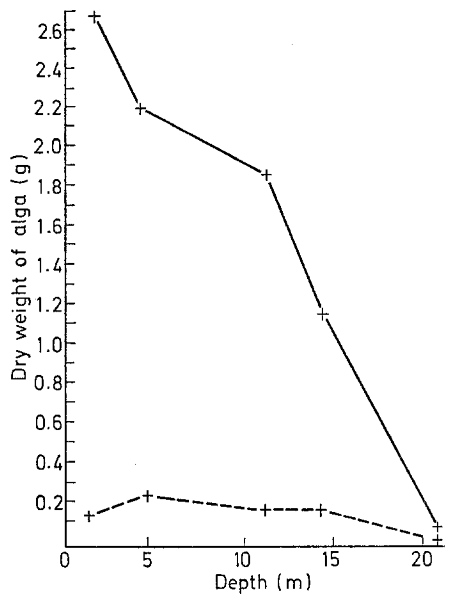


Fig. 2. Growth of green filamentous alga on protected (continuous line) and unprotected (broken line) plates placed at different depths and left *in situ* for 30 days

## Growth of "Lithothamnion" and Importance of Fish Grazing as Means of Providing Surfaces Suitable for its Settlement

Growth of "lithothamnion" was compared on two settlement plates from 0.8 m depth. The protected plate, which had been covered by a thick mat of green filamentous alga, did not have any "lithothamnion" growing on its upper surface; the unprotected plate, which due to the grazing activities of herbivorous fish, had a much thinner covering of green alga, had numerous patches of "lithothamnion" over its upper surface. This indicates that the rasping and grazing activities of herbivorous fish promotes growth of "lithothamnion" by helping it to compete with the green filamentous alga. It has already been stated that coral rubble within territories guarded by *Pomacentrus lividus* is covered by a thicker mat of green alga than that which occurs on rocks outside their territories. These rocks within pomacentrid territories are also poorly cemented, and may be easily dislodged, whereas other rocks are usually more firmly cemented. "Lithothamnion" plays an important role in helping to cement loose fragments, and this experiment suggests that its growth would be inhibited on rocks within pomacentrid territories, since most herbivorous fish are excluded from such areas by the aggressive behaviour of *P. lividus*.

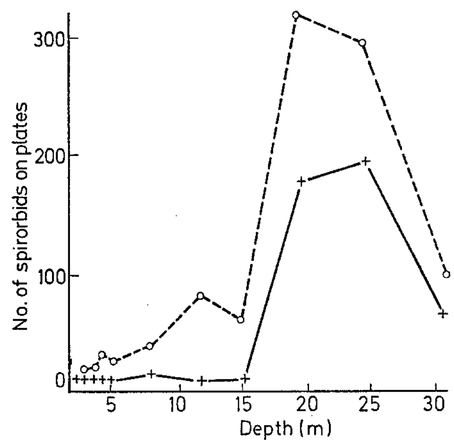


Fig. 3. Number of spirorbid tube worms settling on protected (continuous line) and unprotected (broken line) settlement plates placed at different depths and left *in situ* for 30 days

## Settlement of Spirorbinae (Polychaeta: Serpulidae) on Exposed Surfaces at Different Depths

Fig. 3 shows the numbers of spirorbids settling on different plates. The graph suggests that green filamentous alga on protected plates at shallow depths effectively inhibited spirorbids from settling. Reduced algal growth at greater depths led to more tube worms settling on protected and unprotected plates. A peak of settlement occurred at approximately 20 m, which corresponds with the depth at which a sharp decline in growth of green alga was recorded (Fig. 2). At greater depths, increased sedimentation tended to inhibit settlement of invertebrates.

## Discussion

The experiments described above relate the behaviour of certain fishes to important aspects of coral-reef ecology. Several authors (eg. Hiatt and Strasburg, 1960; Botros, 1971) have commented on the comparative lack of algae on coral reefs in view of the large numbers of herbivorous fish. The settlement studies described above show that green filamentous alga grows very quickly and settles in shallow zones over large areas of the reef. This important source of primary production is utilised by many reef fishes, and the intensity of grazing and rasping by these fish is so great, that most rocks have only a thin patchy matting of the green alga. Smith (1960) describes pomacentrids known to occur in the Red Sea, and states in the introduction to this family: "They occur mostly in the warm parts of all oceans, usually in and about coral, in parts in vast numbers, sometimes hovering in clouds of countless numbers close to steep coral faces and about coral heads. Some appear to live in shallower water among weeds."

Within territories occupied by *Pomacentrus lividus*, the latter's aggressive behaviour prevents intensive algal grazing and, therefore, a thicker, more uniform, matting of green alga is permitted to grow. This, in turn, inhibits settlement and growth of "lithothamnion", thus decreasing the amount of cementation between loose coralline fragments. Randall (1970, and personal commnication dated 3 April, 73) states that he has observed *P. lividus* behave in the same way in Tahiti, where they often live among "staghorn" *Acropora*; their pasture is the collar of algae growing on the dead basal portions of the branches of this coral. Several other species of pomacentrid show similar behaviour, and Randall believes that the schooling of herbivorous fish such as siganids and acanthurids may be related to the aggressive territorial behaviour of pomacentrids. He writes: "As a school they can move into an area occupied by the territorial pomacentrids. Each individual damsel fish is hopelessly outnumbered and can't drive off the whole school which goes through its algal supply like a lawnmower."

Abel (1960) has discussed some aspects of behaviour of *Acanthurus sohal*. Loosely formed schools of this surgeon fish succeed in feeding within territories guarded by *Pomacentrus lividus*, and Randall observed schools of *Siganus rostratus* in Tahiti invade territories occupied by *P. lividus* in a similar manner.

Bakus (1964, 1967, 1969) emphasised the important role played by rasping fish (especially surgeon fish and parrot fish) in controlling distribution of many coral-reef invertebrates. He points to the importance of defence mechanisms for survival of coral-reef invertebrates, and cites thick calcareous shells and tubes or embedded tubes as being partly responsible for certain molluscs and polychaetes escaping from fish predation on coral reefs. It is relevant to note here that the two serpulid species most commonly found in shallow water near the reef crest are both species which appear to have adapted well to this requirement for protection against fish predators. The most common spirorbid in this zone is usually *Pileolaria militaris* Claparède (see Vine, 1972). This is a ubiquitous species in coral-reef areas. It has a comparatively thick calcareous tube, which is often camouflaged and protected by an encrusting cover of "lithothamnion". The tube is also larger than that of most other spirorbids. Its operculum, in which embryos are brooded, has an armour of spines which would presumably discourage many small predators. Tentacles are orange in colour, and are extremely sensitive to any diminuition in light intensity. The worm withdraws very rapidly into its tube at the approach of any potential predator.

The most abundant species in the sub-family Serpulinae is usually a member of the genus *Spirobranchus*, whose calcareous tubes are deeply embedded within coral skeletons and whose colourfully pigmented branchial crowns display very rapid withdrawal reactions in response to vibrations or decrease in light intensity. A further discouragement to fish pursuing worms which withdraw into their tubes is a median sharp calcareous spine, which usually extends above the aperture of the tube. As evidence that fish predation is an important factor controlling distribution of Serpulidae, it may be added that Abel (1960) observed *Runula* sp. attacking serpulids in the Red Sea, and Hiatt and Strasburg (1960) recorded serpulids in gut analysis of many reef fishes.

Motoda (1940) showed that damage caused to corals by scarids is often sufficient to kill whole colonies. Bakus (1969) and Dart (1972) have suggested that removal of green alga by herbivores (especially echinoids and fish) is important for successful recolonisation by reef-building corals. In areas which have suffered intensive predation by *Acanthaster planci* (crown of thorns sea star), a green filamentous alga rapidly covers dead coral skeletons in shallow water. The experiments described in the present paper provide some evidence to support the view that settlement of invertebrates such as corals depends on surfaces being prepared by coral-reef herbivores. Randall (1972) has also stated: "Plant and detritus feeding animals may be among the more important consumers of newly transformed starfish. Many of these animals such as fishes, echinoids and gastropods are not very discriminating as they graze. Small benthic animals, though ingested incidentally, may be eaten in great numbers".

*Pomacentrus lividus*, by its aggressive behaviour, reduces the area of algal covered rocks grazed by fishes, thus reducing the area suitable for settlement of invertebrates.

Further investigations are required to fully elucidate the effects which pomacentrids such as *Pomacentrus lividus* have on influencing survival of invertebrates. It is apparent, however, that grazing and rasping by coral-reef fishes restricts distribution of many coral-reef invertebrates. It is also true that, were it not for such intensive feeding by herbivores, fewer invertebrates would find suitable settlement surfaces, and many loose fragments would not be so firmly cemented together, leading to less consolidation of reef structure.

## Summary

1. Many coral reefs in the Sudanese Red Sea support large numbers of the small pomacentrid fish *Pomacentrus lividus* Bl. Schn. which frequently form colonies consisting of a thousand or more fish.

2. *P. lividus* displays aggressive behaviour towards most fish which attempt to feed within its territories.

3. Aggressive behaviour of *P. lividus* has the following ecological effects: (a) green filamentous alga flourishes on rocks protected by *P. lividus*; (b) few corals or other sedentary invertebrates settle on algal-covered rocks within pomacentrid territories; (c) coralline rubble inhabited by *P. lividus* is poorly cemented; (d) diversity of fish fauna is reduced in areas where large numbers of *P. lividus* form extensive territories.

4. *Acanthurus sohal* Forskal intermittently protects "home range" knolls from members of its own species and from larger herbivorous fish such as parrot fish. At other times, it swims over large areas of the reef, often in loosely formed schools; it feeds primarily on green filamentous alga.

5. Herbivorous fish in schools are more successful at invading pomacentrid territories than are isolated individuals.

6. Green filamentous alga grows at shallow depths (optimum range upper 10 m; maximum depth 20 m) over large areas of the reefs.

7. In areas not protected by pomacentrids, acanthurids, scarids, chaetodontids, balistids, and siganids are primarily responsible for cropping the algae, so that it forms only a thin patchy matting over dead corals.

8. "Lithothamnion" plays an important role in cementing loose coralline rubble at shallow depths, but its settlement is inhibited by rich growths of green filamentous alga.

9. Spirorbid tube worms are inhibited from settling by rich growths of green filamentous alga.

10. While rasping and grazing fishes restrict distribution of certain invertebrates, their active removal of green filamentous alga in shallow zones provides many surfaces suitable for settlement by "lithothamnion" and invertebrates.

*Acknowledgements.* I would like to thank members of the Cambridge Coral Starfish Research Group with whom I have worked in Port Sudan, especially Dr. R. F. G. Ormond, R. Moore, S. Head, and Miss P. Casey, with whom I have discussed some aspects of this paper, and who encouraged me to complete this work. Investigations were carried out as part of the Cambridge Coral Starfish Research Group project into population control of *Acanthaster planci*, and this work was funded by a grant from the British Government Overseas Development Administration. I should also like to thank Dr. C. H. Roads, who is administrative director of the Cambridge Coral Starfish Research Group. Dr. J. H. Randall kindly allowed me to quote personal correspondence, and I am grateful to him for drawing my attention to some relevant published papers. I am happy to thank Mrs. G. Sanders for preparing the typescript.

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Date of final manuscript acceptance: September 27, 1973. Communicated by J. H. S. Blaxter, Oban