Population ecology of the intertidal anemone *Actinia tenebrosa* Farquhar (Cnidaria: Anthozoa)

A thesis presented for the degree of
Doctor of Philosophy in Zoology,
in the University of Canterbury,
Christchurch, New Zealand

by

JOHN R. OTTAWAY

1977

ABSTRACT

The population ecology of the intertidal anemone *Actinia tenebrosa* Farquhar, 1898, was studied at Kaikoura, New Zealand, from 1972 to 1976 inclusive. Chapters in this thesis discuss geographical distribution of the species, synonymy, reproduction, pedal locomotion, intraspecific aggression, population dynamics and longevity.

Except where due acknowledgement has been made, this thesis is solely the work of J.R. Ottaway. None of this material has been submitted in any other thesis for any other degree.

CONTENTS

LIST OF FIGURES

Figure | Page

LIST OF TABLES

CHAPTER ONE

GENERAL

1.1 INTRODUCTION

Early naturalists wrote lengthy and detailed accounts on the natural history of sea anemones (e.g. Dicquemare 1773, 1775, 1777; Johnston 1846; Dalyell 1848; Gosse 1860; Stephenson 1928, 1935; Parker 1919) based on their careful qualitative observations in the laboratory and field. Although more than 800 actinian species have now been described (Carlgren 1949), there is still an almost complete lack of quantitative ecological data, even in more recent studies.

To my knowledge, only one comprehensive study has previously been undertaken on the population ecology of an actinian species (Dunn 1975a, b; 1977a, b, c), probably because of the inherent problems in marking, recognising, and then following individual anemones. To a large extent, Dunn overcame these problems by careful selection of a suitable population for study, by using transparent overlay maps to trace movements, and by observing her subject Epiactis prolifera frequently, sometimes daily (Dunn 1977a, b). Similar methods were used in the present study of the intertidal Actinia tenebrosa.

This thesis examines the population ecology of A. tenebrosa and, except for reproductive cycle data, is based mainly on field observations. Aspects of the behaviour, ecology and reproduction have been discussed previously (Ottaway & Thomas 1971; Ottaway 1973, 1974, 1977b; Ottaway & Kirby 1975), but those studies were based mainly on laboratory data. Here, reproductive cycle, pedal locomotion, intraspecific aggression, population dynamics, growth rates, and longevity of a wild population are discussed. For convenience, the following terminology has been adopted:

Adults - living, healthy *Actinia* with mean column diameters larger than 15 mm. These have well-developed acrorhagi, and would probably develop gonads under the appropriate environmental conditions.

Juveniles - tentaculate *Actinia* less than 15 mm column diameter (CD). Brooded juveniles and free-living juveniles less than 10 mm CD rarely have acrorhagi; juveniles larger than 10 mm usually had at least a few (Chapter 3).

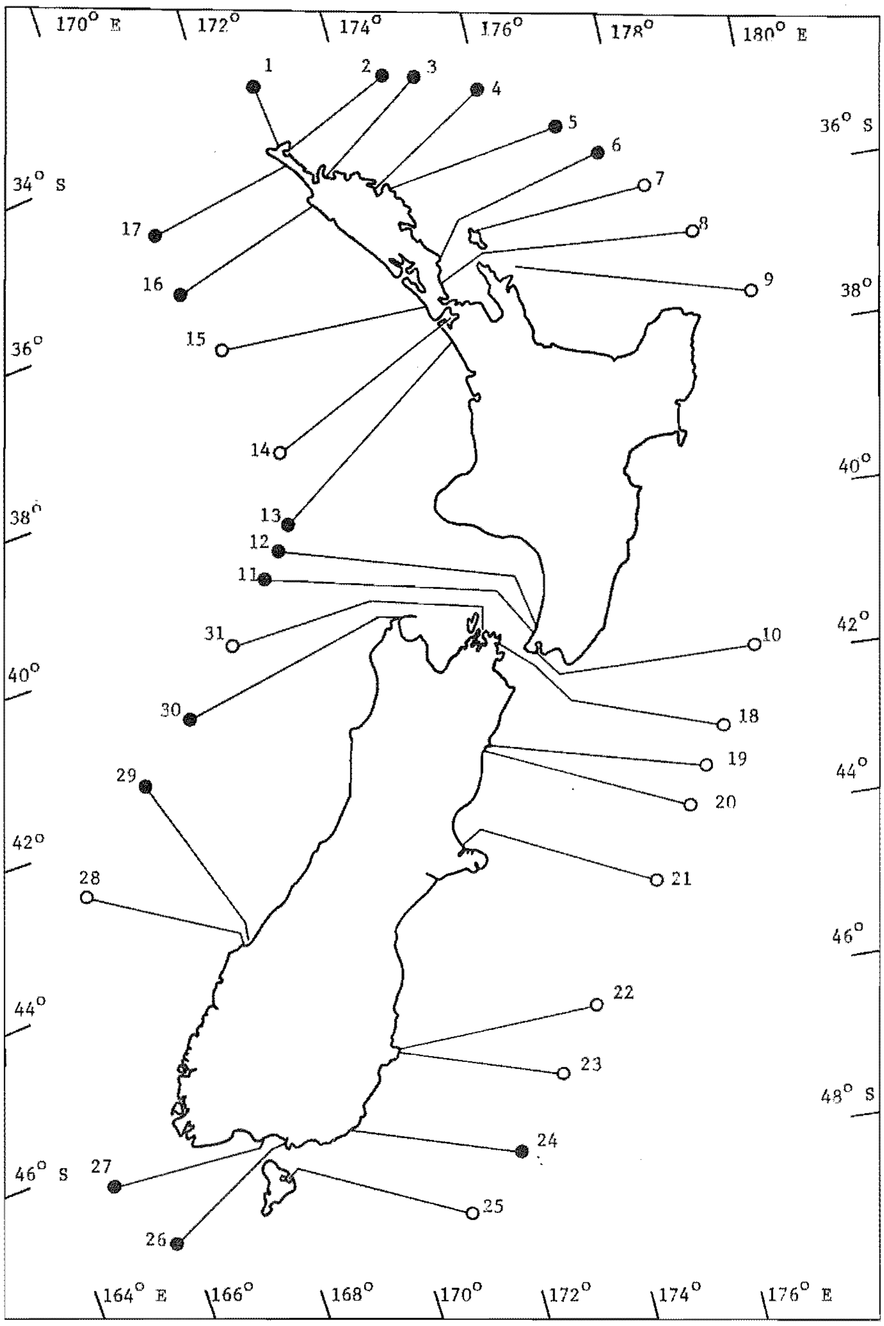
A third category, that of subadults, should properly have been used to describe tentaculate *Actinia* that had developed acrorhagi but had not reached breeding condition. This would include most specimens in the size range 11 - 17 mm CD. That category was not used, however, due to the impracticability of determining whether a non-breeding specimen had the potential to breed or not at that immediate time. In addition, there appeared to be considerable variation in the size and age at which anemones first developed acrorhagi and gonads (Chapter 3).

FIGURE 1: Distribution records of *Actinia tenebrosa* in New Zealand.

○——— : published previously; ●——— : unpublished previously.

1: Hoopers Point (W.J. Ballantyne, personal communication 1975).

2: Ohao Point (Ballantyne, pers. comm. 1975). 3: Taipa (author's observation). 4: Waitangi (author's obs.). 5: Taupiri Reef (Ballantyne, pers. comm. 1975). 6: Leigh (author's obs.). 7: Needles Point, Great Barrier Island (Dellow 1955). 8: Whangaparaoa Peninsula (Dellow & Cassie 1955). 9: Red Mercury Island (Saies, Beever, Hay & Woods 1972). 10: Wellington (Farquhar 1898; Parry 1951), Island Bay (Parry 1951), Worser Bay (Oliver 1923). 11: Pukerua Bay (author's obs.). 12: Paekakariki (author's obs.). 13: Port Waikato (Ballantyne, pers. comm. 1975). 14: Manukau Harbour (Stuckey & Walton 1910). 15: Piha (Morton & Miller 1968). 16: Herekino Harbour (Ballantyne, pers. comm. 1975). 17: The Bluff, Ninety Mile Beach (Ballantyne, pers. comm. 1975). 18: Queen Charlotte Sound (Farquhar 1898). 19: Kaikoura Peninsula (Ottaway 1975a). 20: Goose Bay (Ottaway 1975a). 21: Taylors Mistake (Knox 1969). 22: Little Papanui (Batham 1958). 23 Quarantine Island (Ottaway 1975a). 24: Tautuku Beach (S. Sampson, pers. comm. 1977). 25: Stewart Island (Stuckey 1909). 26: Barracouta Point (author's obs.). 27: Riverton Rocks (author's obs.). 28: Jackson Bay (Ottaway 1975a). 29: Open Bay Island (C.H. Hay, pers. comm. 1975). 30: Wharariki Beach (W.C. Clark, pers. comm. 1976). 31: Outer Chetwode Island (Ottaway 1975a).


170° E
172°
174°
176°
178°
180° E
36° S
38°
40°
42°
44°
46°
48° S
34° S
36°
38°
40°
42°
44°
46° S
164° E
166°
168°
170°
172°
174°
176° E
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31

1.2 TAXONOMY AND GEOGRAPHICAL DISTRIBUTION

Class ANTHOZOA

Order ACTINIARIA

Family ACTINIIDAE

Genus *Actinia* Linnaeus, 1758

Description

Carlgren (1949, p. 49) revised the diagnosis of the genus.

Actinia tenebrosa Farquhar, 1898

Synonymy

Actinia tenebrosa. Farquhar, 1898, pp. 527, 535 (*sp. nov.*). Hutton, 1904, p. 314. Stuckey, 1909, pp. 375, 377, 380-1, fig. 5, pl. 23. Stuckey & Walton, 1910, p. 541. Stephenson, 1922, p. 266. Carlgren, 1924, pp. 196-200, fig. 14. Dakin, Bennett & Pope, 1948, pp. 208, 214, 222, 223. Carlgren, 1949, p. 50. Carlgren, 1950a, pp. 131, 132. Carlgren, 1950b, pp. 121-3. Parry, 1951, pp. 87, 100-101. Dakin, 1952, p. 136, pl. 22. Carlgren, 1954, pp. 571-2. Dellow & Cassie, 1955, pp. 327, 330, 331. Cleland & Southcott, 1965, p. 170. Morton & Miller, 1968, figs. 94, 97. Knox, 1969, p. 542. Ottaway & Thomas, 1971, pp. 63-78, fig. 5. Ottaway, 1973, pp. 103-123, figs. 2, 4. Ottaway, 1974, pp. 73-83. Ottaway, 1975a, pp. 53-55, 59.

Actinia australiae. Carlgren, 1900, p. 52 (*nomen nudum*). Carlgren, 1924, p. 196.

Isactinia tenebrosa. Morton & Miller, 1968, pp. 101, 158, 272, 278, fig. 96, pl. 6. Heath & Dell, 1971, p. 56, fig. 162. Saies *et al*., 1972, pp. 41, 52.

Description

Actinia tenebrosa has been fully described by Carlgren (1924, pp. 196-200; 1950a, p. 132).

Geographical distribution

The species occurs around most of New Zealand and offshore islands (Ottaway 1975a; Figure 1). It is also abundant on many parts of the Australian coastline and offshore islands south of the Tropic of Capricorn (Ottaway 1973).

Remarks

Farquhar (1898) briefly described the external appearance of *A. tenebrosa* and assigned the anemone to the genus *Actinia* because of the very close similarity between *A. tenebrosa* and the common *mesembryanthemum* variety of the genus type, *Actinia equina* Linnaeus, 1758 (*compare* Johnston 1847, pl. 36; Gosse 1860, pl. 6; Stephenson 1928, pl. 5, 6; Stephenson 1935, fig. 64; Russell & Yonge 1936, pl. 16; Morton & Miller 1968, pl. 6; Heath & Dell 1971, fig. 162). Blackburn (1937) considered that *A. tenebrosa* was so similar to *A. equina* as to warrant synonymising the two species, but to date no other author has shared this opinion. In the seventy years following Farquhar's (1898) description, all authors who have examined *A. tenebrosa* agreed with the generic placing, including Carlgren (1924, 1950a) who described the morphology and cnidom in detail.

Morton & Miller (1968) first referred to *Isactinia tenebrosa* and clearly synonymised this with *Actinia tenebrosa* (1968, p. 625; *cf*. fig. 94 with fig. 96; *cf*. p. 278 with fig. 97); however, the transfer of *A. tenebrosa* to *Isactinia* is unwarranted. The main diagnostic character separating these genera is the presence or absence of marginal spherules, defined by Carlgren (1949, p. 8) as "vesicles situated on the parapet or in the fosse, at least sometimes with an aperture and provided with atrichs, basitrichs and spirocysts". The true marginal spherules of *A. tenebrosa* contain atrichs (Carlgren 1950a, p. 132) and can be concealed in the deep fosse. The pseudospherules of *Isactinia* contain basitrichs only, and are situated at the margin (Carlgren 1949, 1954; Parry 1951).

There has been some question as to whether Actinia tenebrosa Farquhar, 1898, is the same species as Actinia papaver Drayton, 1848 (Carlgren 1950a, p. 132; Cleland & Southcott 1965, p. 170). Drayton (1848) described Actinia papaver as

"Animal, with the exterior smooth; body depressed, 2¼ inches thick at middle, much dilated above and below (3 inches in breadth); margin of base faintly crenulate, upper margin not tuberculate, scarcely undulate; tentacles numerous, nearly 3/4 of an inch long, stout, subulate, in 3 series; mouth 3/4 of an inch long, prominent."

Actinia papaver was illustrated in Dana (1856, Plate 4, Figure 29). Drayton (1848) also gave the following information:

"From the rocks exposed to the surf, Wollongong, Illawarra, New South Wales.

This species is found most abundant on rocks exposed to the surf, a little above low-water mark; they are, therefore, for a short time exposed out of water, at the receding of the waves, until the tide covers them again. The colour of the body is a rich brownish-purple, with regular longitudinal lines of a darker purple, crossed by finer transverse lines; tentacles red, the inner darkest, disk and sides of mouth a deep brownish-purple; mouth within, dark orange.

Another variety of this species was seen with a brownish-green body and disk, and tentacles of the same colour, but paler."

The anemone described could have been an exceptionally large specimen of Actinia tenebrosa, but this is uncertain, since Drayton mentioned neither the prominent blue acrorhagi characteristic of the genus Actinia nor morphology or cnidom. Milne Edwards (1857, p. 238-240) was clearly familiar with Actinia equina and had no doubts that papaver was not in the same genus. His transfer of the species to the actinostolid genus Paractis, however, seems to have been based solely on the information provided by Drayton and Dana (Milne-Edwards 1857, p. 249). Clubb (1908) and Carlgren (1949) agreed with this generic placing, and thought that *Paractis papaver* was also found at a depth of 37 m in McMurdo Sound, Antarctica. Hedley, (1915), Johnston (1917), Livingstone (1928) and Pope (1943) thought Dana had described the Australian "Red Waratah Anemone", which was known as *Actinia tenebrosa* in New Zealand, but confusingly these authors still used the name *Paractis papaver*. By Hedley's (1915, p. 68) own information this had to be incorrect, since he noted blue acrorhagi. *Paractis*, as an actinostolid, cannot have marginal spherules.

It is now impossible to determine the species to which Drayton (1848) referred, although it seems likely that it was not *Actinia tenebrosa*. I shall therefore consider *Actinia papaver* to be a *species inquirenda*, and accept Farquhar (1898) as the author of the original description of *Actinia tenebrosa*.

1.3 GENERAL DESCRIPTION OF THE KAIKOURA COAST AND STUDY AREA

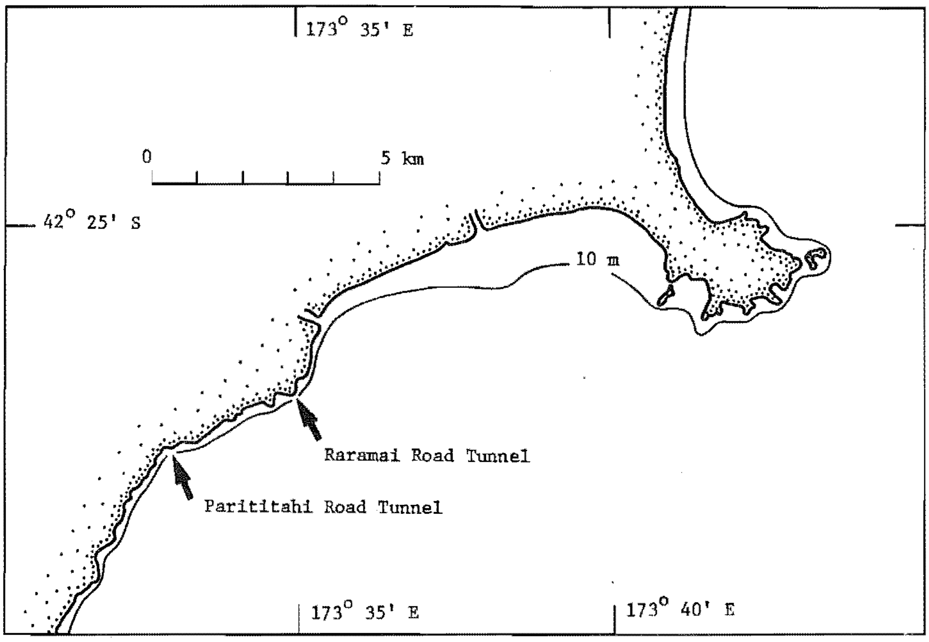
Tides and sea temperatures have been recorded intermittently at Kaikoura for several years since 1967. The tides are semidiurnal, with some diurnal inequalities: mean tidal range is 1.31 m and there may be 0.28 m difference in height of consecutive high tides (Kirk 1976). Morgans (1967a) gave the spring tide range as about 1.6 m. From my observations, the spring tide range is about 1.8 m and the neap tide range is about 0.8 m. Wave heights in excess of 2.5 m have been recorded at Kaikoura (Kirk 1975) and wave conditions can markedly affect tidal conditions. The annual temperature range of inshore waters is 8.5^{o} - 19.0^{o} C (Dix 1970; Poore 1973; Ottaway 1976a), so Kaikoura is classified as having cold temperate mixed waters (Knox 1960, 1963) with an annual mean fluctuation typical of New Zealand (Oliver 1923). Most rainfall is recorded in late autumn and winter, and during 1941 - 1970 the mean annual rainfall was 865 mm. Shaded air temperatures recorded at the Kaikoura Meteorological Station are usually in the range of 0 - 33^{o} C (data supplied by N.Z. Meteorological Service).

The main study area is a 3.2 km section of intertidal coast (173^{o} 34' E, 42^{o} 27' S) which is 10.5 km west 25^{o} south of the township of Kaikoura (Figure 3). The north-eastern limit of the study area is at the Parititahi Road Tunnel, and the south-western limit is at the Raramai Road Tunnel. This coast is made up of alternating areas of stable rock outcrops, stable reef platforms, semi-stable boulder beaches and unstable shingle beaches. Torlesse greywacke is the dominant rock. *Actinia tenebrosa* can be found on all intertidal formations except on the unstable shingle beaches. A census of *Actinia* was made in April 1972, and at that time more than 6×10^{4} adults were estimated to be present within the study area.

FIGURE 2: Aerial view of the study area and surrounding regions. The hills running along the coast shade the intertidal areas for much of the year. The snow-capped Seaward Kaikoura Range, which can be seen in the background, also has a marked effect on the climate during winter. Arrows indicate (from left to right) the Parititahi Road Tunnel and Colony #1, Colony #2, Colony #3, and the Raramai Road Tunnel. The distance between the two tunnels is about 3.2 kilometres.

FIGURE 3: Map of the study area and the Kaikoura Peninsula. Arrows indicate the positions of the Parititahi Road Tunnel (southernmost) and Raramai Road Tunnel (northernmost), which were the limits of the study area.

The offshore line indicates the approximate position of the 10 metres depth contour.


173° 35' E
0
5 km
42° 25' S
10 m
Raramai Road Tunnel
Parititahi Road Tunnel
173° 35' E
173° 40' E

The coast runs along the base of hills which rise steeply and reach a height of 475 m within 1 km of the sea (Figure 2). For several months during winter the entire intertidal study area is permanently shaded by these hills, and even in midsummer most of the area is shaded for much of each day. To the north and south the hills are further from the coast and there is considerably less shading of intertidal regions. There are also significantly fewer _Actinia_ per unit area of stable, rocky shore.

Specimens of _Actinia_ for histology and dissections were collected from all parts of the study area. Intensive observations and detailed measurements were made on three particular groups of free-living anemones (Figure 4), which are designated as Colonies #1, #2 and #3.

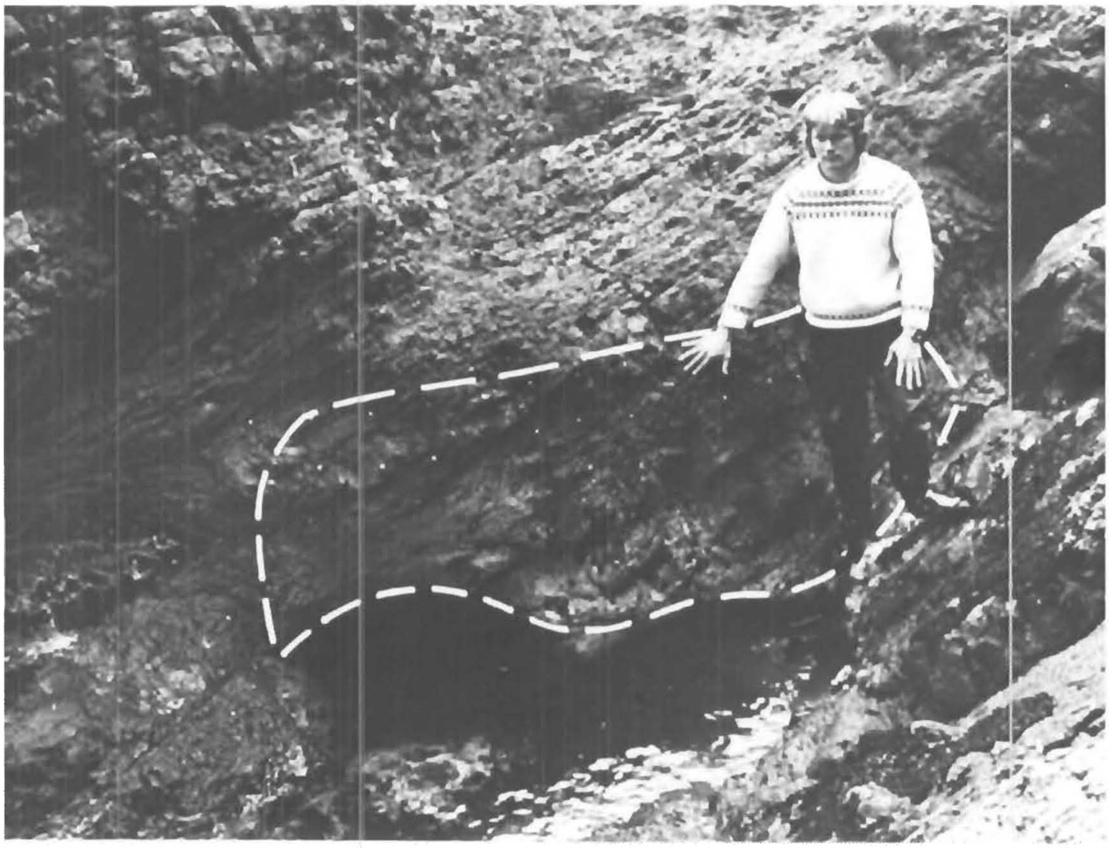
1.4 THE INTENSIVE STUDY AREA

All three Colony areas covered mainly smooth, vertical, stable rock surfaces composed of hard, torlesse greywacke. Colony #1 occupied an area of about 2.5 m^2 and was surrounded by an intertidal reef platform and stable rock outcrops. It was 1 km distant from the nearest other groups of breeding _Actinia_. Colony #2 occupied an area of 3.5 m^2 and was surrounded by mainly semi-stable boulders and some unstable shingle deposits. There were at least several hundred adult _Actinia_ within 6 metres radius of the Colony area. Colony #3 occupied 6 m^2 and was surrounded by stable rock outcrops and large stable boulders. There were over 500 adult _Actinia_ within 6 m radius of the Colony (Figure 4).

FIGURE 4: The intensive study areas. Each Colony was largely shaded from direct sunlight, and was protected from direct wave action by stable greywacke rock formations to seaward.

A. Colony #1 occupied an area of about 2.1 m x 1.2 m (high) on part of a stable cliff formation. It contained 82 adults and 43 juveniles at the start of observations, and is considered as a reproductively isolated subpopulation. The limit of the Colony is outlined.

B. Colony #3 occupied an area of about 5 m x 1.2 m (high) and was part of a large, high density subpopulation of Actinia. Some 115 adults were removed from the Colony face, and replaced with 400 juveniles of all sizes, in order to furnish additional data on growth rates. The actual Colony area (outlined) is part of a stable rock outcrop surrounded by semistable boulders and unstable shingle deposits. This general geological situation was very similar to that of Colony #2.



CHAPTER TWO

REPRODUCTIVE CYCLE AND FECUNDITY

2.1 INTRODUCTION

Information on the reproduction of sea anemones is sparse (Chia & Rostron 1970), and the literature is mainly concerned with aspects of embryology and larval development (e.g. McMurrich 1890; Gemmill 1920; Nyholm 1943; Siebert 1974; Siebert & Spaulding 1976). Although the reproductive modes are known for 110 of approximately 800 described actinian species (Chia 1976), there are only two published accounts of annual breeding cycles: those of Anthopleura elegantissima (Ford 1964) and Actinia equina (Chia & Rostron 1970).

Whether the latter species is hermaphroditic (Dalyell 1848; Cain 1974) or gonochoristic (Chia & Rostron 1970) is unresolved. Rare instances of asexual reproduction have been reported (Elmhirst 1915; Landauer 1924; Stephenson 1935; Stock 1951), but A. equina is considered to have sexual reproduction as the normal mode and is viviparous (Gosse 1860; Stephenson 1928). In the first detailed study of the reproductive biology of A. equina, Chia & Rostron (1970) confirmed that females, males, and also individuals without gonads all brood embryos. Even though they dissected hundreds of brooding adults they found no morulae or blastulae, and only one gastrula. Therefore, they proposed the hypothesis that fertilised eggs are released from the mesenteries at morula or blastula stage to become planktonic: the planulae larvae are supposed to re-enter the coelenterons of adult Actinia, including the males and those without gonads, where they metamorphose to tentaculate juveniles. Later they are released again to settle and attach.

Actinia tenebrosa is morphologically very similar to the common form of A. equina (Ottaway 1975a), and it seems that the two species may have the same mode of reproduction. A. tenebrosa is also viviparous and has been assumed to be gonochoristic (Farquhar 1898; Parry 1951; Morgans 1967b). Females, males, and individuals without gonads all brood young (Carlgren 1924; Ottaway 1974; Ottaway & Kirby 1975). A. tenebrosa thus provides the opportunities to study the annual reproductive cycle of a second species of internally brooding anemone and to examine Chia & Rostron's (1970) hypothesis in context of a closely related species.

2.2 MATERIALS AND METHODS

Twenty-seven collections of Actinia tenebrosa (mean: 68.6 adults/sample; range 50 - 80) were taken from the study area at 28-day intervals from 19 November 1972 - 6 June 1974, and from 11 November 1974 - 16 March 1975. Anemones were gently prised off the rocks with a spatula inserted under the pedal disc, and then they were immediately preserved in individual jars containing 10% neutralised formalin. In each sample, approximately equal numbers of Actinia were taken from stable rock outcrops, stable boulder beaches and unstable boulder beaches. Sampling was biassed towards anemones larger than 10 mm column diameter (CD), though apart from this the collected individuals were chosen at random. The size frequency distribution of specimens is therefore an indication of the size frequency distribution, of Actinia larger than 10 mm CD, in the study area population (Figure 5).

Preserved specimens were dissected 4 - 28 days after collection, by carefully cutting off the pedal disc at about the level of the base of the stomodaeum. Measurements of maximum and minimum column diameters were taken at this level using calipers, and the two values were averaged to give mean size to the nearest 0.5 mm. Adults were examined for the presence, number, size and colour of gonads. Some 287 fertile mesenteries, from 79 adults, were embedded in paraffin wax, sectioned at 8 μm, stained with Heidenhain's haematoxylin, and examined histologically. Dissections were made under a stereoscopic microscope at 16x and 40x magnifications. Brooded juveniles and embryos were extracted, counted, and diameters were measured to the nearest 0.1 mm using an ocular micrometer.

Statistical analyses followed the procedures given by Sokal & Rohlf (1969).

2.3 RESULTS

Sex determination

As with other anemones (Hyman 1940; Ford 1964; Chia & Rostron 1970), the gonads are seen as coloured swellings of the mesenteries, between the mesenterial filament and the longitudinal retractor muscle. The gonads are generally confined to the basal third of the mesentery, and could only be seen after dissection of the animal. It was not possible to determine the sex of intact, free-living *Actinia*. Five gonad colours were observed (Table 1): white, cream or pink gonads, which histological examination showed were testes (Figure 6A), and green or brown gonads, which were ovaries (Figure 6B). Gonad colour was consistent in any particular fertile *Actinia* dissected, and up to 13 fertile mesenteries were examined from particular specimens. Gonads from any one individual were either all testes or all ovaries: there was no histological indication of hermaphroditism. On this basis, all other fertile adults were sexed by the colour of their gonads.

Sex ratios

From sample to sample, females : male sex ratios ranged from 0.4:1 to 5:1. The sex ratio of all fertile adults in all samples was

Table 1: Relationship between colour of gonad and sex

Colour	White	Cream	Pink	Green	Brown	Total
Number of anemones examined	14	16	16	19	14	79
Number of fertile mesenteries examined	43	61	68	60	55	287
Sex	all males	all males	all males	all females	all females	

FIGURE 5: Size frequency distributions of specimens collected for reproductive cycle samples. Ordinate: Column diameter of specimens (mm) after preservation in 10% neutralised formalin. Abscissa: Proportion of specimens, as a percentage of the total number in the particular group, in each size class.

A. Specimens in which gonads were not found (n = 1487).

B. Female specimens (n = 330).

C. Male specimens (n = 192).

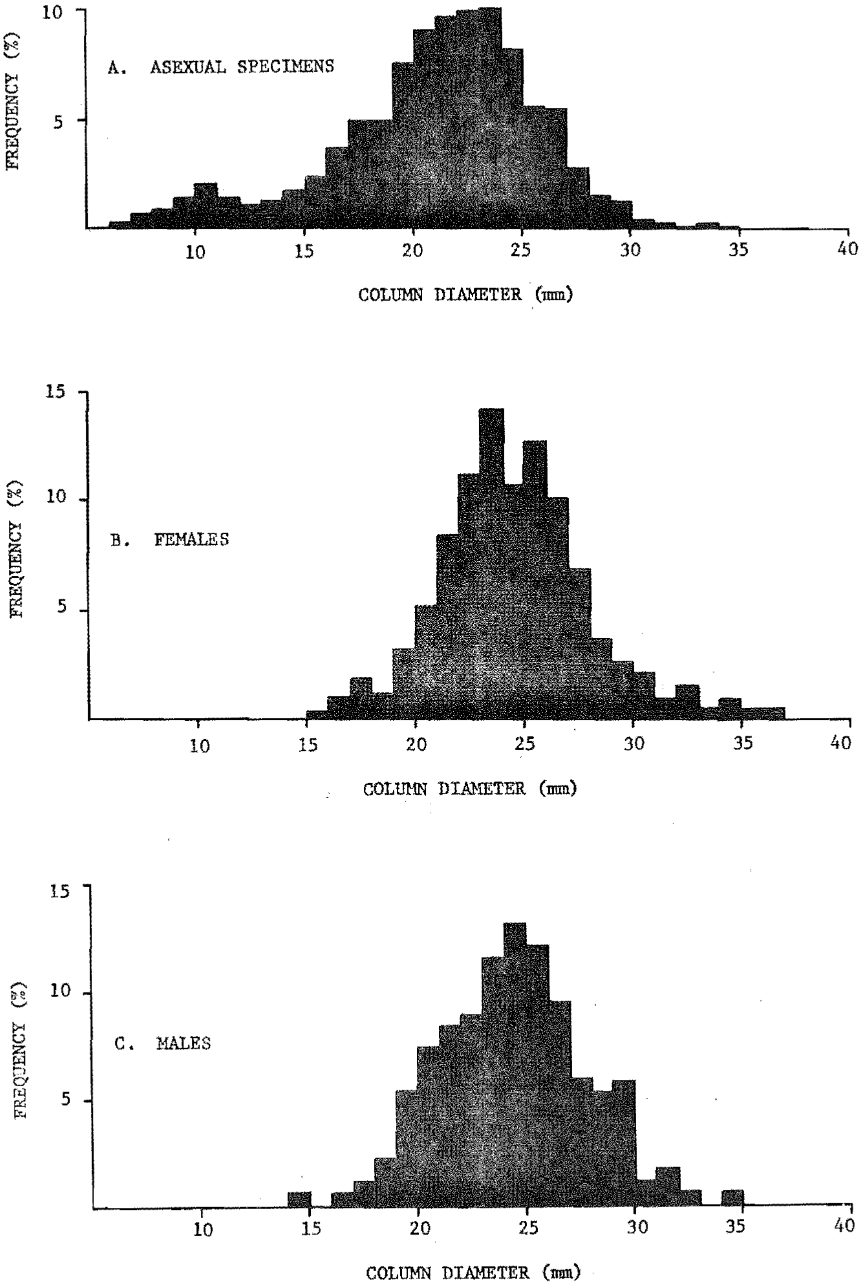

10
5
FREQUENCY (%)
A. ASEXUAL SPECIMENS
10
15
20
25
30
35
40
COLUMN DIAMETER (mm)
15
10
5
FREQUENCY (%)
B. FEMALES
10
15
20
25
30
35
40
COLUMN DIAMETER (mm)
15
10
5
FREQUENCY (%)
C. MALES
10
15
20
25
30
35
40
COLUMN DIAMETER (mm)

TABLE 2: Percentage of males and females, number of fertile mesenteries per fertile adult, and sex ratios for samples taken during the three summer breeding seasons.

Sample number	Date collected	n*	males (%)**	$\bar{x}_m^{+}$ (%)	females (%)**	$\bar{x}_f^{++}$ (%)	sex ratio (♀♀/♂♂)
3	18. 1.73	60	23.3	61	30.0	22	1.29
4	15. 2.73	59	23.7	47	20.3	23	0.86
5	15. 3.73	67	17.9	35	22.4	23	1.25
6	12. 4.73	64	6.3	28	17.2	17	2.75
14	22.11.73	67	4.5	17	11.9	18	2.67
15	20.12.73	62	22.6	47	27.4	21	1.21
16	17. 1.74	67	6.0	28	29.8	17	5.00
17	14. 2.74	74	16.2	30	27.0	14	1.67
18	14. 3.74	80	21.3	28	8.8	14	0.41
22	11.11.74	74	13.5	21	35.1	30	2.60
23	9.12.74	77	27.3	53	49.4	30	1.81
24	6. 1.75	74	25.7	38	41.9	25	1.63
25	3. 2.75	74	14.9	44	31.3	20	2.09
26	17. 2.75	75	18.7	39	37.3	28	2.00
27	16. 3.75	70	15.7	37	34.3	30	2.18

* number of adults in that sample (n)

** number of males or of females as a percentage of the number of adults in that sample

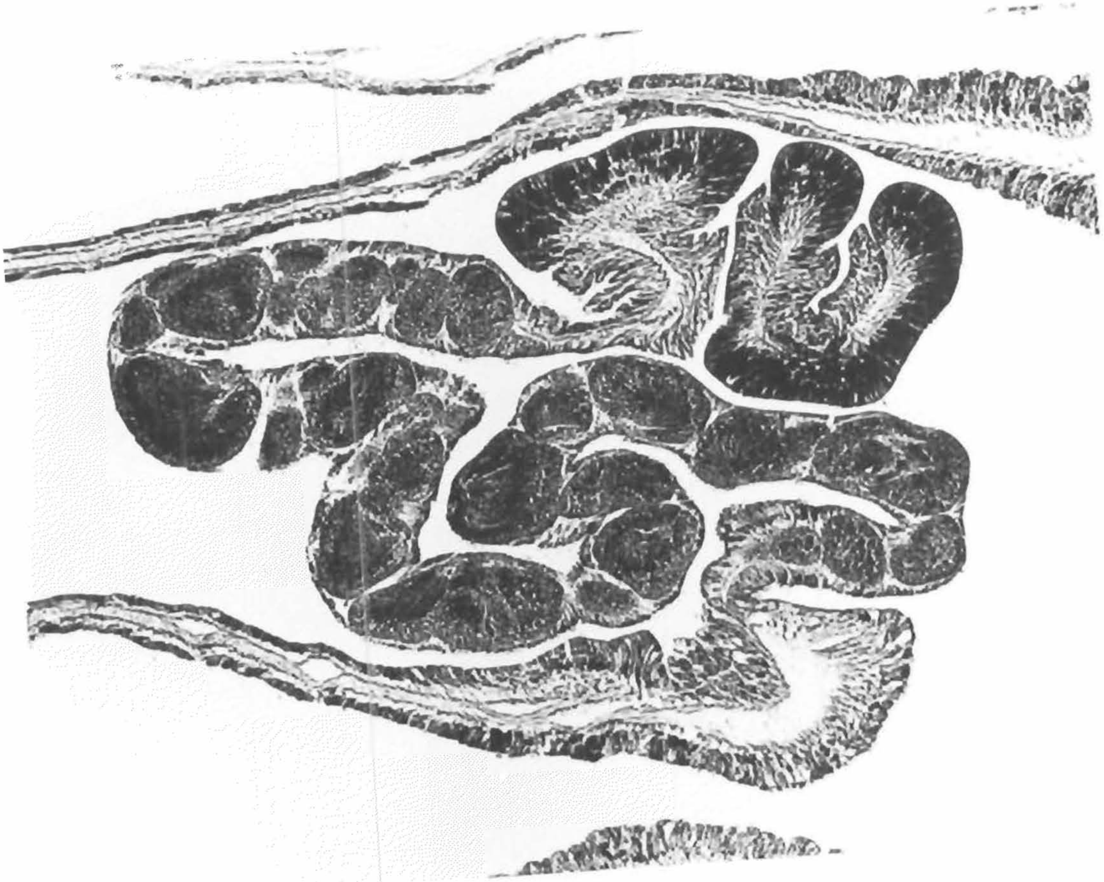
\+ mean percentage of fertile mesenteries per male in that sample ($\bar{x}_m$)

++ mean percentage of fertile mesenteries per female in that sample ($\bar{x}_f$)

FIGURE 6: Transverse sections through gonads of Actinia tenebrosa.

A. Fertile male mesentery.

B. Fertile female mesentery. Mature oocytes have one germinal vesicle. Oocytes are usually, but not necessarily, in a single row, and usually have the some polarisation.



1.72:1 (330 females : 192 males). This is a highly significant difference from a 1:1 ratio ($P<0.001$).

No significant difference was found in a comparison of the means of the minimum sizes of females ($\bar{x}=18.9$) and males ($\bar{x}=19.4$) in 16 samples where at least 3 of each sex were present ($F_s=0.602$; $0.25<P<0.50$), nor was there any significant difference between the mean size of all females ($\bar{x}=24.3$, $n=330$) and all males ($\bar{x}=24.1$, $n=192$; $F_s=0.514$; $0.25<P<0.50$). Since the smallest female found was 15 mm CD, and the smallest male found was 14.5 mm CD, adults were arbitrarily defined, for further analyses, as those individuals $\geqslant$14.5 mm CD after preservation. By this criterion, 1851 of 2013 collected specimens were considered to be adults.

Annual gonad cycle

A. tenebrosa showed most gonad development during the summer months of November - March inclusive. The main peaks of gonad development occurred in January 1973, December 1973 and December 1974, with 53%, 50% and 77% respectively, of adults fertile (Figure 7B). These three peaks coincided closely with the peaks of summer sea temperatures (Figure 7A). A secondary peak of gonad development occurred two months after the peaks of December 1973 and December 1974 (Figure 7B), and it seems quite probable that a secondary peak of gonad development also occurred in the 1972 - 1973 season (Figure 8A). During May - October 1973, a few adults in most samples still had gonads (range: 0 - 8%), but in May and June 1974, 11% and 24% of adults, respectively, were found to have gonads (Figure 7B). Whether this represented a winter peak of gonad development comparable to the summer peaks is not known, but it seems unlikely since relatively few additional embryos were added to those already being brooded (Figure 8A; Figure 9).

FIGURE 7: Inshore sea temperatures at Kaikoura, and the annual reproductive cycle of *Actinia tenebrosa* during 1972 - 1975.

A. Mean inshore sea temperatures at the study area (data from Ottaway 1976a).

B. Percentages of adult *A. tenebrosa* with gonads.

C. Percentage of adult population brooding young.

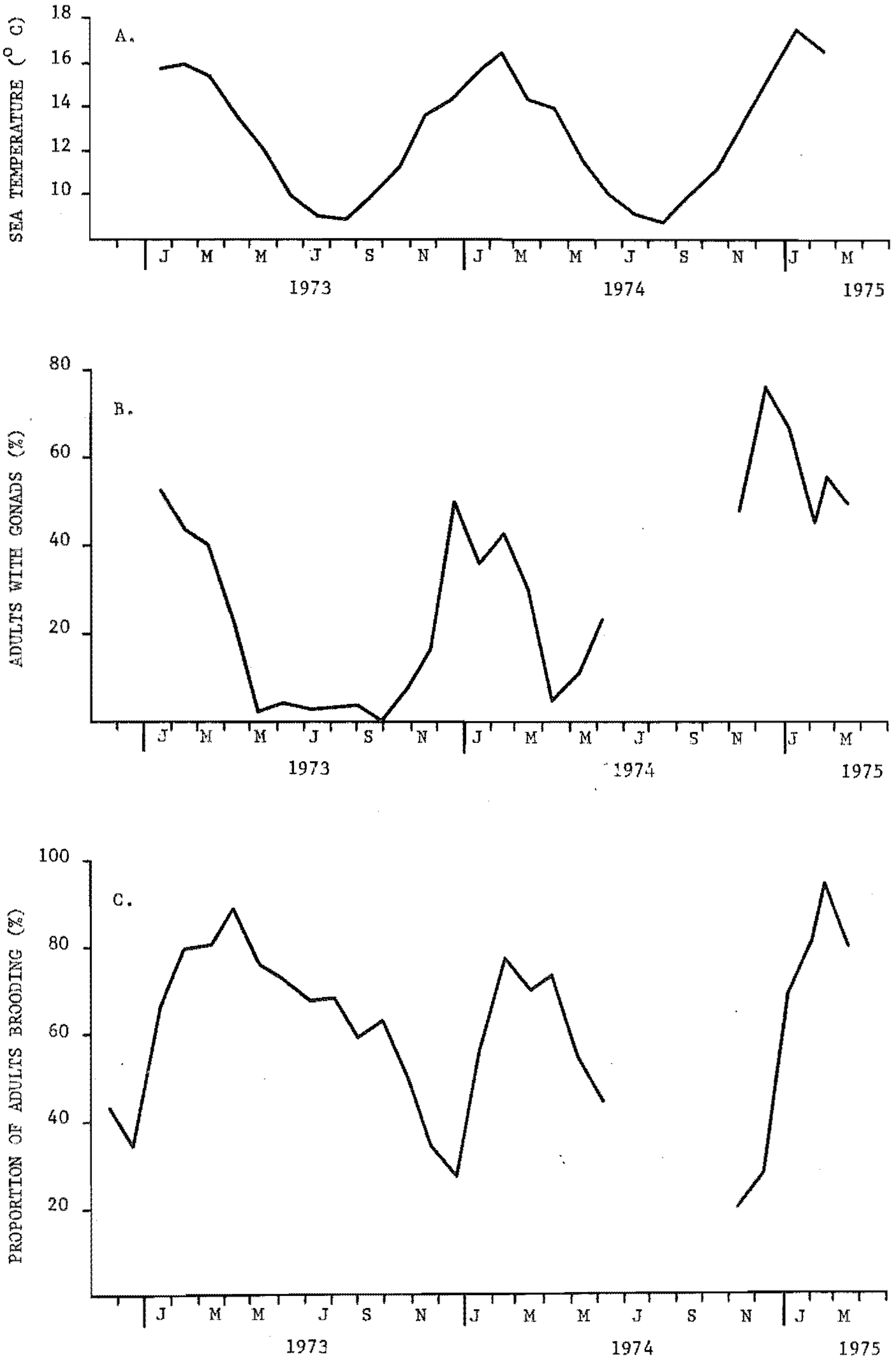
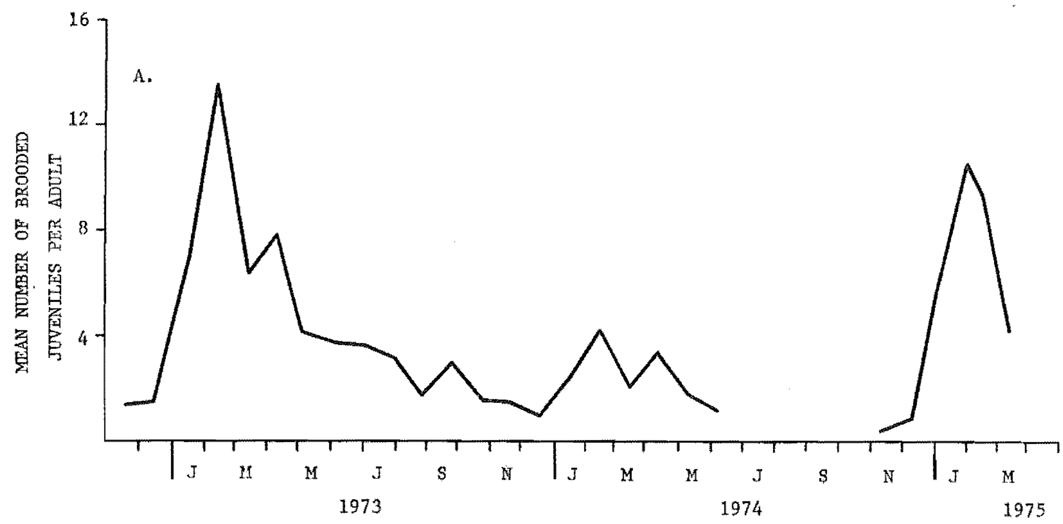

A.
SEA TEMPERATURE (° C)
18
16
14
12
10
J M M J S N J M M J S N J M
1973
1974
1975
B.
ADULTS WITH GONADS (%)
80
60
40
20
J M M J S N J M M J S N J M
1973
1974
1975
C.
PROPORTION OF ADULTS BROODING (%)
100
80
60
40
20
J M M J S N J M M J S N J M
1973
1974
1975

FIGURE 8: Annual fluctuations in size and number of juveniles brooded by <u>Actinia tenebrosa</u> during 1972 - 1975.

A. Mean number of juveniles brooded per adult, including those adults which were not brooding, for each sample.

B. Mean number of brooded juveniles (mm) for each sample.


A.
MEAN NUMBER OF BROODED JUVENILES PER ADULT
16
12
8
4
J
M
M
J
S
N
J
M
M
J
S
N
J
M
1973
1974
1975

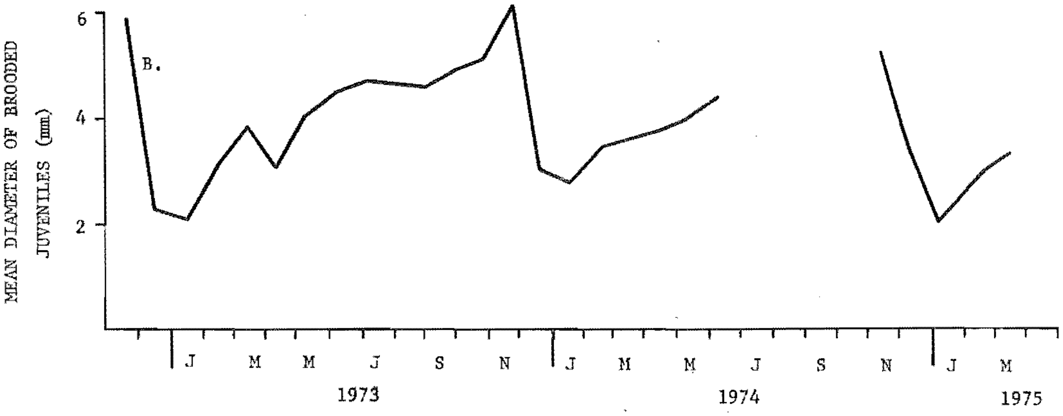
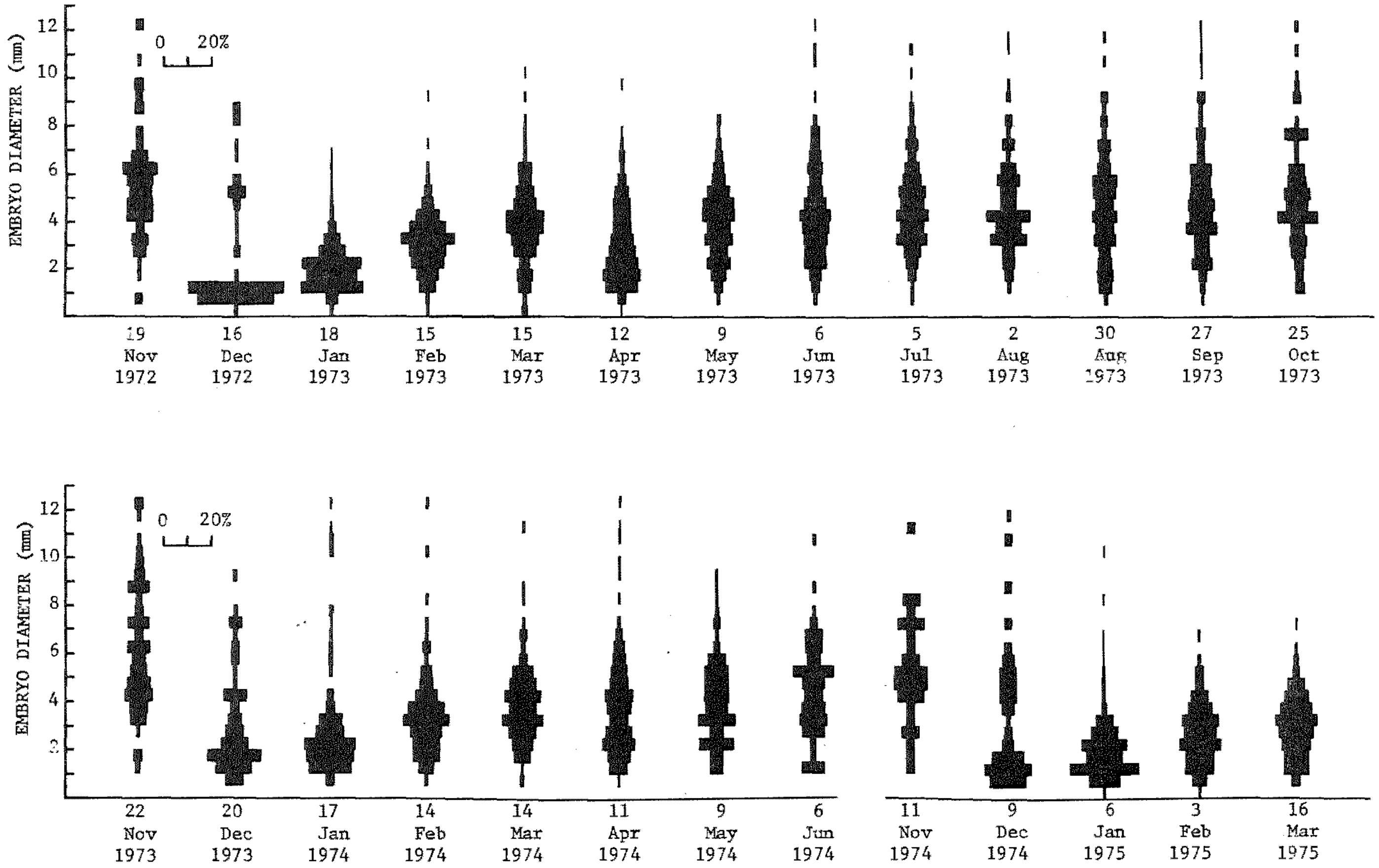

B.
MEAN DIAMETER OF BROODED JUVENILES (mm)
6
4
2
J
M
M
J
S
N
J
M
M
J
S
N
J
M
1973
1974
1975

FIGURE 9: Size frequency distributions of larvae and juveniles dissected from the coelenterons of brooding *A. tenebrosa*, which were collected at approximately 28-day intervals between November 1972 and March 1975. Scales indicate 20% of the total number of embryos from any one collection.


EMBRYO DIAMETER (mm)
12
10
8
6
4
2
0 20%
19 Nov 1972
16 Dec 1972
18 Jan 1973
15 Feb 1973
15 Mar 1973
12 Apr 1973
9 May 1973
6 Jun 1973
5 Jul 1973
2 Aug 1973
30 Aug 1973
27 Sep 1973
25 Oct 1973
EMBRYO DIAMETER (mm)
12
10
8
6
4
2
0 20%
22 Nov 1973
20 Dec 1973
17 Jan 1974
14 Feb 1974
14 Mar 1974
11 Apr 1974
9 May 1974
6 Jun 1974
11 Nov 1974
9 Dec 1974
6 Jan 1975
3 Feb 1975
16 Mar 1975

During the 1972 - 1973 and 1974 - 1975 summer breeding seasons, it was quite common to find males with 80 - 90% of all mesenteries bearing large testes (up to about 1.2 mm wide x 3.5 mm in height), and females with 70 - 80% of all mesenteries bearing large ovaries (up to about 0.8 mm wide x 2.5 mm in height). Although a similar percentage of adults developed gonads in the 1973 - 1974 summer season, it was rare to find Actinia with more than 70% of all mesenteries fertile. Mean numbers of fertile mesenteries per fertile adult were generally fewer (Table 2) and most gonads seen were small to minute. This is reflected in the mean number of juveniles produced in the three seasons: the peaks were 13.6 juveniles/adult in 1972 - 1973, and 10.5 in 1974 - 1975, but only 3.8 in 1973 - 1974 (Figure 8A).

Annual brooding cycle

Female, male and A. tenebrosa without gonads can be found brooding juveniles and embryos (Carlgren 1924; Ottaway 1974; Ottaway & Kirby 1975), and in the present study at least 20% of adults were brooding at any one time. Fewest adults contained young in November or December, at the time that gonads were developing, but the proportion of brooding adults rapidly increased to reach peaks of 89%, 77% and 94%, respectively, in the three summers which were observed (Figure 7C). Thus, the peak of brooding was 2 - 3 months after the peak of gonad development (Figure 7B).

Considering all adults, the mean number of brooded juveniles was 4.01, even though only 62% of adults dissected were brooding. The mean number of juveniles per adult per sample was 0.4 - 13.6 (Figure 8A), fewest juveniles being brooded at the time that gonads were developing, and most being brooded 1 - 2 months after the peak of gonad development. Juveniles were released throughout the year, although most were released in January, February and March. The mean size of brooded juveniles was

FIGURE 10: Frequency distribution of number of embryos per brooding adult Actinia tenebrosa (1149 brooding adults). Considering all adults (n = 1851), the mean number per brood was 4.0; considering only the brooding adults, the mean number was 6.5. The number of juveniles per brood, found in this study, ranged from 0 to 98.

FIGURE 11: Frequency distribution of sizes of all embryos from all samples (7,400 embryos). Planulae sizes (n = 42) ranged from 0.3 mm to 0.6 mm column diameter; tentaculate embryos were 0.5 mm to 12.6 mm column diameter.

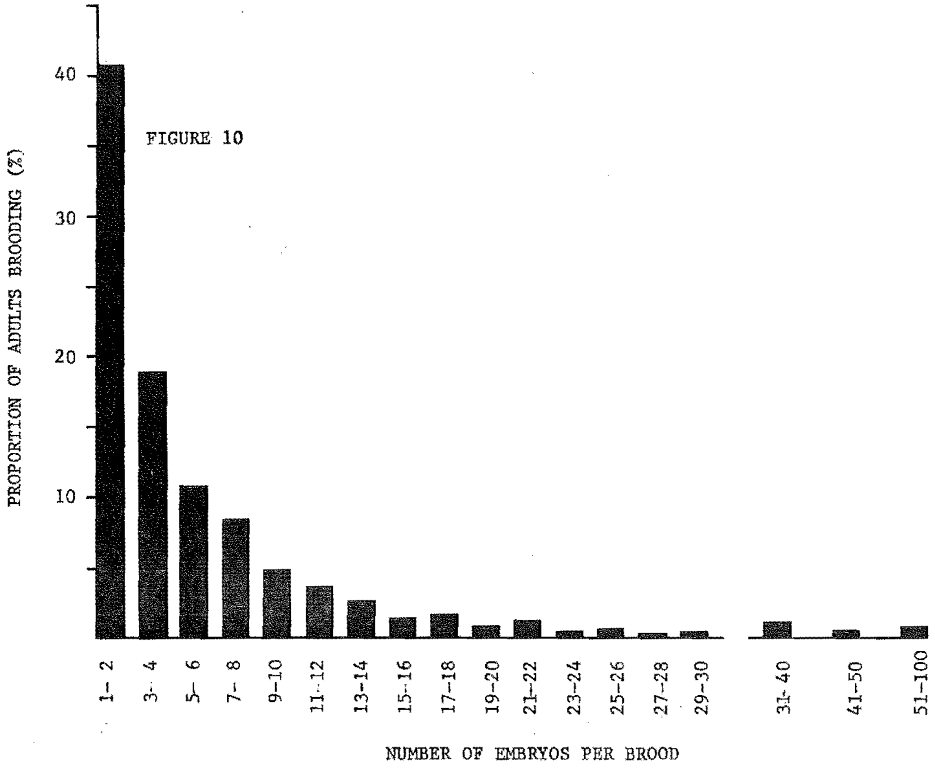


FIGURE 10

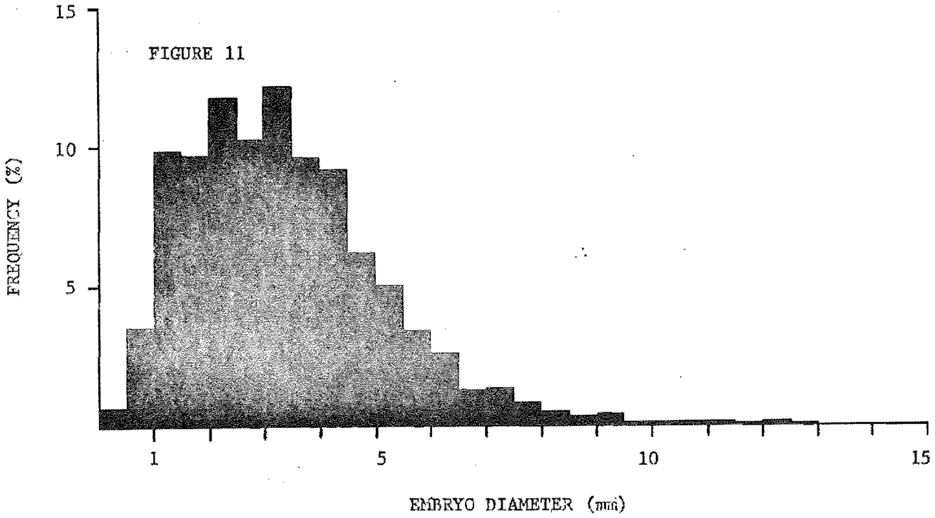


FIGURE 11

greatest at the beginning of December, when it was about 6 mm CD, and was least about the beginning of January, when it was about 2 mm CD (Figure 8B). From examination of the size frequency distributions of brooded embryos (Figure 9), it seems that some embryos are brooded for almost a full year, during which time they may reach 13 mm CD. Only a small proportion of embryos, however, grow to more than 7 mm CD before they are released, and only rarely would embryos be brooded for more than one year.

The frequency distribution of embryos per brooding adult A. tenebrosa (Figure 10) is very similar to that found for A. equina (Chia & Rostron 1970). The maximum single brood size found by Chia & Rostron (1970) was 55, and by Dalyell (1848), 200. In the present study, the maximum found for A. tenebrosa was 98, although in a non-random collection 220 tentaculate young were found in a single brood (Ottaway 1973). During February, March and April, the size range of embryos contained within individual broods was quite small. Later in the year, as the mean number of embryos per brood decreases (Figure 8A), the size disparity increases (Figure 9), indicating that all of the embryos in the same brood do not grow at the same rate. Of almost 7,400 embryos found, 42 were planulae, with diameters 0.3 - 0.6 mm, and the rest were tentaculate young. Most of the latter were 1 - 6 mm CD (Figure 11). The smallest tentaculate embryos were 0.5 mm CD, with 6 newly-formed tentacles, the largest was 12.6 mm CD, with almost 50 tentacles and several poorly developed acrorhagi. No morulae, blastulae or gastrulae were found.

There was no significant difference between the proportions of females brooding (68.2%) and males brooding (65.6%). There was a significant difference between the proportions of apparently asexual Actinia brooding (60.3%) and females brooding (Table 3), but as

TABLE 3: Relationships between sex and brooding in _Actinia tenebrosa_.[**]

Sex	Number brooding	Number not brooding	Totals	% brooding
female	225	105	330	68.2
male	126	66	192	65.6
apparently asexual[*]	611	402	1013	60.3
Totals	962	573	1535 = n	62.7

---

[*] Only adult specimens from those samples containing males and females considered.

[**] Using the G-test statistic (Sokal and Rohlf 1969), there is a significant difference between proportions of females and apparently asexual adults brooding ($\chi^2_1 = 6.646$; $P < 0.01$); there is no significant difference, in the proportions brooding, comparing females with males, or males with the apparently asexual adults.

FIGURE 12: Correlations between column diameter of adult specimens and the number of brooded juveniles, for collections taken on 3 and 17 February 1975. Correlation coefficients were calculated using only specimens greater than 15 mm column diameter. ● : one value

○ : two values.

A. Male specimens (23 degrees of freedom, r = -0.0853).

B. Female specimens (49 d.f., r = 0.0463).

C. Apparently asexual specimens (71 d.f., r = 0.2618).

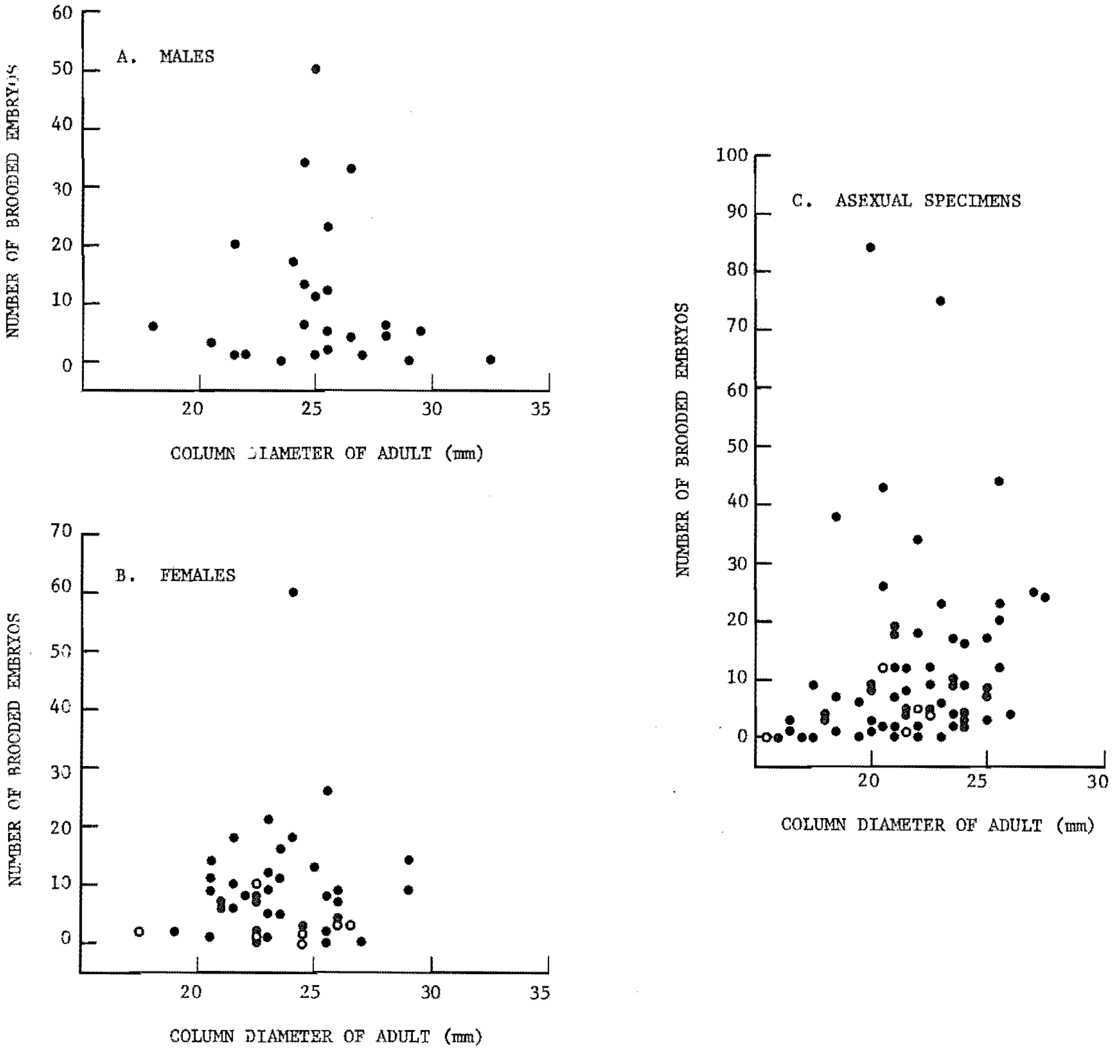

A. MALES
NUMBER OF BROODED EMBRYOS
0
10
20
30
40
50
60
20
25
30
35
COLUMN DIAMETER OF ADULT (mm)
B. FEMALES
NUMBER OF BROODED EMBRYOS
0
10
20
30
40
50
60
70
20
25
30
35
COLUMN DIAMETER OF ADULT (mm)
C. ASEXUAL SPECIMENS
NUMBER OF BROODED EMBRYOS
0
10
20
30
40
50
60
70
80
90
100
20
25
30
COLUMN DIAMETER OF ADULT (mm)

TABLE 4: Relationship between sizes of dissected specimens, from all collections, and numbers of embryos brooded.

Size range of dissected specimens (mm)	Number of specimens	Proportion brooding (%)	Mean number of embryos/specimen
4.0 - 5.9	4	0.0	0.00
6.0 - 7.9	16	6.3	0.13
8.0 - 9.9	36	0.0	0.00
10.0 - 11.9	53	1.9	0.04
12.0 - 13.9	36	5.6	0.17
14.0 - 15.9	66	7.6	0.12
16.0 - 17.9	141	31.9	1.16
18.0 - 19.9	216	51.9	2.19
20.0 - 21.9	358	64.0	3.80
22.0 - 23.9	423	66.4	4.05
24.0 - 25.9	332	69.6	4.86
26.0 - 27.9	202	75.3	5.87
28.0 - 29.9	85	76.5	5.98
30.0 - 31.9	25	64.0	6.88
32.0 - 33.9	11	63.6	2.27
34.0 - 35.9	7	57.1	17.57

discussed below this may be a consequence of the smaller average size of Actinia in the asexual group. There was no significant difference in the numbers of embryos brooded by males ($\bar{x}$=7.01) and females ($\bar{x}$=8.40; F_s=3.84, $0.25<P<0.50$), but the mean size of embryos brooded by males ($\bar{x}$=3.10 mm, n=883) was significantly greater than the mean size brooded by females ($\bar{x}$=2.95 mm, n=1,890; F_s=5.46, $P<0.025$).

For individual samples there was little correlation between sizes of collected specimens and numbers of brooded juveniles, the latter usually showing a very wide variance (e.g. Figure 12); however, considering all collected specimens in the range 4 - 36 mm CD (n=2011), the mean number of embryos brooded increased with increasing size of adults (Table 4). As mentioned previously, the smallest Actinia found with gonads was 14.5 mm CD, and while 62% of all specimens above this size were brooding, only 2.8% (4 specimens, each brooding one or two embryos) of smaller specimens were brooding. The smallest brooder collected was 7 mm CD and was brooding 2 tentaculate young both about 2mm CD. It seems most likely that all three anemones originated from the same brooding adult, with the smallest two already contained by the largest at the time of release. Several brooded juveniles actually dissected from adults were found to be brooding other juveniles, as sometimes occurs in A. equina (Gravier 1916). The small embryos are probably ingested, but still remain unharmed (Ottaway 1974), as the large ones feed on food particles within the coelenteron of the brooding adult.

No correlation was found between the sizes of collected specimens and the sizes of brooded embryos.

2.4 DISCUSSION

Information on the larval development and reproduction of internally brooding Actinia is apparently contradictory and remains to be reconciled. Authors have described ciliated, pre-Edwardsia stage embryos (Dalyell 1848) and planula-form larvae (Appellöf 1900; Stephenson 1928). Gillespie (1931) reported that eggs of A. equina develop to ciliated blastulae and then directly into "a cylindrical form ... which develops tentacular buds". Chia & Rostron (1970), however, found no morulae or blastulae, and only one gastrula, from 823 dissected adults: they proposed that most of the early larvae become planktonic, to re-enter the coelenterons of adults as planulae and only then to metamorphose to tentaculate young anemones. This explained the presence of brooded embryos in males and adults without gonads, as well as in the females. A consequence of their hypothesis is that juveniles contained in an adult should be derived from a number of different matings, and would be expected to show a range of phenotypes characteristic of the population as a whole.

The scant available evidence suggests otherwise: brooded juveniles have phenotypes which are characteristic of the individual brooding adult (Dalyell 1848; Den Hartog 1961), even when the adults are taken from phenotypically diverse populations (Cain 1974). An alternative hypothesis, that A. equina is a hermaphrodite (Dalyell 1848) which mainly self-fertilises and retains larvae within the parent (Cain 1974), was rejected by Chia & Rostron (1970).

The present study has demonstrated many similarities between A. equina and A. tenebrosa, such as overall sex ratios, gonad development as determined by histology of preserved specimens, the apparent absence of brooded morulae, blastulae and gastrulae, brooding of juveniles throughout the year, and the frequency distribution of brooded embryos per adult. The only major difference from the data presented by Chia & Rostron (1970) is that most A. tenebrosa are brooding in late summer, whereas most _A. equina_ are brooding in winter months. Nevertheless, I suggest that my data indicates labile gonochorism in _A. tenebrosa_, that is, consecutive sexuality, whereby adults change from one sex to the other within the one breeding season. Brooding adults would therefore be the maternal parents of their brooded embryos. While cross-fertilisation is most probable, the possibility of some self-fertilisation is not dismissed. Transfer of embryos from one brooder to another is also not dismissed, but the occurrence must be rare, and such embryos would probably be tentaculate young which had been released ready for settling and attachment.

Grouping all fertile specimens, there was no significant difference in the mean or minimum sizes of males or females, there was no significant difference in the number of embryos brooded by males or females, but males brooded significantly larger embryos than females. By my hypothesis, those adults that developed ovaries at the start of a breeding season would later become apparently asexual, and then apparently males, but in the intervening period their brooded juveniles would have had several months in which to grow. Those adults that originally developed testes would not receive a brood of embryos until some months later, after they too had developed their own ovaries. Thus, if males contained embryos at all such embryos would normally be larger than those contained in adults functionally females at that time. Unfortunately, because of the relatively small number of fertile anemones in any one sample (maximum: 41), the disparity in sex ratios, and the very wide variance in numbers per brood, it was not possible to meaningfully analyse the means and variances of numbers and sizes of embryos brooded within samples by males and females. For that, collections each containing at least 150 adults would have been necessary, and logistically such sample sizes were not feasible.

The form of labile gonochorism suggested for *A. tenebrosa* has not been recorded in cnidarian species, although hermaphrodites are known in all 9 orders of Anthozoa (Tardent 1975). Furthermore, previously unsuspected modes of reproduction have been described only recently for the well-known, common actinians *Cereus pedunculatus* and *Epiactis prolifera*. Rossi (1971, 1975) found that *C. pedunculatus* has distinct sexual races, which, according to environmental conditions, may be parthenogenetic and viviparous, protogynously hermaphroditic and viviparous, or gonochoristic and oviparous. Dunn (1975a,b) found that *E. prolifera* is a gynodioecious hermaphrodite, in which small specimens are female and larger ones are hermaphroditic. Previously, *E. prolifera* had been described as gonochoristic (Hand 1955).

I reject Chia & Rostron's hypothesis on several grounds: firstly, the stage of hatching from mesenteries and the time for development to planulae is not known. Embryos may hatch at morula or even blastula stage, and may develop directly to planulae without a "typical" gastrula stage. In *Stomphia didemon*, development from morula to early planula takes 2 days (Siebert 1973), in *Tealia crassicornis*, about 4 days (Chia & Spaulding 1972). Both of these species shed their eggs into the plankton, and development of the brooded, lecithotrophic *Actinia* embryos to Edwardsia stage larvae, when they start actively capturing food within the brooder's coelenteron, may be much more rapid. The probability of finding pre-planula stage larvae during random sampling would be correspondingly quite small.

Secondly, there is a marked difference in the proportions of *Actinia* brooding between the groups less than 15 mm CD (3% brooding) and greater than 15 mm CD (6% brooding). My explanation is that, except in rare instances where released tentaculate young are captured by other *Actinia* in the population, the development of ovaries is one necessary prerequisite for an individual to brood. If planulae were captured from the plankton by all free-living Actinia, efficiency of capture should depend in part on surface area of the oral disc and tentacles. Thus, Actinia of 14 mm CD should be only marginally less effective than Actinia of 15 mm or 16 mm CD. Clearly, this is not so.

Finally, Chia & Rostron (1970) commented on the small number of embryos per brood, when most females produce hundreds of eggs. It seems likely that, as in many marine invertebrates (Kinne 1970, p.487), temperature fluctuations synchronise the development of gonads and release of gametes in Actinia; however, the quantity of gametes released, or the production of gonads at all, in one season and from year to year, is probably a function of some other prerequisite factor. The amount of food an anemone has captured before and during the breeding season is an obvious suggestion (Dalyell 1848), but it is difficult to assess (Chia & Rostron 1970) and no attempt was made in the present study. Since there is no evidence that Actinia adults move together to copulate (Chapter 3) as observed in Sagartia troglodytes (Nyholm (1943), free-swimming sperm must be shed into the sea to be planktonic for a period before they enter females and find ripe oocytes. Such a chance event would lead to a wide variance in the numbers of eggs fertilised between particular individuals, and dense aggregations should have proportionally higher mean brood sizes than scattered, solitary Actinia, providing the latter do not employ alternative modes of reproduction such as self-fertilisation or parthenogenesis. If, however, effectiveness of sperm capture is related to size of the capturing individual, larger females should have more eggs fertilised, and therefore brood more embryos. Such a relationship was seen (Table 4).

Thus, I suggest that the observed population of Actinia tenebrosa consists of cross-fertilising labile gonochorists, which have the potential to change from one sex to the other during each breeding season.

Chia (1976) has described seven patterns of sexual reproduction found in actinian species. From earlier conclusions (Chia and Rostron 1970), Actinia equina should be considered to have either a larviparous-pelagic-lecithotropic pattern of larval development or an oviparous-pelagic-lecithotropic pattern, yet he classified the species as viviparous, in common with Actinia bermudensis (Walton 1918) and A. tenebrosa (Farquhar 1898; Carlgren 1924; Parry 1951). The reason for this inconsistency was not mentioned. Viviparity, where fertilisation is internal and the larvae are released at a post-Edwardsia stage of development, is thought to have the lowest rate of dispersal and the highest rate of offspring survival, of the seven patterns seen in actinians, and is only ecologically advantageous in situations of limited nutrient supply for gamete production (Chia 1976, p.268). While Chia's logic appears to be basically sound, I question whether his conclusions are entirely so. At least four species of anemones in New Zealand are known to be viviparous: the intertidal Actinia tenebrosa, Epiactis thompsoni, which is usually found in shallow subtidal waters living on rock substrata, Epiactis mortenseni, which is epiphytic on large brown algae, also in shallow subtidal waters (Ottaway 1975c), and Bunodactis chrysobathys, which is found attached to bottom fauna in depths of 45 - 110 m (Parry 1951). It is difficult to conceive why these species should be under any more limited nutrient supply than other actinian species, sharing the same habitats, which are not known to be viviparous. Chia (1976) also considers that viviparity, or brooding, is not the best method for the dispersal and survival of an actinian species in the long term. While his argument is convincing, it may be at fault, at least using the criteria of numbers, biomass and geographical distribution for intertidal species.

Of the many intertidal actinian species described for New Zealand and Australia (Parry 1951; Carlgren 1950a, 1950b, 1954), A. tenebrosa is not only one of the most abundant but it is also one of the most widely distributed (Chapter 1). Comparative studies on other actinian genera could provide much more valuable information on this question.

CHAPTER THREE

PEDAL LOCOMOTION AND INTRASPECIFIC AGGRESSION

PEDAL LOCOMOTION

3.1 INTRODUCTION

It has been known for many years that sea anemones can move by pedal locomotion (e.g. Dicquemare 1775; Johnston 1846; Gosse 1860; Zahl & McLaughlin 1959) and it seems likely that all species with "a well-differentiated pedal disc have some powers of locomotion" (Parker 1919, p.24).

Many of the accounts, however, are somewhat anecdotal (e.g. Tugwell 1856; Cotte 1922; Livingstone 1928) and most describe the behaviour of anemones kept in aquaria (Parker 1915, 1917a,b, 1919; Pantin 1952; Batham 1965; Ottaway & Thomas 1971; Robson 1976), but, Ross (1974, p.303) notwithstanding, some species, including Actinia equina, sometimes initiate pedal locomotion apparently as an escape response from prolonged adverse stimuli (Jennings 1905; Batham & Pantin 1950c), unfavourable environments (Hargitt 1907), aggressive conflicts with other actinians (Abel 1954; Bonnin 1964; Francis 1973b; Williams 1975; Sebens 1976) or attack by predators (Fleure & Walton 1907; Edmunds, Potts, Swinfen & Waters 1976; Dunn 1977b; Ottaway 1977b). Although attempts have been made to quantify such laboratory observations on locomotion (Osburn 1914; Parker 1917a), very few quantitative field data have been published. Dunn's (1977b) work on E. prolifera provides a notable exception, but "there is a good deal still unknown about the movements of whole colonies or groups of anemones" (Fleure & Walton 1907).

3.2 MATERIALS AND METHODS

Attempts to mark or tag Actinia have not proved successful (Ottaway & Thomas 1971). Individuals were therefore identified by position and size recognition, using a technique modified from Fager (1968) and similar to that described by Dunn (1977b).

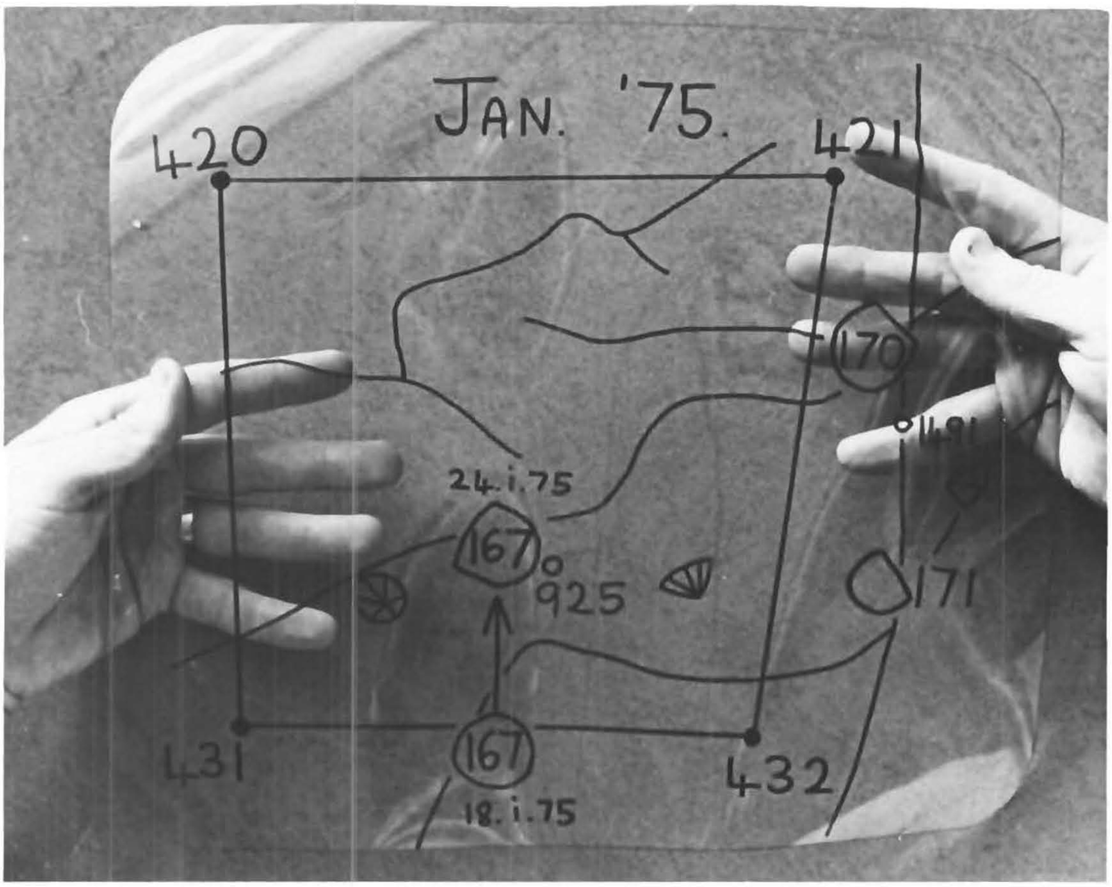
In March 1973 a set of individually numbered tags were embedded into the vertical rock substratum of Colony #1 to form the points of a grid extending past the limits of the area occupied by Actinia. Tags were placed so that if the actual point locations were projected onto a vertical, plane surface standing parallel to the main surface of the colony area, horizontal and vertical lines could be drawn to connect the projected points into grid squares with sides of 0.2 m. The actual rock area covered by each grid square was in the range 0.04 - 0.1 m^2, depending on the curvature of that area of rock surface. Full-scale overlay maps were drawn on transparent plastic sheets using waterproof felt-tipped pens. Each map, representing one grid square and part of adjoining squares, showed the numbered tags which were used as permanent fixed reference points, geological features of the rock surface, locations of the Actinia present, and sizes of those anemones (Figure 13).

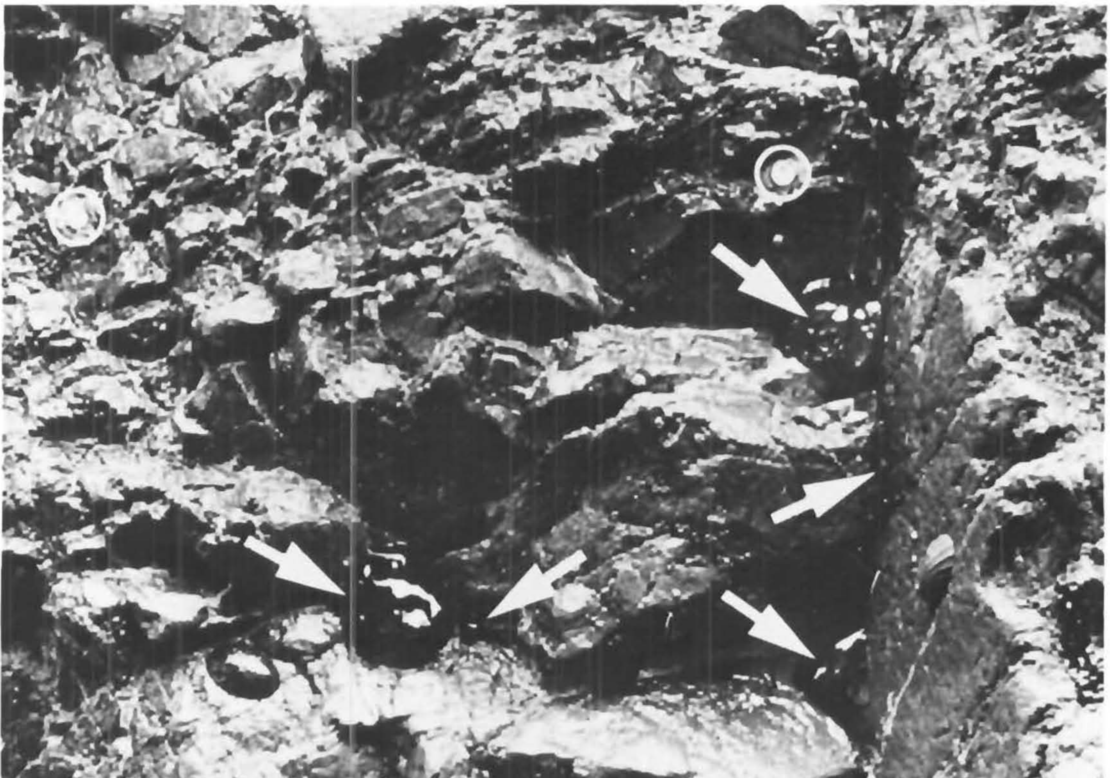
Between 24 November 1973 and 30 March 1975, the anemones on Colony #1 were checked during 104 low tide periods (about once every 4-5 days) and then about monthly until 3 December 1975. A total of 111 visits and about 15,300 observations were made, each observation consisting of 4-8 items of information regarding a particular anemone. On the first sighting, anemones were assigned individual reference numbers. On subsequent visits, except on a few occasions when

FIGURE 13: Method used to locate and follow individual Actinia on the intensive study areas.

A. Typical map, showing adult and juvenile anemones present in a particular grid square on Colony #1 in November 1974. Waterproof felt-tipped pens were used to mark information, such as size and position of anemones, directly onto overlay maps drawn on clear plastic sheets.

B. The actual area of Colony #1 represented by the map above. Individually numbered tags (circled) were embedded into the rock to provide fixed permanent reference points. The positions of adults 167, 171, and 170, and juveniles 925 and 1491 are arrowed.


JAN. '75.
420
421
170
491
24.i.75
167
925
171
431
167
432
18.i.75



circumstances such as inclement weather resulted in a curtailment of observations, all anemones were identified and checked for presence, location, visible wounds, general condition, and other specific information that is discussed elsewhere in this thesis.

3.3 RESULTS

Movements of more than 5 mm by juveniles and 15 mm by adults were discernable. Three main patterns of pedal locomotion were evident:

(1) Actinia which showed no appreciable change of location at all. Relatively few juveniles were seen to move, although most juveniles survived less than 10 days from the time of settlement (Chapter 4). Some of the anemones which survived the entire 738 days of observations also showed no locomotion (Tables 5,6; Figure 14).

(2) Actinia which showed frequent small moves, that sometimes approached almost continuous slight activity, but which generally stayed within a quite restricted area. Some 81.4% of juveniles moved less than 50 mm (Table 6), and 76.3% of adults moved less than 250 mm (Table 5), but the majority of these juveniles and adults were not seen more than 30 mm away from their original positions. For example, adult 204 was seen only once outside an area 70 mm x 50 mm (Figure 14), even though it moved a total distance of 325 mm in 2 y.

(3) Actinia which generally fitted into one of the above two categories, but which for relatively brief periods also exhibited sustained and usually directed locomotion, taking the animals some distance from their original position.

The greatest total distances moved, in 2 y, were 1555 mm for adults and 625 mm for juveniles; the greatest rates of locomotion observed were 210 mm/day for adults and 81 mm/day for juveniles.

TABLE 5: Total distances moved by adult Actinia tenebrosa on Colony #1. Seventy-eight individuals were followed for 738 days; two individuals were followed for 623 days.

	Distances moved (mm)				
	≤50	51 - 250	251 - 500	501 - 1000	≥1000
Totals	36	25	13	5	1
Percentages	45	31.3	16.3	6.3	1.3

TABLE 6: Total distances moved by juvenile *Actinia tenebrosa* on Colony #1. Only juveniles seen at least twice between November 1973 and February 1975 inclusive were considered (n = 257).

	Distances moved (mm)					
Time observed (days)	≤10	11 - 50	51 - 100	101 - 250	251 - 500	≥501
1 - 20	71	8	0	4	0	0
21 - 100	51	14	7	6	1	0
101 - 200	22	4	3	2	0	0
201 - 738	24	15	12	9	3	1
Totals	168	41	22	21	4	1
Percentages	65.4	16.0	8.6	8.2	1.6	0.4

These maximum rates are considerably less than those observed for A. tenebrosa under laboratory conditions (Ottaway & Thomas 1971).

In some instances it was possible to associate such movements with external factors. Locomotion was observed following:

a. Physical injury. Actinia damaged by the impact of moving stones or floating logs moved actively for several weeks afterwards.

b. Physical shocks. Actinia covered by shingle usually moved rapidly upwards soon after being uncovered.

c. Repeated desiccation appeared to initiate movement in adult 227. After a series of low tides coinciding with warm dry weather, during which this anemone was repeatedly desiccated, it moved 750 mm in 4 days (30 December 1973 - 3 January 1974), directly downwards. On 8 January 1974, however, Actinia on Colonies #1 and #2 were severely desiccated for 4 h by a warm, dry wind, and during this period many anemones shrunk to almost 30% of their original volume. There was no increased locomotion following this, and all but a few juveniles recovered within one week. In summer especially, many juveniles settled and attached in positions where they were subjected to repeated desiccation; most of these died within a few days without moving appreciably from the site of settlement.

d. Biological interference. Crowding or crushing of Actinia, especially of the juveniles, by limpets, chitons or whelks, were followed by small, rapid moves (20 - 30 mm in one day) away from the source of irritation.

e. Wounding from intraspecific aggression. When an adult moved into contact with another, one or both usually reacted aggressively with an "acrorhagial response". Wounded anemones moved directly and rapidly away from the wounding anemone. Intraspecific aggression generally only modified the direction and rate of pedal locomotion of an already

FIGURE 14: Patterns of pedal locomotion and aggression observed in Actinia tenebrosa on Colony #1.

Adults 57, 58, 59, 60: Moved 40 - 130 mm in 738 days (24 November '73 to 3 December 1975) and were in close contact with each other for most of that time. No aggression was observed between these adults.

Adult 163: Moved 95 mm in 2 y, but remained within 20 mm of original position.

Adults 166, 197, 198: No appreciable locomotion in 2 y.

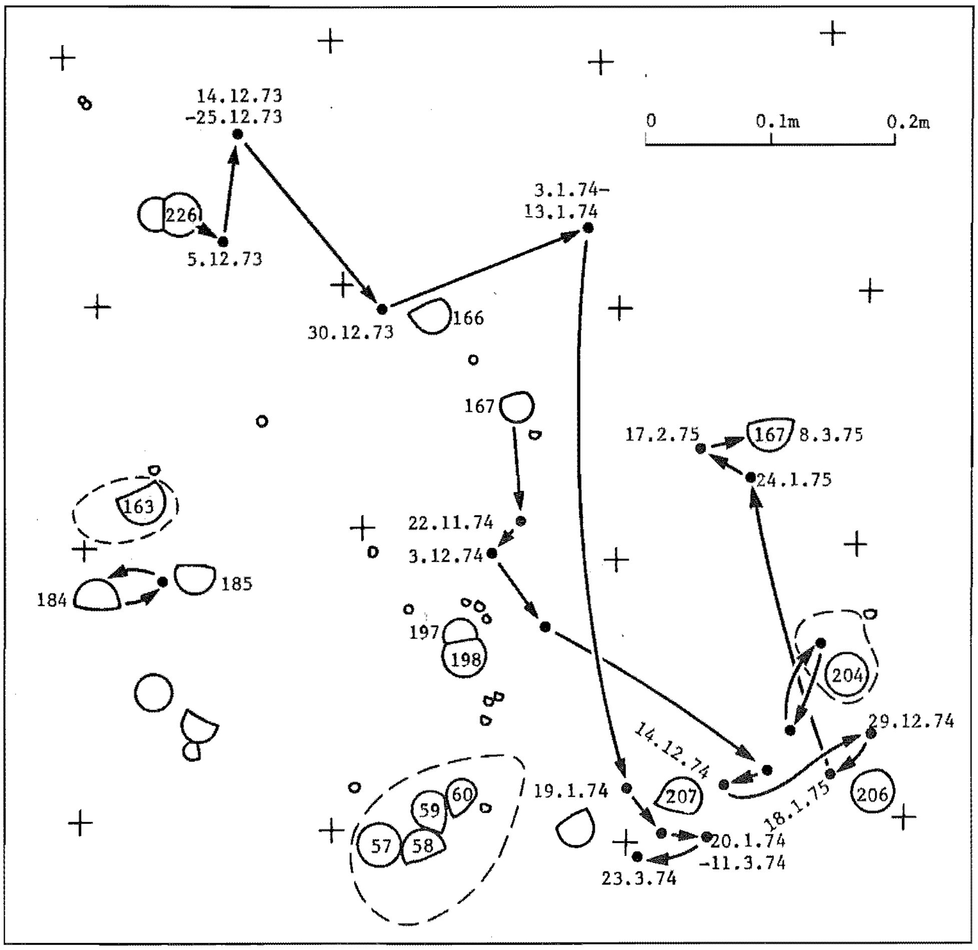
Adult 167: Did not move appreciably until 17 November '74, 358 days after the start of observations. Moved 420 mm in the next 27 days, mainly following cracks and contours in the rock surface. Between 14 December '74 and 29 December 1974, adult 167 abruptly changed direction and moved 120 mm, possibly as a result of a non-wounding contact with adult 207. Adult 167 then contacted adult 204, was wounded, moved away 45 mm, contacted adult 206, was wounded again, and moved away 235 mm between 18 January '75 and 24 January '75. It moved only 70 mm in the next 9 months.

Adults 184, 185: Adult 184 was seen to move between the position shown and adult 185. The latter did not move appreciably at any time. On four occasions, adult 184 slowly approached adult 185, but then quickly moved away. On two of these occasions (4 April and 19 April '74), 184 was seen to have acrorhagial wounds inflicted by 185.

Adult 204: Moved 325 mm in 2 y, mainly within an area about 70 mm x 50 mm. On only one occasion (14 February '74), was seen outside this area. Aggressive conflicts with adults 208 (25 October '74 and 29 December '74), 167 (18 January '75) and 227 (3 December '75), resulted in those anemones moving away, carrying 4 - 6 acrorhagial wounds. Adult 204 was never visibly wounded.

Adult 226: Moved a total of 960 mm, which took it 610 mm away from the position where it was first seen. This was one of the largest net movements observed.

Dashed lines indicate areas within which particular anemones confined their movements.


14.12.73
-25.12.73
0
0.1m
0.2m
226
5.12.73
3.1.74-
13.1.74
30.12.73
166
167
17.2.75
167
8.3.75
24.1.75
163
22.11.74
3.12.74
184
185
197
198
204
29.12.74
14.12.74
18.1.75
206
207
19.1.74
60
59
57
58
20.1.74
-11.3.74
23.3.74

moving anemone (Figure 14), although in a few instances both anemones moved away from the point where the fight had occurred. This behaviour will be described in detail.

INTRASPECIFIC AGGRESSION

3.4 INTRODUCTION

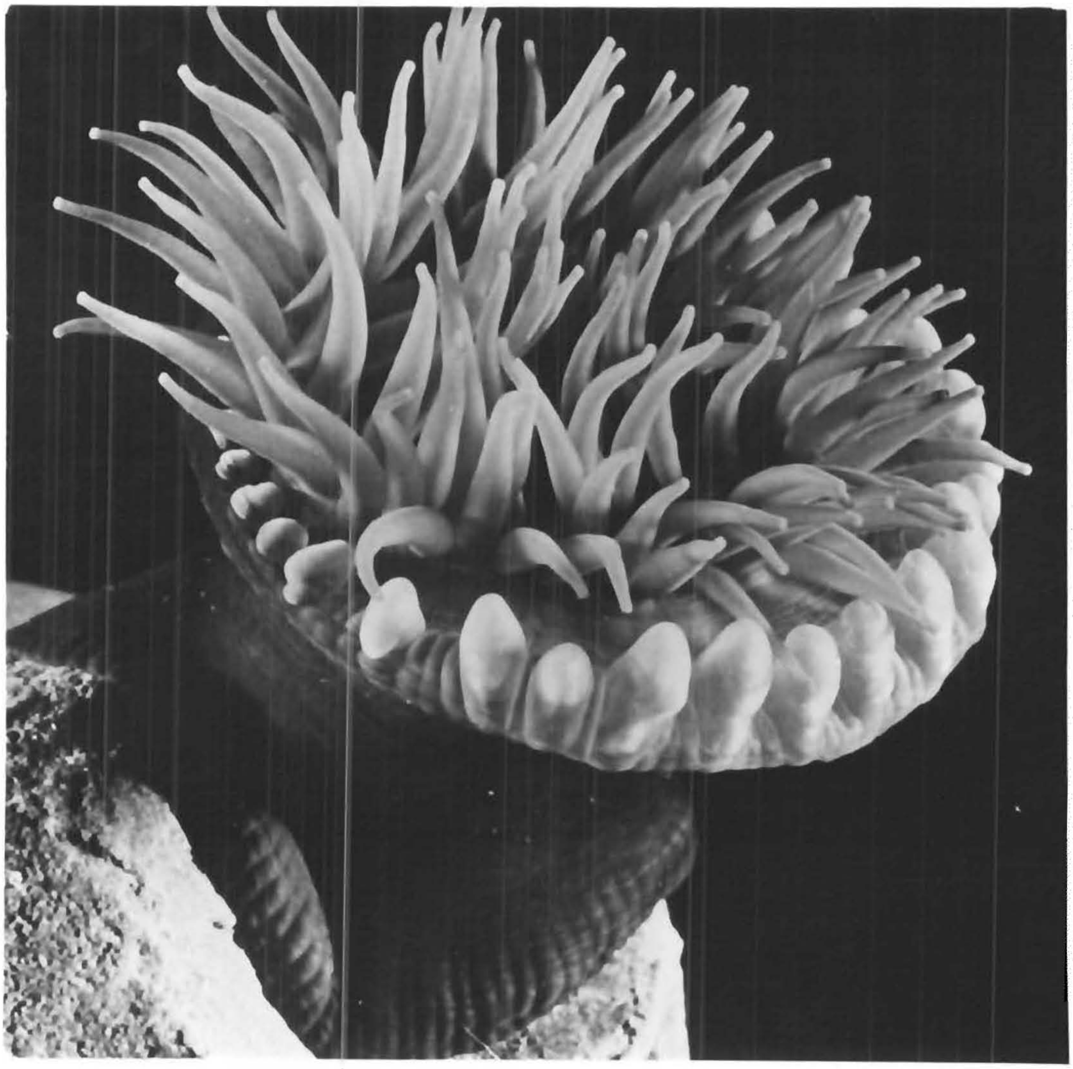
In the laboratory, an "acrorhagial response", in which one anemone inflates its acrorhagi and then attacks another, can be elicited by contact of two anthozoans, only one of which need be an actinid with acrorhagi (Bonnin 1964; Francis 1973b; Bigger 1976); however, this response is normally associated with intraspecific aggression between two genetically dissimilar individuals (Abel 1954; Bonnin 1964; Francis 1973b, 1976).

Ottaway & Kirby (1975) noted that Actinia tenebrosa exhibits intraspecific aggression, but this behaviour has not been described previously for the species.

3.5 ACRORHAGI

Acrorhagi, or marginal spherules, are specialised structures found in Actiniidae (Carlgren 1949) and are only used during some forms of aggressive behaviour (Abel 1954). The acrorhagi of A. tenebrosa are simple or slightly compound, and contain only atrichous nematocysts (Carlgren 1950a). Bigger (1976) considers these atrichs should be described as holotrichous isorhizas (holotrichs) following the terminology of Mariscal (1974). The spherules of Actinia are usually hidden in the deep fosse of the oral disc (Carlgren 1924, 1949; Parry 1951), they number about 24 in adults and they are conspicuous when inflated (Figure 15). The colour is consistent for any particular

FIGURE 15: _Actinia tenebrosa_ showing uncovered, expanded acrorhagi. These number about 24 in total, and are usually hidden in the deep fosse of the oral disc.



anemone, but may be white, pink or most commonly lavender blue. Of more than 7,300 brooded juveniles dissected from adults, only a few of the very largest, those greater than 12 mm CD and with almost 50 tentacles, possessed acrorhagi. These spherules were poorly developed and numbered fewer than five. From my field observations it seems that acrorhagi normally develop after a juvenile has been free-living for at least several months and has grown to more than 10 mm CD. All examined specimens greater than 15 mm CD possessed well-developed acrorhagi.

3.6 LABORATORY OBSERVATIONS OF AGGRESSION

Methods

The collection of specimens and the general conditions for keeping Actinia in the Edward Percival Marine Laboratory have been described previously (Ottaway & Thomas 1971; Ottaway 1975b). Adult specimens were collected from different locations within the study area, brought to the laboratory, and allowed to attach individually to small stones kept in running-seawater aquaria. Once the animals were attached and expanded, they were brought together in pairs as described by Bonnin (1964) and Francis (1973a), until some tentacles of one contacted tentacles of the other (Figure 16A).

Results

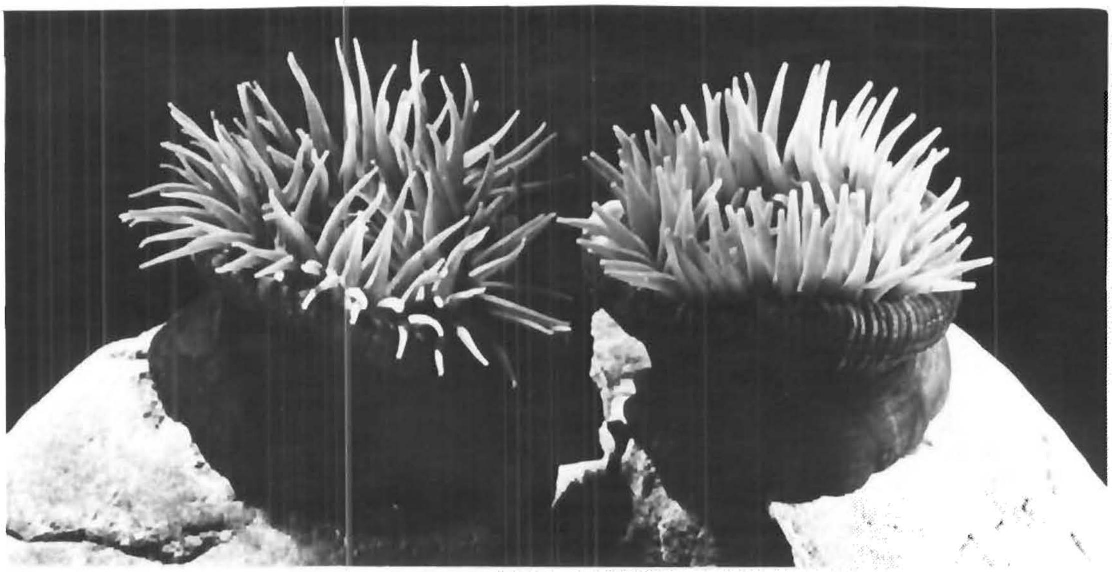
Adults brought together responded to the initial two or three contacts by a rapid and almost complete withdrawal of all tentacles. By about the fourth contact, *"l'un devient l'agresseur, l'autre sa victime"*, as observed by Bonnin (1964) for Actinia equina. The aggressing anemone inflated acrorhagi on the side of tentacle contact with the other (Figure 16C), swept downwards with tentacles retracted, acrorhagi inflated, but only the margin of the oral disc making contact with the column of the other anemone (Figure 17A), and then swept upwards to force

FIGURE 16: Intraspecific aggression in Actinia tenebrosa.

A. Two anemones are placed together so that their tentacles touch. Acrorhagi are deflated and covered by the margins of their oral discs.

B. After several tentacle contacts, one anemone (right) commences to uncover and inflate acrorhagi, while the other withdraws its tentacles.

C. The aggressive anemone fully inflates acrorhagi near the site of tentacle contact with the other, and then "leans" in that direction.



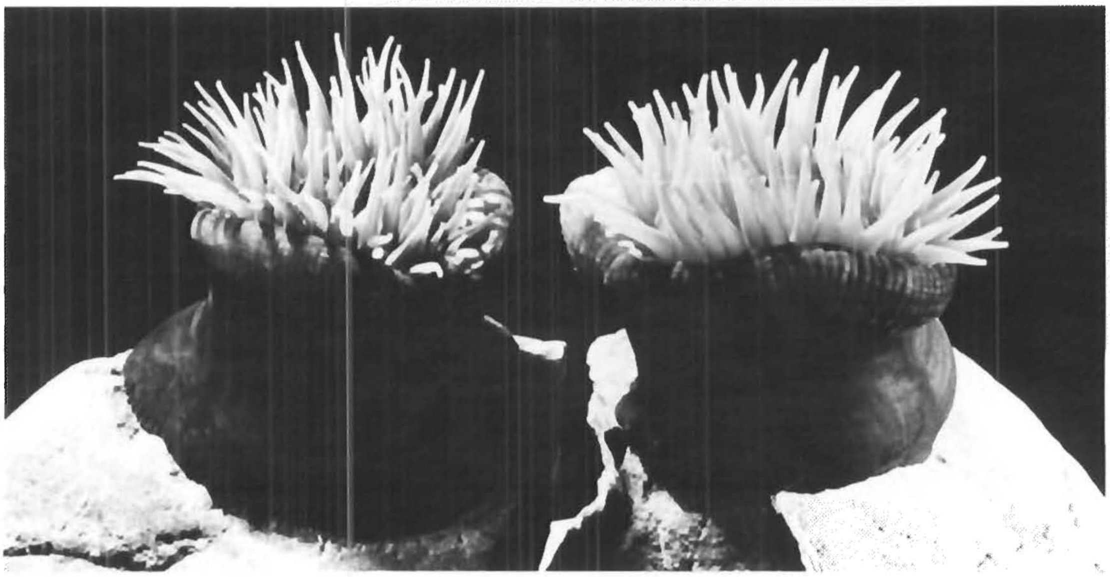
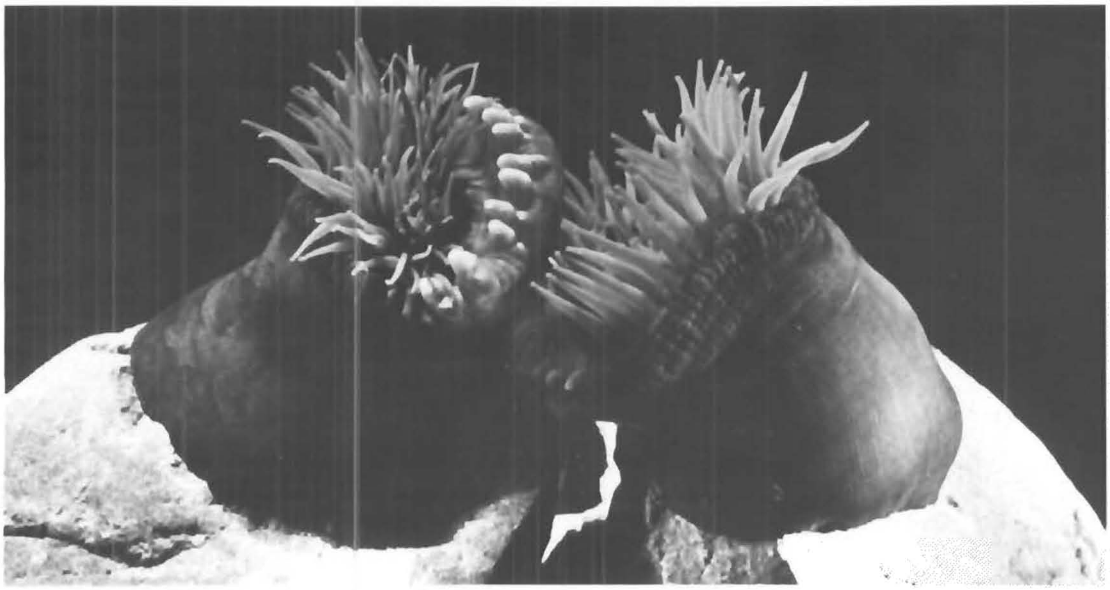


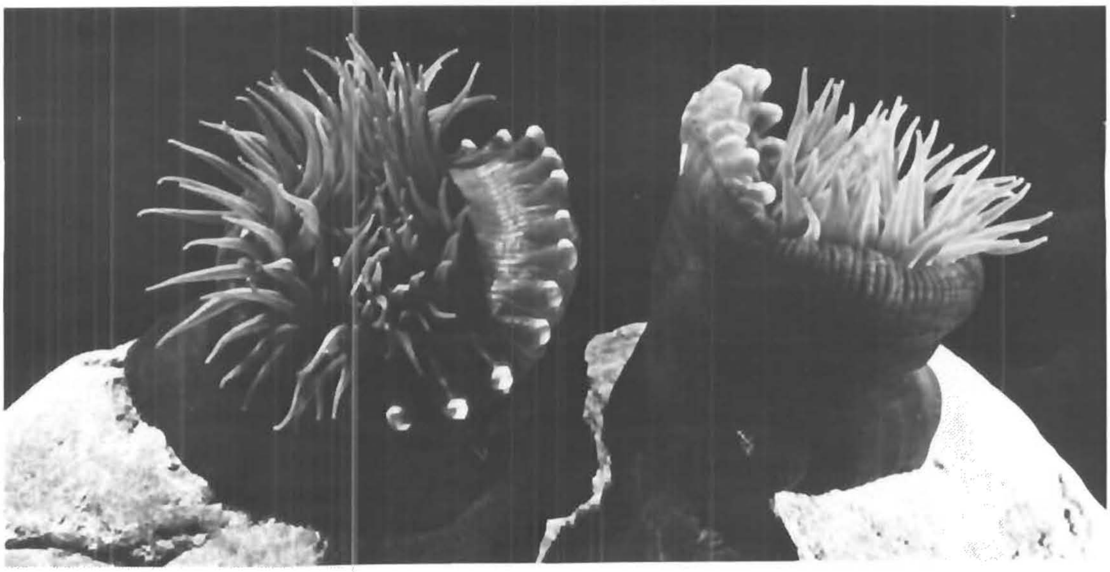
FIGURE 17: Intraspecific aggression in *Actinia tenebrosa*.

A. The aggressive anemone sweeps downwards, but the inflated acrorhagi do not contact the column of the victim (left).

B. On the upward, return motion, the aggressor's acrorhagi are dragged along the column of the victim, and acrorhagial ectoderm remains attached to the victim's column.

C. The aggressor then pulls away, partially deflating acrorhagi. In this instance, the victim then also showed an "acrorhagial response"; however, this was unsuccessful, as the aggressor (right) was leaning too far away to be contacted.





the inflated acrorhagi onto the column of the victim (Figure 17B). It seems likely that, at this point, acrorhagial nematocysts are fired into the victim's ectoderm as described by Bonnin (1964), because acrorhagial ectoderm is released from the aggressor to remain firmly attached to the column of the victim (Figure 18), as for A. equina. Then, "*In der Regel rücken beide Tiere voneinander ab, eines von ihnen* (almost invariably the victim in my observations on A. tenebrosa) *meist in besonders augenfälliger Weise*" (Abel 1954). The time between initial inflation of acrorhagi to deflation at the end of the sequence described, after which the anemones separated, was 2-5 minutes. The victim's column contracted around the immediate area of the wounds and stayed in that condition for 5-10 days while the foreign acrorhagial tissue was evident.

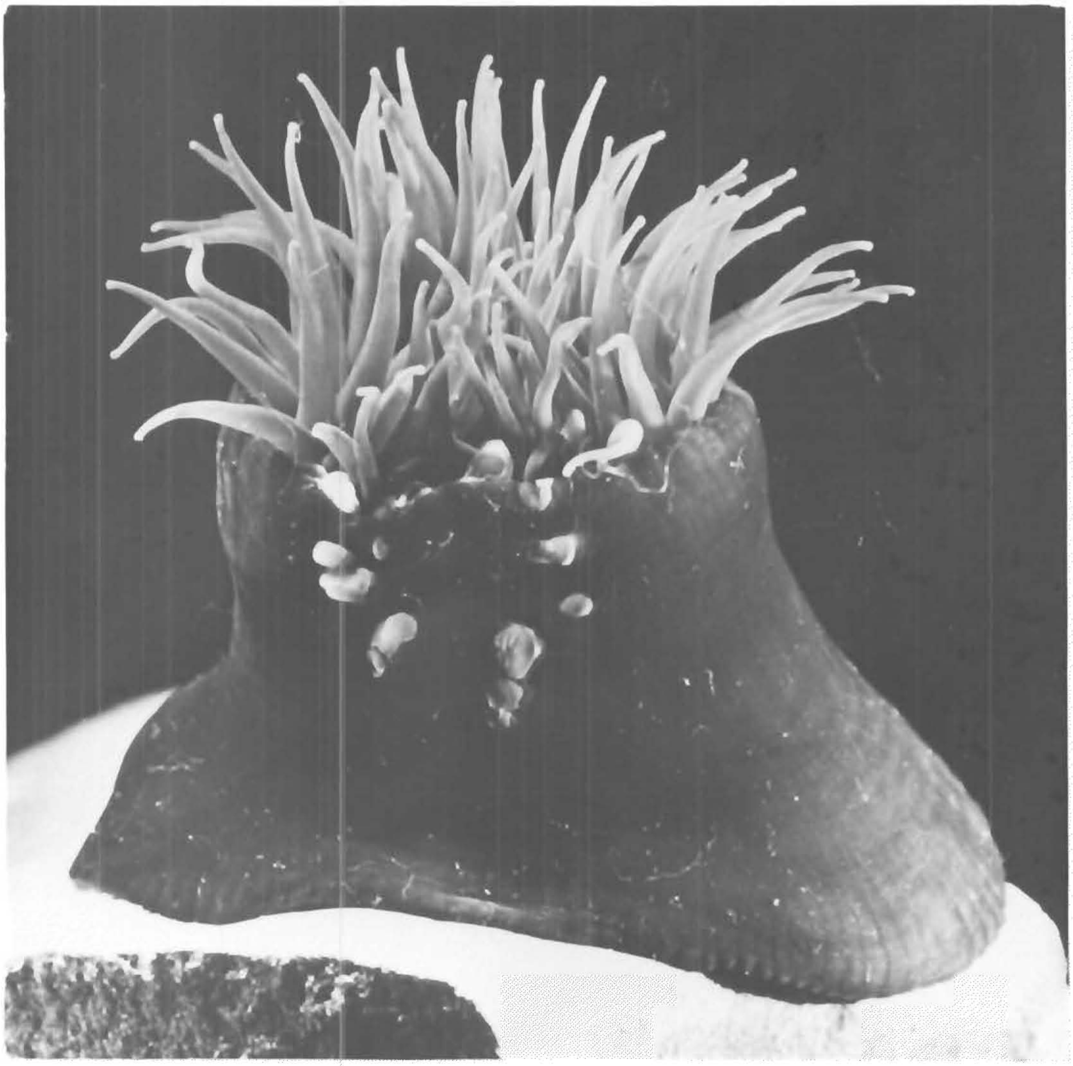
Localised ectodermal necrosis usually occurred after several hours and mesenterial filaments sometimes extruded through small ruptures that formed at the sites of particularly severe column wounds. Locomotion of the anemones was somewhat restricted, because the rocks used in these experiments were quite small, but movements of 100 mm within 2 h of wounding were not uncommon. Victims always moved directly away from the side of the attack.

3.7 FIELD OBSERVATIONS OF AGGRESSION

Methods

Location and identification of Actinia on Colony #1 were discussed previously (Section 3.2). The presence of acrorhagial wounds on a particular anemone was evidence that an aggressive conflict had taken place within the prior 10 days, and because of the frequency of my observations the time of the fight could be estimated to within a few days. Furthermore, the placement of the wounds on the victim indicated the location of the aggressor. No aggressive conflicts were seen

FIGURE 18: *Actinia tenebrosa* showing acrorhagial wounds on its column, as a result of intraspecific aggression.



actually in progress in the field, but these are of very short duration and the anemones were observed at low tides when their tentacles are retracted and covered by the margin of the column.

Results

Fifty-four adult/adult conflicts were recorded, involving 36 of the 82 adults present (44%). Two Actinia only were always involved in each fight, a few adults were involved in as many as 6 fights (Table 6) with 3 other adults (Table 7), but 70% of protagonists were involved in only one fight during 2 y of observations. An adult that moved into contact with another was usually the only one of the two wounded, and wounded anemones always moved away from the point of the fight.

The mean number of acrorhagial scars per wounded anemone was 3.7 (range 1 - 9), and wounds were obvious for 5 - 10 days, as in the laboratory experiments. There was one adult/subadult fight recorded, in which both anemones were wounded, and four adult/juvenile fights. Three of the juveniles recovered from their wounds; the fourth died several days after 7 acrorhagial wounds, covering 50% of its column, had been inflicted. Not all intraspecific contacts led to aggression: some adults were in close contact with 1 - 3 others for 2 y without showing evidence of either wounds or aggression (Figure 14). Other individuals, however, repeatedly fought and separated whenever they came into contact: adult 215, for example, moved into contact with adult 216 on six occasions between 4 August 1974 and 24 January 1975, and in each instance adult 215 was wounded and moved away.

3.8 DISCUSSION

In the past it has been found difficult to identify and track individual actinians, and, probably as a consequence, there have been few published observations on pedal locomotion of wild anemones. The

TABLE 7: Number of successful attacks directed to, and received from, other Actinia on Colony #1 in 2 y of observations.

		Observed number of successful attacks directed to other adults (n = 51*)						
		0	1	2	3	4	5	6
Observed number of successful attacks received (n = 54*)	0	-	9			1		
	1	6	5	2	1			
	2	2	3					
	3	1	1	1	1		1	1
	4							
	5							
	6			1	1			

* three Actinia were wounded by an undetermined aggressor.

TABLE 8: Frequency of aggression and victimisation recorded on Colony #1.

		Number of other adults to which attacks were directed			
		0	1	2	3
Number of other adults from which attacks were received	0	46	7		
	1	9	13	1	1
	2	2	1		
	3		1	1	

most detailed study to date is that of Dunn (1977b), who followed 40 adult *Epiactis prolifera* for up to 11 weeks. Much of the movement by *E. prolifera* was apparently random, and the net distance travelled was less than 36% of the gross distance. *Anthopleura elegantissima* has been seen to move under natural conditions (Ford 1964; Dayton 1971), and so has *Actinia tenebrosa* (Guiler 1950, 1954; Ottaway & Thomas 1971). Though the previous field observations on *A. tenebrosa* were rather superficial, they are consistent with the present work and suggested, to borrow words from Dalyell (1848, p.201), that *A. tenebrosa* "is endowed with a very slow locomotive facility, rarely exercised".

Pedal locomotion was not common in the observed population: most juveniles died without moving from the point of settlement and some *Actinia*, of all sizes, were present for 2 y without showing perceptible locomotion. Even considering only those anemones which survived for a minimum of several months, a higher proportion of adults moved than did juveniles, and adults moved further in terms of both absolute distances and relative distances (absolute distance travelled/ pedal disc diameter). Many of the movements recorded were small, apparently random, and over long periods often left an anemone close to the location where it was first observed. Such movements seem to be analogous to the "slight inherent activity which continues even in the absence of environmental gradients", which have been observed for *A. tenebrosa* (Ottaway & Thomas 1971) and *Metridium senile* (Batham & Pantin 1950a,b,c) in experimental situations. Unfortunately, few causes were observed to account for the larger, directed movements also recorded in the field. Where causal factors were ascribed, they were consistent with Pantin's (1965) hypothesis that, in coelenterates, particular and sometimes complex motor responses are usually evoked by simple, single, key stimuli. In the present instance, directed pedal locomotion was apparently initiated as an escape response from prolonged physical shocks, sources of physical injury, interference from molluscs, or repeated desiccation. Shorter intermittent moves, apparently in response to more subtle environmental factors, almost invariably followed a large initial move, until the anemone settled down into a suitable nook or crack in the rock surface.

Mackie (1974) reviewed locomotion in actinians, and proposed four classes: escape locomotion, locomotion in relation to sex, locomotion related to feeding, and locomotion related to substrate selection. All moves observed in the present study, that were related to environmental factors, could be classed as escape locomotion. It is not known whether the short, intermittent moves were directed towards location of a suitable microenvironment, though this seemed to be the end result, or away from unsuitable microenvironments. Since actinians do not have well-developed exteroceptive senses (Pantin 1965), the latter explanation seems more likely.

Intraspecific aggression was rare in *A. tenebrosa* and rarely initiated pedal locomotion, but it always modified the direction and rate of motion of at least one of the protagonists. Victims moved rapidly and directly away from the aggressor, and because of the nature of acrorhagial wounds this behaviour also fits with Pantin's (1965) hypothesis of key stimuli. Acrorhagial ectoderm from the aggressor remained attached to the victim, by nematocysts, for about 5 days, and during that time presumably would have been a source of prolonged irritation. In some instances, topographical features of the rock surface prevented a victim moving more than a few centimetres away from an aggressor; after the acrorhagial wounds healed victims sometimes repeatedly moved back into contact with aggressors, with the same results. There was no evidence that victims "learnt" to stay away from aggressors, in the sense of learning discussed by Ross (1964) and Robson (1964), or that healthy, adjacent anemones responded to any anthopleurine-like alarm pheromones (Howe & Sheik 1975) released by victims.

It is remarkable that the function of acrorhagi remained undiscovered until comparatively recently (Abel 1954), since the prominent acrorhagi of actinids were often noted (e.g. Johnston 1846; Milne-Edwards 1857; Farquhar 1898; Carlgren 1924; Stephenson 1928; Van Urk 1952). Gosse (1860, p. 180) actually described what can now be interpreted as the result of intraspecific aggression in _Actinia equina_: "Below these (acrorhagi of the oral disc), scattered down the side of the column, were four or five more blue worts; more irregular in form and shape, but still well defined, and perfectly similar in their azure hue to the spherules". The original observations on intraspecific aggression have now been extended, with further work on _Actinia equina_ (Bonnin 1964), _Anthopleura elegantissima_, _Anthopleura artemesia_ (Francis 1973a, b) and _Anthopleura krebsi_ (Bigger 1976).

The aggregations formed by _Anthopleura elegantissima_ may each contain several hundred or more anemones. Individual aggregations are largely the result of asexual reproduction (Hand 1955), and are regarded as clones (Ford 1964; Francis 1973a, b). Individuals within any particular clone (clonemates) are genetically identical, although there may be sexual and morphological differentiation (Francis 1976), but they do not fight amongst themselves. Individuals from different clones are genetically different, and react aggressively when they come into contact (Francis 1973a, b). This appears to be intraspecific competition for space, the latter being a resource limiting the spread of clonal aggregations. Such aggressive behaviour could increase the probability of survival and reproductive success of clonemates and their post-laryal progeny (Francis 1973b).

A similar argument could explain the observed behaviour of *A. tenebrosa*: adults which did not react aggressively on contact may be genetically similar, while those that did react may be genetically dissimilar. In contrast to *Anthopleura elegantissima* (Francis 1976), however, both aggressive and non-aggressive adult *A. tenebrosa* have similar numbers of acrorhagi and seem to reproduce equally well (Chapter 2).

Brooded *A. tenebrosa* appear to have identical genotypes to the brooding adult (Ottaway & Kirby 1975) and the juveniles are released ready for immediate attachment (Ottaway & Thomas 1971). Once released many of the juveniles that successfully settle and attach may do so within a few millimetres of their nurse adult (Chapter 4). While space *per se* did not appear to be a limiting resource for the observed populations of *A. tenebrosa*, suitable settling sites for juveniles probably are quite scarce (Ottaway 1973). Thus, in addition to maintaining themselves between general vertical limits which are suitable for the survival of settling juveniles (Ottaway & Thomas 1971), and moving away from adverse stimuli, it is suggested that adults may also respond to more subtle factors to actively maintain position in a favourable microhabitat. The aggressive behaviour described, in which *Actinia* of putatively dissimilar genotypes actively repel each other on contact, may effectively establish and maintain space onto which progeny are likely to settle, with increased prospects for survival, may also avoid unnecessary competition for food (Meadows and Campbell 1972a), and yet may still allow the adults to remain close enough to facilitate breeding (Chapter 2).

CHAPTER FOUR

POPULATION DYNAMICS AND ENVIRONMENTAL FACTORS

4.1 INTRODUCTION

The first published observations on actinian population dynamics recorded that three species in a particular area "considerably suffered" when parts of a cliff fell down on them (Dicquemare 1777). With two exceptions (Fager 1968; Dayton 1971), subsequent reports have given few details other than that the sizes of observed populations changed between two points in time (e.g. Fleure & Walton 1907; Stock 1951; Van Urk 1952; Den Hartog 1954, 1961; Crisp 1964; Crisp *et al* 1964; Moyse & Nelson-Smith 1964).

In this chapter, fluctuations in the size of the population of *Actinia tenebrosa* on Colony #1, over 3 y, are described. The "emersion factors" of temperature and desiccation (Lewis 1964) are examined in detail, since these are thought to be important determinants of the intertidal distribution of *Actinia* (Van Urk 1952, 1953; Den Hartog 1961; Ottaway 1973), and an attempt is made to relate the observed population changes to physical and biological factors of the environment.

4.2 MATERIALS AND METHODS

Censuses

The method of identifying and tracking individual *Actinia* has been described (Chapter 3.2). In addition to the area occupied by the Colony #1 adults (about 5 m^2), all surrounding areas below high water of spring tides, for a radius of over 12 m (an additional area of about 120 m^2), were searched for the presence of juveniles. Complete censuses were taken at about 4 - 5 day intervals between November 1973 and March

1975, approximately once per calendar month between March 1975 and December 1975, and then again on 19 December 1976. All *Actinia* present were measured approximately once per calendar month between November 1973 and December 1975 (Figure 19). Measurements were of maximum and minimum column diameter just above the pedal disc; they were taken with calipers to the nearest 0.5 mm and were averaged to give a single value for that individual at that census.

Newly-settled juveniles are pale pink, and for about 3 weeks are distinct from older, darker juveniles. After the initial sighting, all anemones were individually followed until they disappeared from the area (Chapter 3.2). Notes were kept on whether the anemones were wounded, desiccated, or otherwise appearing unhealthy, and whether they were being interfered with by other organisms. In some instances, interference was not seen but could be reasonably inferred; for example, fresh radula marks indicated recent movements of grazing molluscs.

Macroclimate records

Total rainfall and total sunshine data were obtained from daily records taken at the Kaikoura Meteorological Station (N.Z. Meteorological Service), 10.5 km NE of the study area. The rainfall data is probably a good indication of rainfall at the study area. The sunshine data, and my *in situ* observations on shading effects of the nearby hills (Chapter 1), were used to calculate approximate total sunshine on the study area. Over 200 visits were made to the study area for various purposes, during which such observations as sea conditions and shingle movements were routinely noted.

Microclimate records

About 1050 h of temperature data (over 5000 probe-hours) and 349 h of relative humidity (RH) data were accumulated and analysed. Temperatures were recorded during most weather conditions experienced at Kaikoura. Relative humidities were taken only at low tides near the actual rock surface inhabited by the adults of Colony #1, not during heavy rain, and most often during daylight hours in warm or dry weather. No measurements were taken during phenomenally heavy rainfalls or during a hurricane that occurred in the periods of observations. Instruments were routinely checked against those in use at the Kaikoura Meteorological Station, and discrepancies between instruments were within those given by manufacturer's specifications.

Three instruments were used:

a. A Grant Model D Miniature Temperature Recorder (Grant Instruments, Cambridge, England), with 8 bead thermistor probes, was used to measure water and surface temperatures in the range -5° to 45° C ($\pm 0.5^{\circ}$ C). Records were taken from each probe once every 15 minutes, for the periods 1200 h 31 October 1973 - 1200 h 14 November 1973 (NZST), and 1900 h 4 December 1973 - 1900 h 20 December 1973. Probes were placed on the ectoderms of adult *Actinia* and on immediately adjacent bare rock surfaces at the lower and upper limits of the anemones' range, in the middle of the range, in the sea 1.2 m below low water of spring tides, and on an exposed rock in the upper "splash zone".

b. A Zeal Zeatron GPE Thermistor Unit (G.H. Zeal, London, England) with 6 needle and disc thermistor probes, was used for spot measurements of temperatures in the range -10° to 50° C ($\pm 0.5^{\circ}$ C).

c. A Wallac-Oy EP-400 Thermohygrometer (Wallac-Oy, Turku, Finland) was used for spot measurements of RH in the range 15% to 90% ($\pm 2\%$) and air temperatures in the range -20° to 40° C ($\pm 0.6^{\circ}$ C). Most readings were taken near shaded adult *Actinia* towards the upper limit of the anemones, at 5 minute intervals, on 106 low tides during the period 2 November 1973 - 12 November 1974.

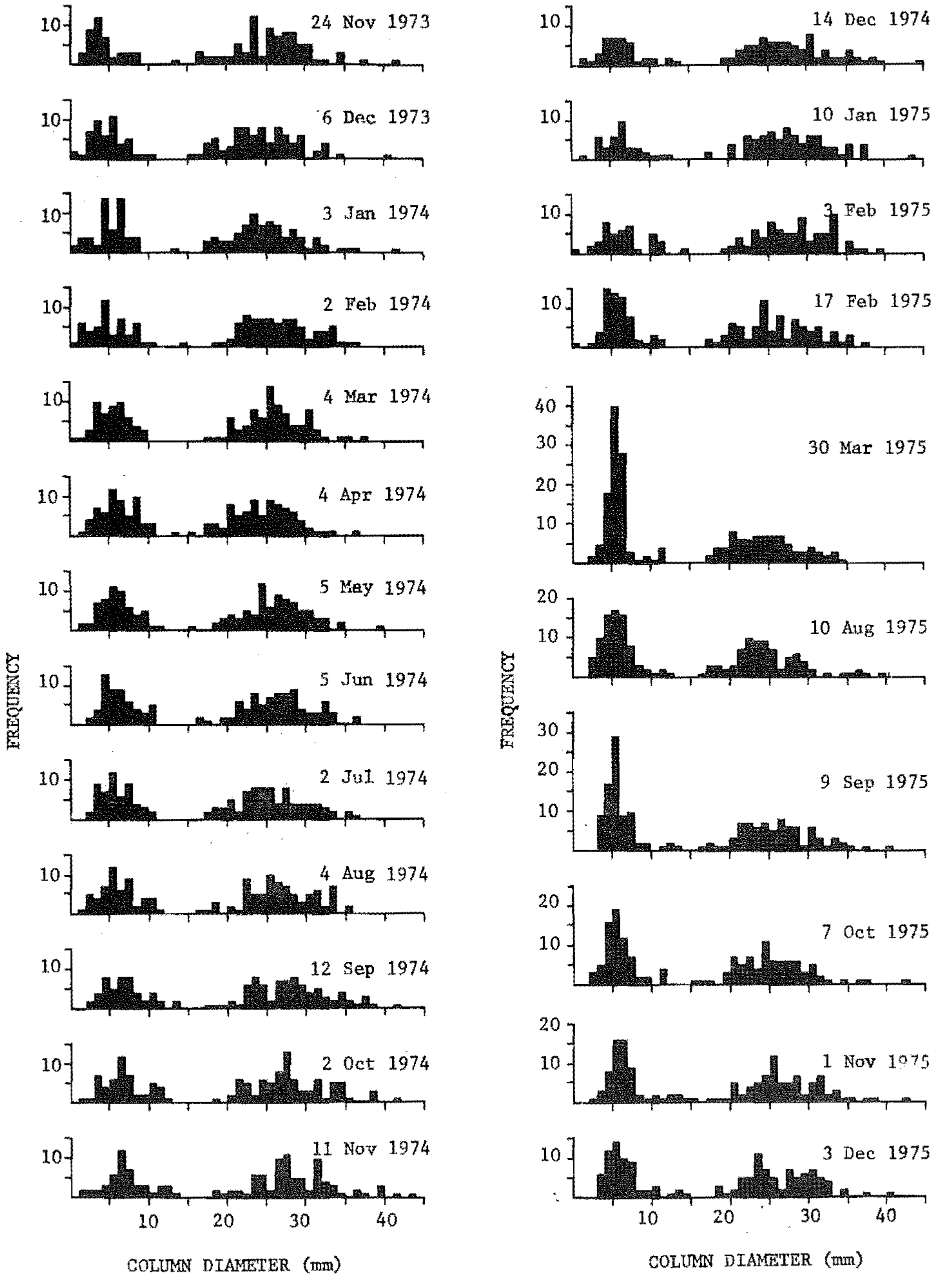
4.3 POPULATION DYNAMICS

The area occupied by the Colony #1 adults was mainly sheltered from direct sun, wind and wave action (Chapter 1). Above and to both sides of the Colony were solid, bare rock faces, on which physical extremes regularly occurred at low tides as a consequence of exposure to the prevailing weather. Downward movement of the anemones was restricted by the solid rock floor of a shallow, permanent, intertidal pool, although the lower limit of the Colony adults was 0.3 m above this, and above the water level in the pool at low tides. Juveniles occasionally settled away from the Colony face, but no immigration or emigration by pedal locomotion was observed. Such movements would certainly have been detected had they occurred (Chapter 3). Absence of an individual was taken to indicate mortality, and for the purposes of this Chapter the two terms will be used synonymously. Recruitment of juveniles from other sources than the Colony adults was possible, but rather improbable (discussed below), since the Colony was about 1 km distant from the nearest other groups of breeding _Actinia_. Thus, the Colony will be considered as an isolated, discrete breeding population, with no immigration and no effective emigration.

Population size structure

Measured individuals were in the size range 0.5 - 44.5 mm CD. In all censuses, two major size groups were evident (Figure 19): _Actinia_ less than 15 mm CD ("juveniles") and those greater than 15 mm CD ("adults"). Juveniles were usually 2 - 11 mm CD and adults were usually 17 - 36 mm CD. Individuals normally showed daily fluctuations in CD which, to a large extent, were a result of the tide-related semidiurnal expansion and contraction cycle. To minimise the effects of these fluctuations, anemones were always measured at low tide when all tentacles were fully retracted and covered; nevertheless, such

FIGURE 19: Population size structure of _Actinia tenebrosa_ on Colony #1, between November 1973 and December 1975. In each census, most _Actinia_ less than 15 mm CD were newly-settled juveniles. Only five of 48 juveniles (10%) present in November 1973 survived 1 y. There was little change in the population of anemones larger than 15 mm CD: of 82 originally present, 78 (95%) survived over 2 y, and 77 (94%) survived over 3 y.


FREQUENCY
10
24 Nov 1973
6 Dec 1973
3 Jan 1974
2 Feb 1974
4 Mar 1974
4 Apr 1974
5 May 1974
5 Jun 1974
2 Jul 1974
4 Aug 1974
12 Sep 1974
2 Oct 1974
11 Nov 1974
10
20
30
40
COLUMN DIAMETER (mm)
FREQUENCY
14 Dec 1974
10 Jan 1975
3 Feb 1975
17 Feb 1975
30 Mar 1975
10 Aug 1975
9 Sep 1975
7 Oct 1975
1 Nov 1975
3 Dec 1975
COLUMN DIAMETER (mm)

fluctuations still amounted to almost ±15% of the mean CD, over a period of a month. Greater fluctuations were rarely observed. Excluding those associated with growth, they followed such events as extreme desiccation or physical injury, and were negative.

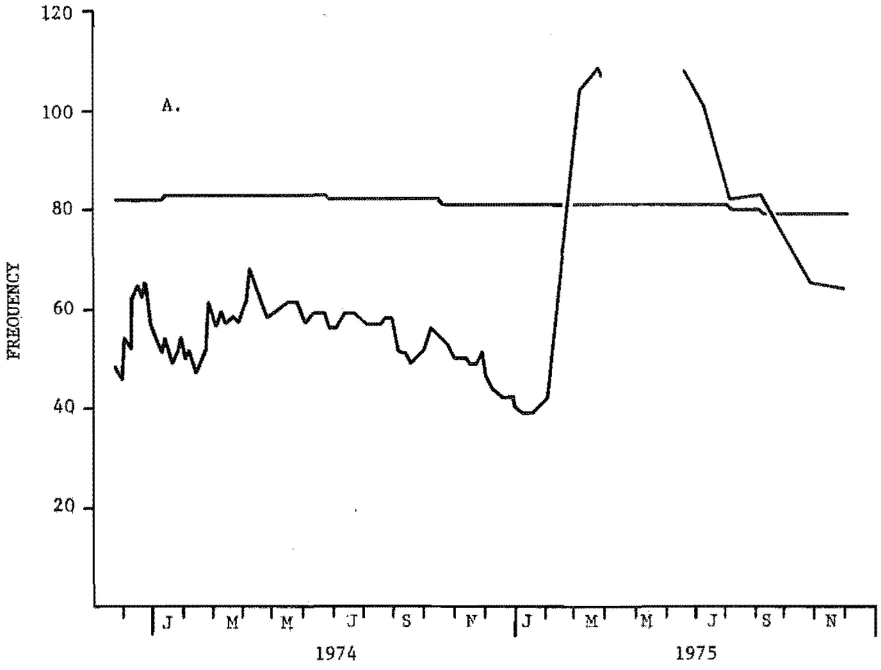
The mean size of adults was 26.5 mm CD; the mean size of all juveniles was 6.0 mm CD. From census to census, and also seasonally, the mean CD of the adult and juvenile populations varied, in the ranges 24.6 - 28.6 mm and 4.3 - 7.1 mm respectively. The mean size of the juvenile population was largely influenced by the size of newly-settled individuals, since most juveniles present at any particular time were less than 2 months old (Chapter 5). By contrast, 95% of the adults first seen in November 1973 were still present in December 1975. Mean size fluctuations in the adult population appeared to be related to reproductive cycle (Chapter 2). Adults reached maximum mean size about the time that gonads were fully developed, and reached minimum mean size several months later, after spawning. The seasonal increase in mean size of adults probably reflects an actual increase in biomass of tissue, which is lost during spawning and release of brooded juveniles, rather than just an increase in volume of coelenteric fluid. Biomass analyses were not undertaken to confirm this.

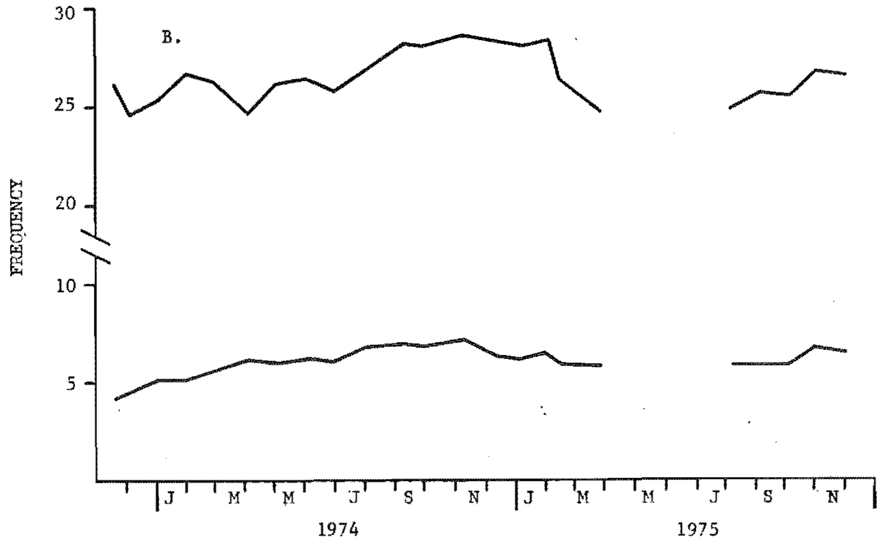
The division of the total population into two groups at 15 mm CD is arbitrary, and some of the smaller "adults" may well have never developed gonads. The anemones were disturbed minimally in order to avoid modifying their natural behaviour and rates of mortality. It was impossible to assess the gonad state of intact anemones (Chapter 2). The juvenile group was also heterogeneous, including pink, newly-settled juveniles (0.5 - 12 mm CD) without acrorhagi, darker, red, "old" juveniles (3 - 12 mm CD) without acrorhagi, and large "old" juveniles (11 - 15 mm CD) with acrorhagi. This last group should properly be

FIGURE 20: Summary of population changes on Colony #1, between November 1973 and December 1975 inclusive. Complete censuses were not taken between April 1975 and June 1975.

A. Fluctuations in the numbers of adults (upper line) and juveniles (lower line) present.

B. Fluctuations in the mean sizes of adults (upper line) and juveniles (lower line) present.


A.
FREQUENCY
120
100
80
60
40
20
J
M
M
J
S
N
J
M
M
J
S
N
1974
1975


B.
FREQUENCY
30
25
20
10
5
J
M
M
J
S
N
J
M
M
J
S
N
1974
1975

included with small non-breeding adults, as subadults; however, the one division into juveniles and adults was found to be most practical.

Settlement and mortalities

The adult population remained quite stable over the 3 y of observations. Eighty-two adults were present in November 1973, by January 1974 one juvenile had grown to the extent that it was classified as adult, 2 adults died in 1974 and 2 died in 1975 (Figure 20). In 1976, one adult died and two juveniles grew to adult size. Over 3 y the net change in the adult population was therefore a decrease of 2 (-2.4%). In total, 409 newly-settled juveniles were observed, with a mean size of 5.5 mm CD (Figure 21). The mean settlement rate was 3.0 juveniles/adult/year for 1973 - 1974, and 1.9 juveniles/adult/year for 1974 - 1975. The latter figure is probably low, because censuses were made only monthly after March 1975. Both figures do not take into account juveniles settling further than 12 m from the Colony.

Fecundity of *Actinia*, as determined from the dissection of preserved specimens, was discussed previously (Chapter 2). From time to time, juveniles could be seen and counted through the column walls of brooding adults: 72% of the adults were recorded brooding juveniles in at least one season and 39% were seen brooding in two seasons. The mean size of brooded juveniles, estimated while they were within the adults, appeared to increase at about 1 mm/month. The greatest number of juveniles seen in one adult on one occasion was 60, with a size range of 0.5 - 2.5 mm CD. Since all juveniles brooded by a particular adult are unlikely to be seen at one time, or even *at all* while brooded, the maximum number of juveniles seen on any one occasion during a breeding season, in any one adult, can be used as a *minimum* estimate for the number of juveniles brooded and presumably released by that adult in that season. Summing all such minimum estimates, at least 1085 tentaculate young were brooded in 2 y by the adults of Colony #1 (mean: 6.8 juveniles/adult/year). This agrees well with the minimum estimate, of 1141 juveniles (7.2 juveniles/adult/year) from dissections of adult Actinia collected elsewhere during those years (Chapter 2). The proportion of initially successful settlements in the area searched was therefore, at most, 38% (409/1085), and was probably considerably less.

The juvenile population fluctuated in the range 39 - 108 (Figure 20A), but over 2 y there was a net increase of 16, a 33% increase on the number of juveniles originally present. Forty-eight juveniles were originally present, on 24 November 1973, and 16 others settled in that month. Of these, five (8%) survived for 2 y. At the beginning of December 1973, 1974 and 1975 there were, respectively, 53, 47 and 64 juveniles present. In the 1973 - 1974 season, most juveniles settled during November to April inclusive; in the 1974 - 1975 season the main peak of settlement started in February (Table 9). It was not determined whether release of juveniles is stimulated by particular environmental cues, but, as discussed before, there was also a marked difference in gonad development and offspring production in those two seasons (Chapter 2). Monthly mean sizes of settling juveniles were in the range 3.9 - 8.5 mm CD, and during most months both quite small and quite large juveniles were found newly-settled (Table 9). The absolute size range was 0.5 - 13.3 mm CD.

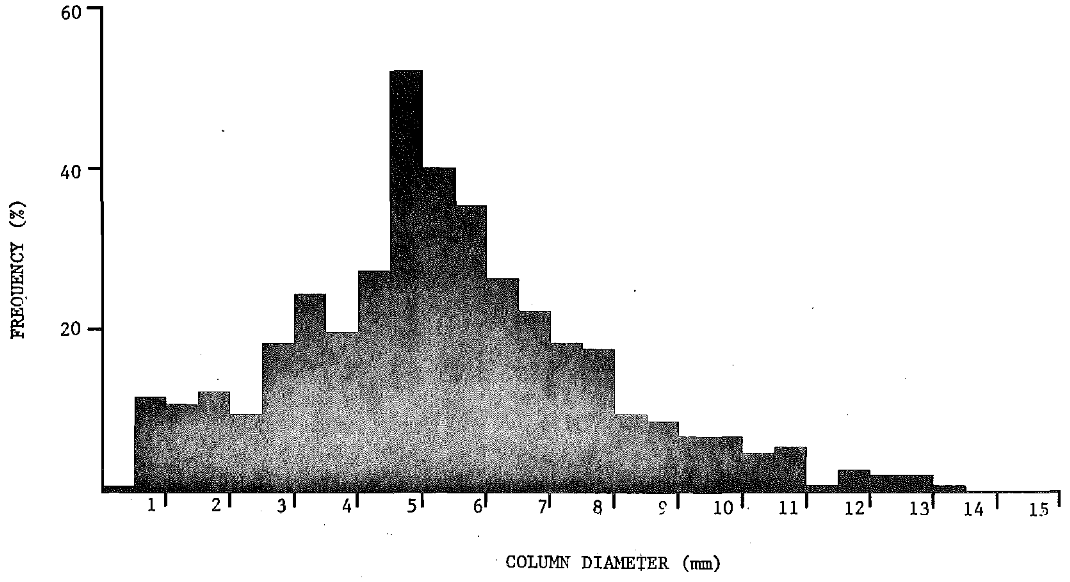
Newly released juveniles appear to be ready for immediate attachment to any hard surface they first contact (Ottaway & Thomas 1971). Juveniles usually settled on bare rock, though occasionally on the shells of gastropods and even algae. Over 60% of juveniles settled within 50 mm of some adult, which was probably their brooder

TABLE 9: Number and size of juveniles settling per month on Colony #1 during the period of intensive observations, 24 November 1973 - 30 March 1975.

Month		Number settling	Column diameters (mm)	
			mean	range
1973	November	30	4.55	1.25 - 12.00
	December	65	5.31	1.00 - 12.00
1974	January	28	3.91	0.75 - 10.00
	February	33	5.11	0.50 - 10.50
	March	20	5.69	1.00 - 10.25
	April	25	6.81	3.00 - 10.75
	May	9	4.77	1.25 - 7.00
	June	9	6.08	1.50 - 11.00
	July	4	6.94	5.50 - 8.00
	August	1	(3.50)	
	September	7	8.43	5.00 - 12.50
	October	10	8.45	3.00 - 13.00
	November	5	7.15	3.00 - 11.00
	December	4	7.06	3.50 - 13.25
1975	January	4	5.31	3.25 - 8.25
	February	49	5.39	1.00 - 11.00
	March	51	5.34	1.00 - 9.25

(November 1973 - October 1974 inclusive: 81.6 adults (mean), 241 newly-settled juveniles; November 1974 - October 1975 inclusive: 79.6 adults (mean), 148 newly-settled juveniles; 2-year average = 2.4 NS juveniles/adult/year.)

FIGURE 21: Size frequency distribution of juveniles (n = 409) settling on Colony #1, between November 1973 and December 1975 inclusive.


60
40
20
FREQUENCY (%)
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
COLUMN DIAMETER (mm)

since it was common to find 2 - 5 juveniles, of similar size, settling about the same time in a tight group near the pedal disc of an adult. Over 95% of observed juveniles settled within 0.5 m of adults, that is, within the 5 m^2 defining the Colony. A surrounding area of about 120 m^2 was regularly searched, but few further juveniles were found. About 4% of juveniles settled 0.5 - 5 m away from the nearest adult, and less than 1% were found on rock surfaces 5 - 12 m distant. Juveniles found settled away from the Colony survived only several months at most, and much more commonly only a few days.

Similar results were seen on Colony #3. The Colony occupied an area of about 15 m^2 on a solid, stable rock outcrop, surrounded by a semi-stable boulder beach supporting a large population of breeding Actinia (Chapter 1). Some 110 adults were originally present on Colony #3, and for several months while these were observed the rate of settlement was 5 - 15 juveniles per week. In 14 months following removal of all the adults, only 13 juveniles settled naturally on the Colony, even though 650 adult Actinia were still present within 15 m of it. Again, this suggests that, on stable rock outcrops, most initially successful attachments occur quite close to the brooding adult.

On Colony #1, juvenile mortality was highest during summer, especially if this coincided with the main period of juvenile settlement for that particular breeding season, but some juvenile mortality occurred throughout the year (Figure 22B). Most juveniles died within 20 days of settlement. This will be discussed in detail below and in Chapter 5.

4.4 ENVIRONMENTAL FACTORS AND CAUSES OF MORTALITY

The physical environment of A. tenebrosa has been briefly discussed before (Ottaway 1973), but there is still a paucity of data concerning climatic extremes experienced by *Actinia* and other intertidal invertebrates in their microhabitats (Lewis 1964; Wolcott 1973). It is usually assumed that intertidal marine invertebrates are in favourable environments when covered by the sea, and are exposed to potentially unfavourable environments when uncovered (e.g. Lewis 1974, p.26). This certainly seems to be true for *Actinia*. The anemones were relaxed, but still quite responsive to prodding, even in the midst of heavy rainfall and gales, when waves of almost 4 m height were breaking over the shore. They appear similarly unharmed by silt and other suspended particulate matter in the water. With rare exceptions, *Actinia* is found in positions sheltered from the direct force of waves, and, by criteria discussed elsewhere (Riedl 1971; Wilber 1971), they appear to be unharmed by the observed extremes of water turbulence and water turbidity *per se*.

This section therefore considers biological factors, gale-associated factors such as low salinities and wave-driven debris or rocks, and especially physical factors associated with emergence. The discussion and assessment of the relative importance of these various factors is largely qualitative and subjective, since most *Actinia* disappeared without any indication of a cause.

Macroclimate

The Kaikoura coast is under fairly direct influence from oceanic currents (Dix 1970), and salinities are normally very close to 35%. Inshore sea temperatures fluctuate in the approximate range 8.5 - 19° C (Ottaway 1976).

Conditions on rocky shores are unlikely to bear any close correlation to conditions measured at a Meteorological Station, nevertheless, the value of daily records from the latter should not be overlooked (Lewis 1964, p.32). The amount of bright sunshine and the

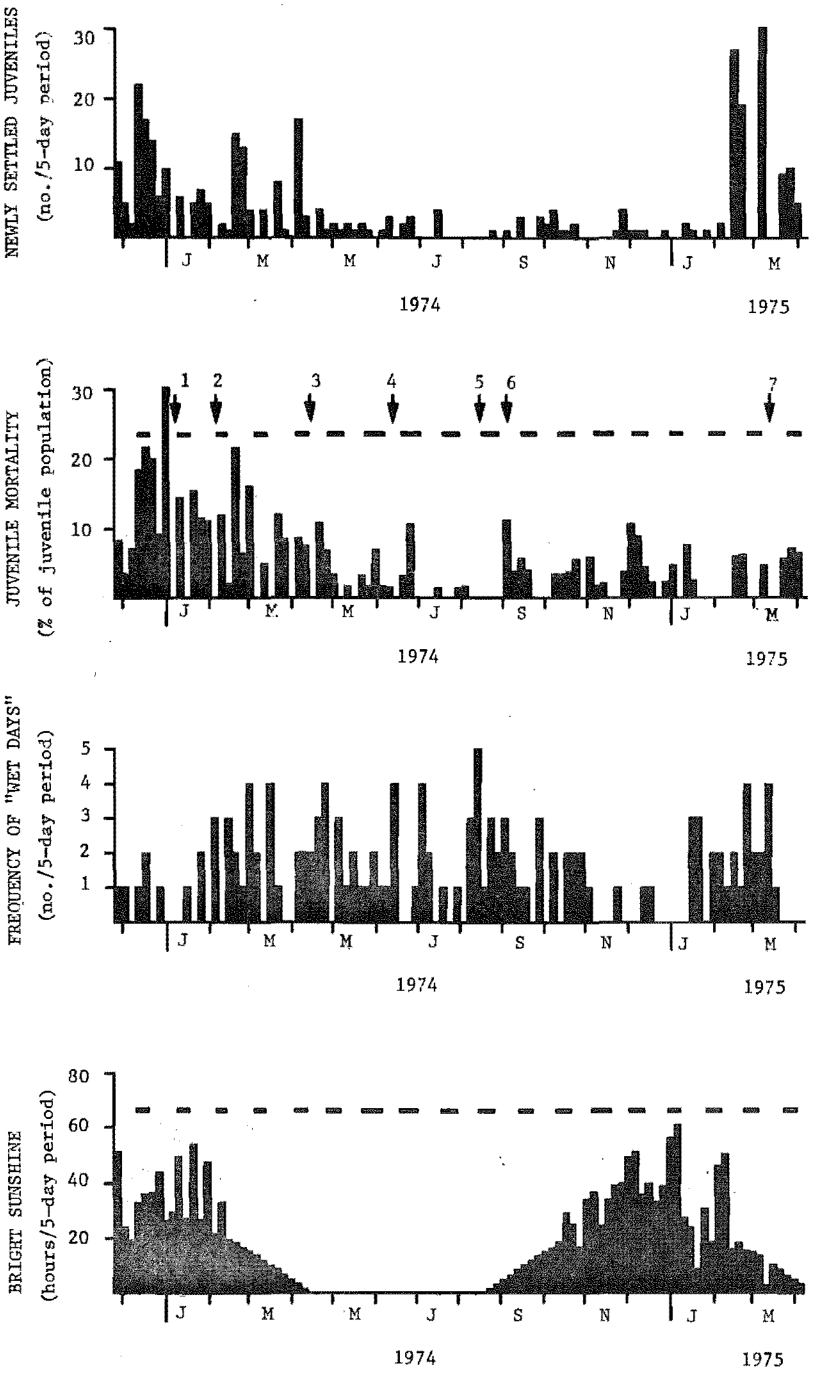
FIGURE 22: Settlement, juvenile mortalities, and macroclimate data for Colony #1, November 1973 to March 1975.

A. Number of newly-settled juveniles recorded per five day period.

B. Juvenile mortalities per five day period, as a percentage of the total number of juveniles present during that period. Occurrences of marked climatic disturbances are arrowed. Solid bars indicate predicted periods of low spring tides occurring during the day. 1: 8 January 1974. Mean R.H. of 37% for 3 h at low tide, mean temperature of 22.5° C (microenvironmental data), and a moderate breeze. 2: 9 February 1974. The hottest day recorded at Kaikoura. Calm air conditions, mean microenvironmental temperature of 25° C for 3 h, and mean R.H. of 64%. 3: 15 to 16 April 1974. 144 mm of rain in 2 days. 21 to 28 April. Moderate to strong gale force conditions, with windspeeds reaching 60 $km.h^{-1}$ and waves of up to 2.5 m height. 4: 15 to 18 June 1974. MOderate to strong gale force conditions, with waves of up to 3.5 m height breaking on the shore. 5: 18 to 19 August 1974. Moderate gale force conditions with waves of up to 3 m height. 22 to 28 August. Fresh to whole gale force conditions, with 68 mm of rain and waves of up to 4 m height breaking on the shore. 6: 2 to 4 September 1974. Strong breeze conditions, with 173 mm of rain and waves of 2 m height. Much forest debris, including floating logs, branches and leaf litter, covering the intertidal regions. 7: 12 March 1975. Moderate gale force conditions, with the heaviest rainfall recorded in one day at Kaikoura, of 205 mm.

C. Frequency of "wet" days (>1 mm rainfall per day) per five day period.

D. Hours of bright sunshine per five day period. Solid bars: as above.


NEWLY SETTLED JUVENILES
(no./5-day period)
30
20
10
J
M
M
J
S
N
J
M
1974
1975
JUVENILE MORTALITY
(% of juvenile population)
1
2
3
4
5
6
7
30
20
10
J
M
M
J
S
N
J
M
1974
1975
FREQUENCY OF "WET DAYS"
(no./5-day period)
5
4
3
2
1
J
M
M
J
S
N
J
M
1974
1975
BRIGHT SUNSHINE
(hours/5-day period)
80
60
40
20
J
M
M
J
S
N
J
M
1974
1975

number of "wet" days, or days on which more than 1 mm of rain was recorded, give a good indication of general conditions on the Kaikoura coast. For example, high temperatures and low relative humidities are unlikely to occur during rainy periods with little bright sunshine. Furthermore, almost 30 years of daily records at Kaikoura give an unequivocal statement of the abnormally severe weather which was experienced during 1973 - 1975.

In the summer, a maximum of 80 h per week of bright sunshine can be recorded at the study area, but the mean is about 47 h per week. For all but the summer months, the coast is shaded to some extent by nearby hills. Between mid-February and mid-October a maximum of less than about 30 h per week is possible; for May, June and July the study area is in continuous shade (Figure 22D). Although there is still some controversy on whether Actinia responds to light per se (Fleure and Walton 1907; Den Hartog 1961; Milia and Geppetti 1964; other literature reviewed by Ottaway 1973), there is still no evidence that A. tenebrosa shows immediate or seasonal responses to changing light levels.

The mean annual rainfall is about 865 mm, with most being recorded in late autumn and winter (Figure 22C). Three months, April 1974, September 1974, and March 1975, were all within 40 mm of the wettest month on record, with rainfalls of 271 mm, 258 mm and 264 mm respectively. The effects of five moderate to strong gales and one hurricane were observed. The heaviest rainfall ever recorded in Kaikoura occurred on 12 March 1975, and was 205 mm in one day, although particularly heavy rainfalls were recorded on 15 - 16 April 1974 (144 mm) and 3 - 4 September 1974 (155 mm). The highest windspeed recorded at Kaikoura, of almost 200 $km.h^{-1}$, occurred on 1 August 1975. The hottest day on record (discussed below in "Microclimate") was on 9 February 1974.

Two types of injury were seen after unsettled weather: impact wounds and damage resulting from the effects of prolonged exposure to water of low salinity. The former injuries occurred whenever logs and rocks were battered against the anemones by wave action; the latter injuries were only observed during the three periods of abnormally heavy rainfall, which were statistically extremely rare events at Kaikoura. Both types of injury are quite distinct from the acrorhagial wounds of intraspecific aggression (Chapter 3), damage resulting from attack by predatory invertebrates (Ottaway 1977b), or the symptoms of a single exposure to conditions of lethal desiccation (Ottaway 1973).

Typical symptoms of impact injuries were extreme generalised contraction, moderate to extreme multiple contusions, rupture of the column or oral disc, and extrusion of mesenterial filaments through ruptures or from the stomodaeum. Symptoms of prolonged exposure to fresh water were moderate generalised contraction, patches of white, necrotic ectoderm, and, if the areas of necrotic tissue included the base, partial detachment of the pedal disc.

Light to moderate rainfall, extreme water turbidity, and very rough sea conditions per se did not appear to harm anemones that had been attached and settled for some time before the event. Established Actinia were almost invariably in positions sheltered from the direct force of the waves, and the usual casualties were newly-settled juveniles that were either insecurely attached, and were washed away, or were in exposed positions that made them susceptible to impact injuries. From abrasion marks on the rock surfaces, and evident damage to juveniles present after storms, impact injuries appeared to be a major factor in gale-associated mortality of newly-settled juveniles. It is not known whether brooding adults released juveniles during turbulent seas: if they did, the juveniles would undoubtedly have been washed away without the opportunity to attach.

Impact injuries were probably responsible for a high proportion of the deaths amongst newly-settled juveniles in April 1974, June 1974 and March 1975. Few juveniles were observed to settle in July and August 1974 (Figure 22A), and it is probably significant that despite intermittent rain (Figure 22C) and moderate gale force conditions there was minimal juvenile mortality for those months. More damage to the anemones occurred during 2 - 4 September, however, than in any other single five day period. As a consequence of frequent intermittent rain and strong wind for most of August, exceptionally heavy rainfall and strong winds in early September 1974 washed a huge quantity of forest material down from the nearby hills. Most of the intertidal region of the entire study area was completely covered with logs, large branches and leaf litter. On 5 September, one adult was found to have disappeared during the preceding gale and seven adults were found to have impact injuries; of these, six eventually recovered. The seventh died on 15 October. Six juveniles (10% of the juvenile population) also disappeared during the storm and three juveniles were injured. Thus, in total, 12% of the Colony #1 population was either injured or killed by impact injuries during that one gale.

During the heavy rainfall of 2 - 4 September 1974, small freshwater streams were formed in crevices running down the rock surface of Colony #1. At low tide, even with the heavy swell, some anemones were exposed repeatedly for perhaps several minutes at a time to these streams. Three of the adults mentioned above, four other adults, and four juveniles developed patches of white necrotic tissue; however, this condition was not apparent several weeks later. Actinia seems to have a high tolerance to the effects of rain and short-term lowered salinities. When Colony #2 was visited on 4 September, during the rainfall, 76 of 151 Actinia present were found to be completely immersed in brackish water, later estimated to be no more than 10‰. During that low tide period, most of those anemones would have been immersed in 10‰ brackish water for about one hour and in 10 - 35‰ for a further two hours. All anemones recovered from that exposure, and the only ones on Colony #2 to show serious injuries were others that had been above the water level of the pool, but in streams of rainwater running down channels in the rock surface.

On Colony #1, the record rainfall of 12 March 1975 resulted in further injuries from exposure to freshwater, but only one adult death and a few juvenile deaths. When seen shortly after the rainfall, adult 114 had areas of white, necrotic tissue surrounding its base, and it was partly detached from the rock substratum. Despite relatively calm weather and seas, 75% of its pedal disc was still unattached when it was last sighted on 27 March. Wave action probably then washed the anemone away from the Colony and into deeper offshore water. Even during the hurricane of August 1975, when winds reached 200 km.h^{-1} but there was little forest debris in the intertidal region, only one adult and several juveniles were killed, by impact injuries, on Colony #1.

By contrast, much higher mortalities often occurred during gales on the semistable boulder beaches. Rock movements crushed and injured the anemones, and later, even in winter, those anemones stranded on the uppermost side of turned boulders could be found lethally desiccated. During the gale of 22 - 28 August 1974, an estimated 60% of Actinia, in some localised areas on these semi-stable boulder beaches, were injured or killed.

Microclimate

During immersion, temperatures in the intertidal region reach a more or less equable level, there are no problems of water loss, and

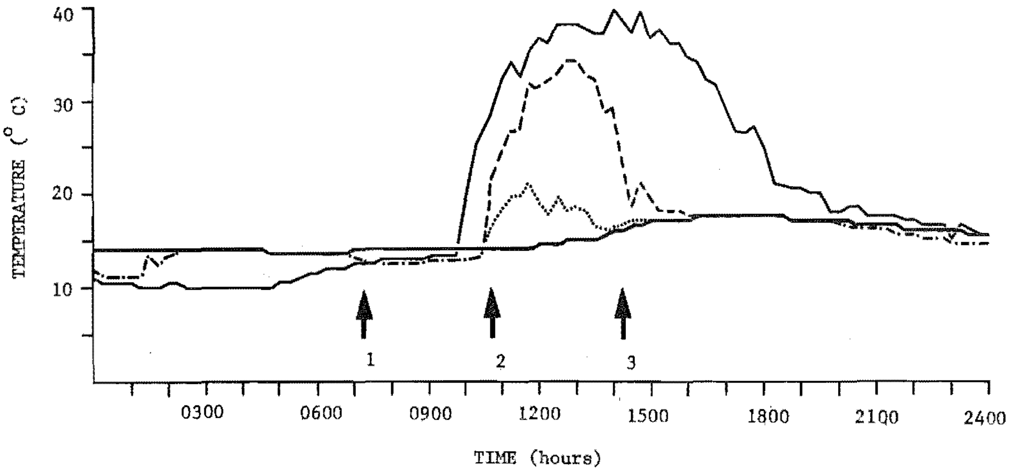
FIGURE 23: Microclimate records of temperature on Colony #1, 10 December 1973. Records were taken on all probes at 15 minute intervals.

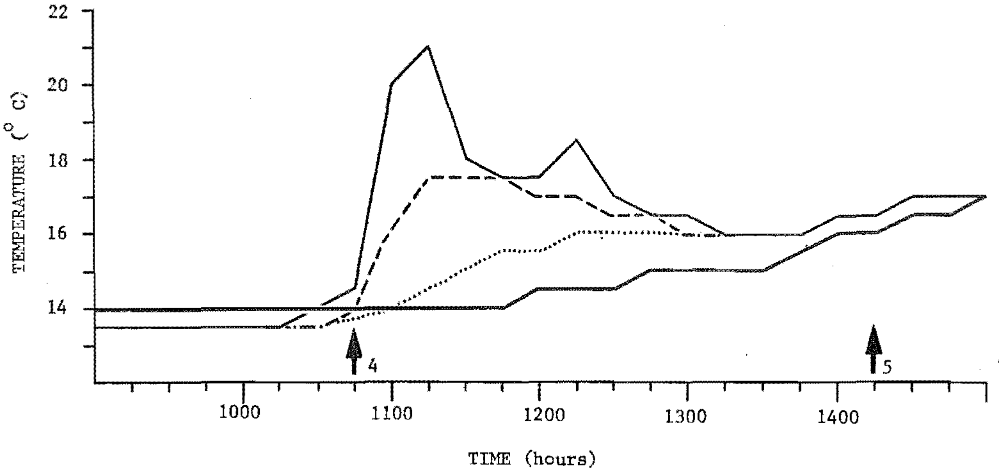
A. Sea and rock surface temperatures for the 24 hour period. 1: highest *Actinia* uncovered. 2: low tide. 3: highest *Actinia* covered.

———— : splash zone rock surface (top line at 1200 h).
– – – – – : rock surface at level of high water of neap tides.
………… : rock surface at midtide level.
━━━━ : sea temperatures in deep pool (bottom line at 1200 h).

B. Sea and ectodermal temperatures of adult *Actinia* during low tide on the fine, summer's day of 10 December 1973. 4: low tide. 5: highest *Actinia* covered.

———— : ectodermal temperature of highest *Actinia* (top line at 1200 h).
– – – – – – : ectodermal temperature of *Actinia* at midtide level.
………… : ectodermal temperature of lowest *Actinia*.
━━━━ : sea temperature in deep pool (bottom line at 1200 h).


40
30
20
10
TEMPERATURE (° C)
1
2
3
0300
0600
0900
1200
1500
1800
2100
2400
TIME (hours)


22
20
18
16
14
TEMPERATURE (° C)
4
5
1000
1100
1200
1300
1400
TIME (hours)

the environment is generally favourable for marine organisms (Lewis 1964, p. 26). Conditions for Actinia are also mild at low tides coinciding with night or light rain. Temperatures were generally quite uniform and in the range 5 - 15° C; relative humidities were 75 - 100%. Microenvironmental extremes were only experienced at low tides during calm, rainless periods.

On frosty winter mornings, air temperatures occasionally dropped to -3° C, but temperatures in the intertidal region rarely dropped below about 3° C, and then for only brief periods. Intertidal anemones, including Actinia equina, can survive short exposures to frost (Dicquemare 1773, 1777), although particularly prolonged periods of such conditions may result in heavy, if delayed, mortality (Van Urk 1952; Crisp, Moyse & Nelson-Smith 1964; Crisp & Southward 1964; Moyse & Nelson-Smith 1964). There is no evidence that temperatures at Kaikoura have ever been sufficiently low to cause mortality of intertidal anemones.

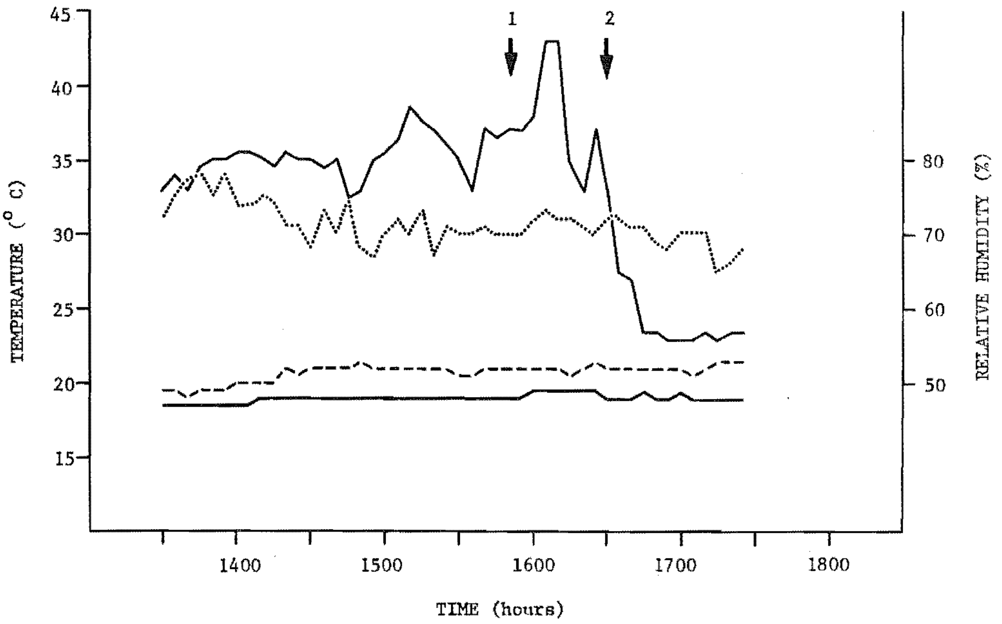
The vertical limits of the anemones on Colony #1 are approximately at the low and high neap tide levels (Chapter 1). Juveniles settled on most surfaces below high water of spring tides. Positions within the limits of the area occupied by the Colony, which was generally quite shaded and protected from the weather, ranged from extremely protected (in permanently shaded crevices) to quite exposed (on small projecting outcrops). There were few of the latter in the Colony area, and physical conditions on those were more equivalent to physical conditions away from the Colony area. Actinia found on exposed rock surfaces were invariably newly-settled juveniles: adults and older juveniles were found in protected positions in the Colony area.

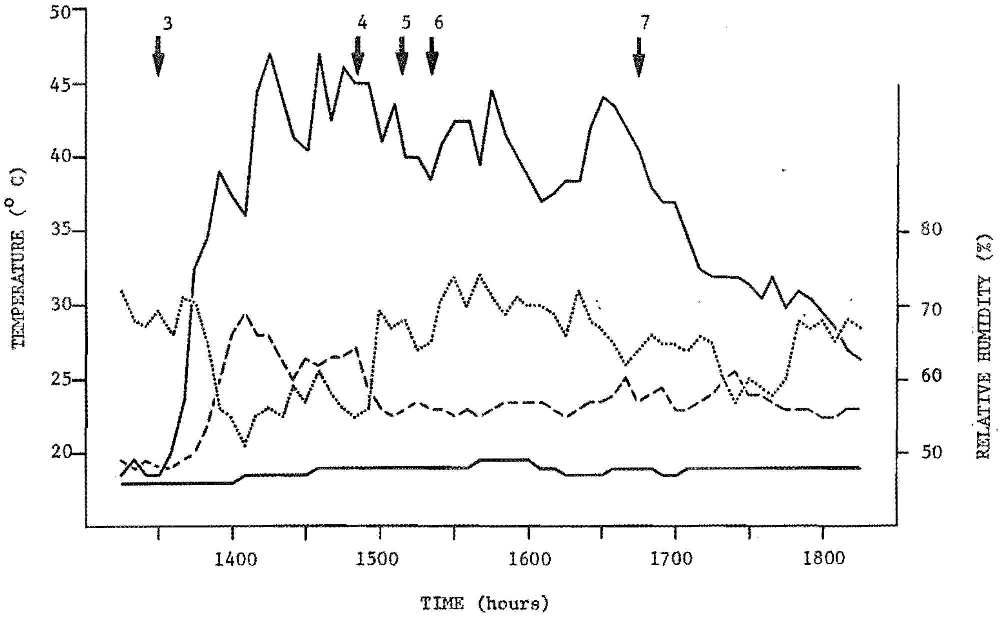
Temperatures in excess of 22° C were very rare in the protected positions, yet temperatures on some of the exposed rock surfaces, less

FIGURE 24: Microclimate records of temperature and relative humidity on Colony #1. Records were taken at 5 minute intervals during low tide periods. ———— : surface temperatures on an "exposed" rock surface near adult *Actinia* (top line at 1400 h). •••••••• : relative humidities near adult *Actinia* in the middle of the Colony area. — — — —: air temperatures near adult *Actinia* in the middle of the Colony area. ━━━━ : water temperatures in the permanent rock pool immediately below the Colony (bottom line at 1400 h).

A. Measurements during a low tide occurring on a fine summer's day, 30 January 1974. There were clear skies, no wind, and calm seas. 1: low tide. 2: all of the Colony was shaded by the nearby hills after this time.

B. Measurements during the low tide occurring on the hottest day on record at Kaikoura, 9 February 1974. Skies were initially cloudless, there was slight to no wind, and seas were calm. 3: all of the Colony was shaded by the nearby hills until 1100 hours (NZST). 4: slight sea breeze for a few minutes. 5: patchy clouds briefly covering the sun. 6: extremely low spring tide. 7: sun covered by patchy clouds of increasing density.


1
2
45
40
35
30
25
20
15
TEMPERATURE (° C)
80
70
60
50
RELATIVE HUMIDITY (%)
1400
1500
1600
1700
1800
TIME (hours)


3
4
5
6
7
50
45
40
35
30
25
20
TEMPERATURE (° C)
80
70
60
50
RELATIVE HUMIDITY (%)
1400
1500
1600
1700
1800
TIME (hours)

than 100 mm from adult Actinia, commonly approached and sometimes exceeded 40° C in summer (Figure 24A). On calm, sunny days, intertidal temperatures stayed within 1 - 2° C of sea temperature for up to several hours after the start of ebb tide. Most Actinia were shaded from the sun, and although ectodermal temperatures could increase by about 7° C during low tide, there could still be differences of over 20° C between shaded (protected) and unshaded (exposed) areas on the Colony. As would be expected, temperatures of anemones and rock surfaces near low water level deviated less from sea temperatures than those of anemones and rock surfaces towards high water level (Figure 23). The maximum recorded ectodermal temperature of an adult was 22° C, the maximum recorded Colony air temperature, near adults, was 29.5° C, and the maximum temperature recorded on an exposed rock surface, on the Colony face, was 47° C (Figure 24B). Temperatures within crevices remained close to sea temperatures; because of the relatively large size of probes, the temperatures of juveniles could not be measured, but these would be more similar to the temperature of the adjacent rock surface than adult temperatures.

While temperature measurements were taken much less frequently in winter, they were especially biassed towards sunny, calm days, and so are reasonably indicative of the upper temperature extremes likely to be experienced in the shaded positions of Colony #1. The highest, shaded mean air temperatures for 1, 2 and 3 h periods were 27°, 25° and 25° respectively, and temperatures over 20° C were only recorded in summer months (Table 10).

Relative humidities were measured in a shaded position near the upper limit of adults. Values were generally 65 - 80% during low tides in the day, and 80 - 90% at night. Relative humidities greater than 90% only occurred during rain or following sudden temperature

TABLE 10: Maximum mean air temperatures and minimum mean relative humidities measured in the microenvironment of <u>Actinia tenebrosa</u> on Colony #1, November 1973 to November 1974. The absolute maximum air temperature recorded was 29.5° C, with temperatures above 22° C being very rare. The absolute minimum R.H. recorded was 28%, with relative humidities below 60% being very rare.

	Month	n*	$\bar{x}$** (hours)	Maximum mean temperatures (°C)			Minimum mean relative humidities (%)		
				1 hr	2 hr	3 hr	1 hr	2 hr	3 hr
1973	Nov	8	2.32	21	21	20	49	49	53
	Dec	14	3.21	20	19	18	62	66	68
1974	Jan	10	2.88	23	23	22	31	36	37
	Feb	21	3.59	27	25	25	56	62	64
	Mar	11	3.77	20	19	19	53	55	56
	Apr	2	3.38	16	15	15	81	81	82
	May	3	3.53	12	11	11	55	58	63
	Jun	3	3.75	12	12	12	68	69	71
	Jul	4	2.67	10	10	10	62	63	64
	Aug	11	3.05	11	11	11	66	66	68
	Sep	9	3.51	16	16	16	55	57	58
	Oct	6	3.57	18	18	17	65	66	68
	Nov	4	3.58	16	15	15	70	71	71

*n : number of visits to Colony #1 on which microenvironmental measurements were taken.

**$\bar{x}$: mean duration of visits for that month. Measurements were taken at five minute intervals for the duration of the visit.

decreases; relative humidities less than 65% occurred in association with warm, gentle breezes or following sudden temperature increases (Figure 24B).

In the shaded areas of Colony #1, relative humidities varied more with the weather than with season. Thus, on a calm, rainless day, RH near adult Actinia was most likely about 70%, even though shaded air temperatures were about 15° higher in summer than in winter. Few relative humidities were measured away from the shaded locations, but indicated that on sunny days unshaded positions had relative humidities of about 55% or less. The lowest mean relative humidities recorded on the Colony area for 1, 2 and 3h were 31%, 36% and 37% respectively (Table 10).

Desiccation was a major cause of juvenile mortality, especially during periods of heavy settlement coinciding with rainfree weather. Newly settled juveniles were often found on exposed areas; those on surfaces in direct sunlight sometimes died within a few hours, but others in shaded positions were also seen to die within single low tide periods. Conditions of 24° C, 60% RH and a slight breeze were sufficiently severe to kill juveniles in 3 h: such conditions were regularly exceeded on exposed positions, and they occasionally occurred elsewhere on the Colony face (Figure 24B) during extremely warm, dry periods. Only juveniles in crevices or positioned against adults were likely to be protected from desiccation.

As mentioned above, no adults deaths on Colony #1 were attributed to lethal extremes of temperatures or desiccation. By contrast, adults (as well as juveniles) were often seen to die of lethal desiccation on the unstable boulder beaches following winter storms. Boulders were occasionally turned over by wave action, leaving the anemones uppermost, and during calm, rainless weather even adult *Actinia* died after exposure to several low tides. Since the coast was shaded and always quite cool during winter, mortality was attributed to desiccation, from repeated exposure to low relative humidities (50 - 60%) and gentle breezes.

There is evidence that *Actinia* may be eurythermal to some extent. *A. tenebrosa* survived several days of extremely hot weather in Western Australia (Hodgkin 1959), which killed intertidal limpets, chitons, mussels and zoanthid colonies.

Biological factors

Even during calm, wet periods in winter, there was still an intermittent mortality of juveniles (Figure 22B), especially of those less than about 8 mm CD. These mortalities were attributed to the biological factors discussed below.

a. Biological interference, from grazing molluscs

Grazing molluscs seem to be a small but consistent source of mortality to juvenile *Actinia*, mainly by dislodging the latter from the substratum so that they wash away. Feeding limpets and chitons regularly moved over the entire rock surface of Colony #1, except that occupied by adult *Actinia*. These molluscs penetrated into narrow crevices and occasionally under the pedal discs of the anemones. *Actinia* greater than about 10 mm CD were able to maintain their attachment to the rock, although they sometimes moved a short distance away from the irritating mollusc. Juveniles less than about 10 mm CD were sometimes forced to detach from the rock, and either washed away or reattached to the shell of the mollusc. The latter juveniles were never seen for very long before they disappeared too. Limpets sometimes moved over and clamped down on small juveniles, which were later seen to be crushed and dead. In other instances, radula marks indicated that a feeding mollusc had passed over the position of a juvenile at about the same time the juvenile had disappeared.

b. *Predation*

Only two instances of predation were observed on the Colony #1 population: in each a gastropod, *Haustrum haustorium*, partially ate the tentacles of juveniles. Both juveniles died soon afterwards (Ottaway 1977a). It seems unlikely that predators have any marked effect on the observed population; however, every year a high proportion of newly-released juveniles and a small proportion of adults must fall to subtidal positions where they cannot move back into the intertidal region. Since *Actinia* are rarely found living subtidally (Ottaway 1973, 1975a, 1977b), and prolonged submergence *per se* apparently does not harm the anemones (Den Hartog 1954; Ottaway 1973), it has been suggested that invertebrate predators may eat *Actinia* that settle below low water of neap tides (Ottaway 1977b).

c. *Starvation*

Several juveniles survived for periods of over a year, while slowly decreasing in size and then finally disappearing. For example, one juvenile survived 380 days after settlement, during which time it shrunk from 5.5 mm CD to 1.5 mm CD. It seems possible that such juveniles starve to death. Some settling positions may be protected from physical extremes of the environment, hazards, and biological interference, but for unknown reasons are unsuitable for capture of food to the extent that some juveniles cannot even maintain size.

d. *Intraspecific aggression*

Fifty-nine fights were recorded between the *Actinia* of Colony #1 (Chapter 3). In only one instance did an anemone die: a juvenile, after 50% of its column had been injured with acrorhagial wounds.

4.5 DISCUSSION

The distribution and abundance of any particular species, both spatially and temporally, is determined by a complex interaction of physical and biological factors of the particular environment (Andrewartha and Birch 1954). Although adult Actinia can and do adjust their positions in response to unfavourable environmental stimuli (Ottaway and Thomas 1971; Ottaway 1973; Chapter 3), there has been no indication that released juveniles actively determine or select the site on which they finally settle. Thus the local distribution of A. tenebrosa may be dependent on a chance combination of events, which Moore (1975) terms "habitat availability and ecological opportunity", to a much greater extent than habitat selection or behaviour (Meadows and Campbell 1972a, 1972b) of the anemones themselves. Vagaries of water movement immediately following the release of juveniles would clearly be a very important determinant of subsequent survival and success for an intertidal invertebrate of this type (Lewis 1968), but this factor was not studied in detail.

Desiccation is another important factor, which directly affects the intertidal distributions of both Anthopleura elegantissima (Dayton 1971) and Actinia tenebrosa. The latter species is most likely to be found on the southern aspects of rocks, and in crevices or shaded hollows rather than on surfaces which are exposed to the wind and sun at low tides. Adults are more resistant to desiccation than juveniles (Ottaway 1973). To survive the juveniles require microhabitats that are considerably more protected and humid at low tides than those of most adults. As a consequence, most settling juveniles cannot survive the physical conditions found at the upper limit of the vertical distribution of adult Actinia, unless they happen to settle in a permanent rock pool. The determinant of the lower limit of the distribution, which is about mean low water of neap tides, has not been investigated in detail. A. tenebrosa has not been reported living subtidally in natural situations, with the one exception of a dubious record by Black (1971), and it has been suggested that juveniles and adults washed away from the shore are killed by predators rather than physico-chemical factors of the subtidal environment (Ottaway 1973, 1977b).

At Kaikoura, Actinia can be found living on stable rock outcrops and semi-stable boulder beaches. It seems that, even when the two habitats are adjacent, the main causes of juvenile mortality on each have different degrees of importance. Stable rock outcrops provide fewer protected microhabitats for Actinia, and may support a relatively denser population of limpets and chitons than do the unstable boulder beaches. On stable rock outcrops, juveniles have a low chance of successfully attaching near the brooding adult, or at all intertidally, and are much more likely to be washed away into deep offshore water. Once attached intertidally, there is still a very high mortality in the first year and subsequently, until a size greater than about 15 mm column diameter is reached. This mortality was attributed mainly to lethal desiccation, or a combined exposure to severe desiccation and warm temperatures, and to the effects of grazing molluscs.

Limpets are known to dislodge settling barnacle larvae (Hatton 1938; Lewis 1954; Southward 1956; Connell 1961), small settled barnacles (Stimson 1970), and they may severely restrict the recruitment and survival of many other sessile species in intertidal communities (Dayton 1971), but limpets and chitons have not previously been noted as an important source of mortality for juvenile Actinia. As found for barnacles and algae (Dayton 1971), however, some of the anemones "eventually attain a size at which they are immune to the bulldozing effect and the grazing of the limpets" and chitons. When all limpets and chitons were removed from Colony #1, however, algal growth was such that some juveniles were smothered in their crevices, and died. These grazing molluscs may therefore be necessary in the environment of *Actinia*, to help maintain clear space in which the juveniles can settle and live.

Once the anemones reach adult size, the annual mortality rate on stable rock outcrops is very low (2%), and was attributed mainly to impact injuries from wave-driven rocks or logs. On the unstable boulder beaches, there is an abundance of suitable microhabitats in which juveniles may settle. Released juveniles that are washed away from the brooding adults are very likely to fall into the shaded, humid spaces underneath nearby boulders. My observations suggest that there is an abundance of food for the anemones on these boulder beaches, and also fewer and smaller limpets and chitons than on the stable rock outcrops. It seems likely therefore that juveniles may have a higher chance of successful settlement on the unstable boulder beaches, a higher chance of surviving their first year, a relatively faster growth rate if the latter is related to food availability (Chapter 5), but a relatively high mortality rate as adults. During most gales, even those which were not particularly severe, some localised areas on the boulder beaches suffered catastropic disturbance, where most boulders were moved or even completely overturned. In such instances, the local *Actinia* population suffered a very high mortality of both adults and juveniles, due in part to the crushing and battering effect of the boulders as they moved, and in part to lethal desiccation of anemones, left uppermost on turned boulders, exposed at low tides following the gale.

Colony #1 is probably representative of many Actinia colonies on stable rock outcrops. Here, no adult mortalities were attributed to lethal extremes of temperature or desiccation, even though the hottest day on record at Kaikoura, and an extremely dry, breezy day, both coincided with extremely low spring tides and occurred during the period of intensive observations. Juveniles living close to adults would be in cool, shaded, humid microenvironments, and because of boundary layer effects, exposed to little or no wind. Such juveniles should survive over 14 hours (Ottaway 1973) of the most extreme temperatures and relative humidities measured. Juveniles living away from the adults, however, especially those on rock surfaces exposed to the sun and wind, would regularly experience temperatures approaching 40° C for 3 hours, relative humidities of about 50%, and slight breezes. One such exposure would lethally desiccate most juveniles (Ottaway 1973), and probably also result in lethal hyperthermia although the juveniles might not actually die until several days after the exposure.

Juvenile settlement was quite variable, both from month to month and from year to year. Juvenile release occurs throughout the year (Chapter 2), but it was not possible to determine if juveniles were released during gales or periods of rough seas. Most settlements on Colony #1 occurred in summer and early autumn. A high proportion of those juveniles settling in summer, however, were quickly killed by desiccation, which is a function of humidity, air movement, temperature, and of the direct solar radiation absorbed (Kinne 1971, p. 846). Although the effects of moving air are well known (Ramsay 1935; Kensler 1967; Foster 1971), wind was previously considered unimportant in the microenvironment of Actinia because at any particular time most individuals are found in sheltered positions (Ottaway 1973).

That wind could significantly contribute to the lethal desiccation of juveniles settling on exposed positions, away from the adults, was completely overlooked. The mildest conditions actually seen to cause lethal desiccation, of a newly settled juvenile on an exposed position, resulted in death of the juvenile in 25% of the time predicted from experiments which were conducted in still air (Ottaway 1973). This marked discrepancy must to a large extent be attributed to a slight breeze. Newly-settled juveniles appeared to be more susceptible to desiccation than older juveniles of the same size, partly because the older juveniles were almost always in sheltered positions, and possibly because there may be physiological changes in the ectoderm of juveniles as they age which decreases permeability of the column wall. The latter suggestion needs experimental verification.

Juveniles that settled very close to adults were less likely to be exposed to extremes of temperature and relative humidities at low tides than those which settled elsewhere; however, in one instance an adult was seen to attack and kill a juvenile (Ottaway & Kirby 1975), and in another instance the positions of abutting adults seemed to prevent a juvenile capturing sufficient food to maintain itself. A juvenile that settled in the middle of a group of adults apparently starved to death over the next year. Juveniles that settled intertidally, but away from the adults, appeared to be much more likely to attach in positions where they were exposed to lethal extremes of the physical environment. In summer, lethal desiccation could occur in one low tide period; in winter, it usually occurred over several days. Severe physical conditions, especially low relative humidities, while most frequent in summer, could occur all year around, but were never recorded during low tides at night.

Throughout the year there was a small, continuing mortality of juveniles which was ascribed to biological factors, since it appeared to be independent of the weather and physical environment. Molluscs are thought to be the main source of this mortality: limpets and chitons were seen to dislodge and crush juveniles, and whelks nibbled their tentacles. Torrential rainfall, brief exposures to seawater of reduced salinity, and prolonged heavy wave action sometimes resulted in injuries to the Actinia on Colony #1 but they did not seem to result in any significant increase in the number of mortalities. Actinia is euryhaline, and can survive at least several hours in seawater of either very high salinity or very low salinity, as can another intertidal anemone, Haliplanella luciae (Shick 1976). Since coelenterates generally exhibit low capacities for ion regulation (Kinne 1971, p.886), the survival of Actinia under such conditions is probably due to a resistance adaptation of high cellular osmotic tolerance.

Both the number of juveniles released and the peak of juvenile settlement varied markedly from year to year, which is in accordance with fluctuations in the size of gonads from year to year (Chapter 2). The Colony #1 population, however, must be considered quite stable. Despite the marked seasonal fluctuations in the number of juveniles present, the resultant change in the numbers present after three years, of juveniles as well as adults, was slight. It seems probable that once a newly-formed colony has increased in size to occupy most of the suitable microhabitats on a stable rock outcrop, the adult population size would reach a limit and stabilise. A marked population change would then only occur after some catastrophe, such as described by Dicquemare (1777), where a cliff fell down or the rock outcrop was in part destroyed by erosion forces, and the anemones suffer accordingly.

Rapid population increases, as are known to occur in Anthopleura elegantissima living on stable rock substrates (Dayton 1971) would be unlikely for Actinia in this situation, since asexual reproduction is rare for the latter species (Chapter 2), and the number of juveniles reaching maturity in any one year seemed independent of the number of offspring produced in the few years immediately preceding. By contrast, marked seasonal and annual fluctuations in population size could quite possibly occur on semi-stable boulder beaches, though the fluctuations on one part of a beach need not necessarily be synchronised with those on another part, even a short distance away. Localised parts of these beaches frequently suffered catastropic disturbances during gales, in which the Actinia population suffered high mortality, but in those breeding seasons where juvenile production was high, settlement and survival of those juveniles were also high. Thus, a rapid increase in the population size could result as a consequence of a good breeding season followed by a winter with gales which were not unduly severe, with many of the juveniles surviving their first year. Rapid changes of this nature have been noted before in Actinia equina populations (Fleure & Walton 1907; Stock 1951; Van Urk 1952; Den Hartog 1954, 1961).

CHAPTER FIVE

GROWTH RATES AND LONGEVITIES

5.1 INTRODUCTION

Most data on growth and longevity of actinians come from observations of animals maintained in aquaria. The size of an anemone is not necessarily related to its age (Stephenson 1928) but is probably more related to its nutritional history. Regularly fed juvenile anemones grow rapidly (Chia & Rostron 1970; Chia & Spaulding 1972) and the ages at maturity have been estimated at less than one year for Epiactis prolifera (Dunn 1977a) to less than "a few years" for Actinia equina (Dalyell 1848; M'Bain 1878). Regularly fed adults, however, may show no appreciable change in size or appearance for 8 y (Ashworth & Annandale 1904). There are longevity records of 78 y for Cereus pedunculatus (Comfort 1964), 66 y for Actinia equina (Ashworth & Annandale 1904), 43 y for Cereus viridis (Torelli 1938), and 21 y for Cerianthus lloydii (Fox 1963). These data, nevertheless, should be interpreted with caution, since longevity of anemones in captivity may be atypical of their longevities in the natural environment (Ottaway & Kirby 1975).

To my knowledge, there are two long-term studies on wild actinian populations, but still very few published data on longevities and growth rates of anemones under natural conditions. Fager (1968) found that 11 of 45 Harenactis attenuata lived for more than 5 years without notable change in size. From the calculated instantaneous exponential mortality rate of those adults, of $0.281.y^{-1}$, mean life expectancy was 3.5 y after the start of observations, and one adult was predicted to live at least 13.5 y. Dunn's study (1975a,b; 1977a,b,c) on Epiactis prolifera did not deal with the above aspects.

This Chapter examines growth rates and longevities of Actinia tenebrosa living under natural conditions.

5.2 MATERIALS AND METHODS

The methods used in identifying, tracking and measuring individual Actinia have been described (Chapter 3.2, Chapter 4.2). Anemones on Colony #1 were measured when first seen and thereafter about once per calendar month between November 1973 and December 1975. A further census was made in December 1976. About 400 juveniles, of size range 2.5 to 15 mm CD, were artificially settled on Colony #3 early in July 1974. The survivors were measured on 15 occasions between 21 July 1974 and 8 September 1975 (mean interval between measurements of 28 days).

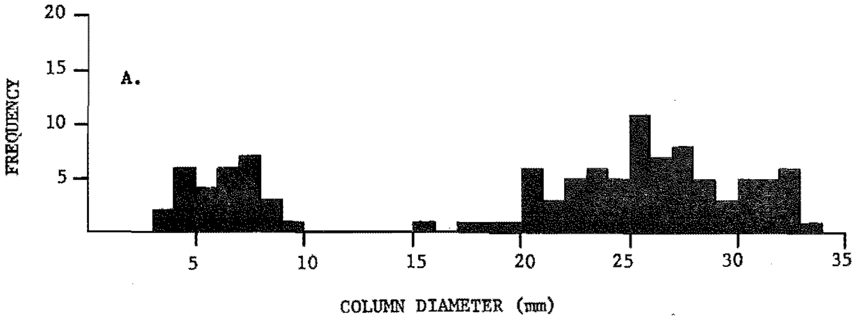
Standard linear regression analyses, of column diameter against time, were used to derive growth equations for all individuals that survived at least 350 days. Results from Colony #1 (n = 82 adults, 28 juveniles) and Colony #3 (n = 189 juveniles) were pooled. Anemones were grouped into six class intervals on the basis of their calculated theoretical column diameters at the start of measurements. Mean and maximum annual growth increments were determined for anemones in each class interval, and these values were used to calculate mean and minimum times for newly-settled juveniles to reach maturity and then approximate maximum size (Figures 25, 29).

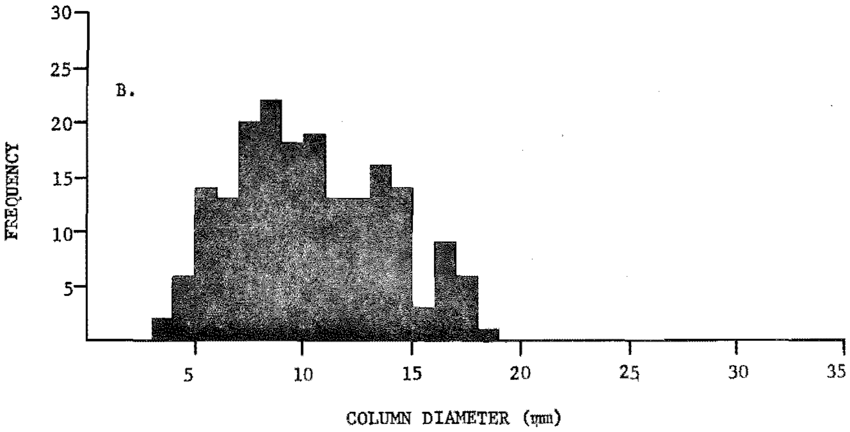
To define the relationship between mortality of observed adult Harenactis and time, Fager (1968) used an exponential equation of the form:

$$N_T = N_0 . e^{-MT} \quad . \quad . \quad . \quad . \quad . \quad . \qquad (1)$$

FIGURE 25: Size frequency distribution of <u>Actinia tenebrosa</u>, from Colonies #1 and #3, which survived longer than 350 days. Size is the theoretical column diameter (mm) of each specimen at the start of observations, calculated from the linear regression analysis of size against time.

A: Colony #1 (n=110); B: Colony #3 (n=189).


20
15
10
5
FREQUENCY
A.
5
10
15
20
25
30
35
COLUMN DIAMETER (mm)


30
25
20
15
10
5
FREQUENCY
B.
5
10
15
20
25
30
35
COLUMN DIAMETER (mm)

where T = elapsed time from the start of observations

N_0 = number of adults seen in first observation period

N_T = number of those adults surviving to time T

e = base of natural logarithms

M = instantaneous mortality rate.

To find the instantaneous mortality rate,

$$M = -\ln\left(\frac{N_T}{N_0}\right).T^{-1} \qquad . \quad . \quad . \quad . \quad . \qquad (2)$$

To find the elapsed time at which a predicted number of adults is left

$(1 \leqslant N_T \leqslant N_0)$,

$$T = -\ln\left(\frac{N_T}{N_0}\right).M^{-1} \qquad . \quad . \quad . \quad . \quad . \qquad (3)$$

To find the mean longevity ($\bar{T}$) of the adults after the start of observations,

$$\bar{T} = M^{-1} \qquad . \quad . \quad . \quad . \quad . \qquad (4)$$

There was no indication of senescence in the observed population of *A. tenebrosa*, and all evidence indicated that the mortality of adults was independent of their age or size. Thus, equations (1) to (4) above will also be applied here, to describe the relationship between mortality of *Actinia* and time.

5.3 GROWTH RATES

Representative growth patterns are shown in Figures 26 and 27. Many anemones showed large, short-term decreases in size following extreme desiccation or particularly heavy rainfall (Chapter 4), and a few showed large long-term size decreases following physical injuries (Figure 28). Adults also showed annual size fluctuations that appeared to be correlated with reproductive cycle: many adults showed a mean

FIGURE 26: Representative examples of positive growth rates observed for _Actinia tenebrosa_. Graphs are derived from standard linear regression analyses of column diameter (mm) against time (days) from start of observations, 24 November 1973.

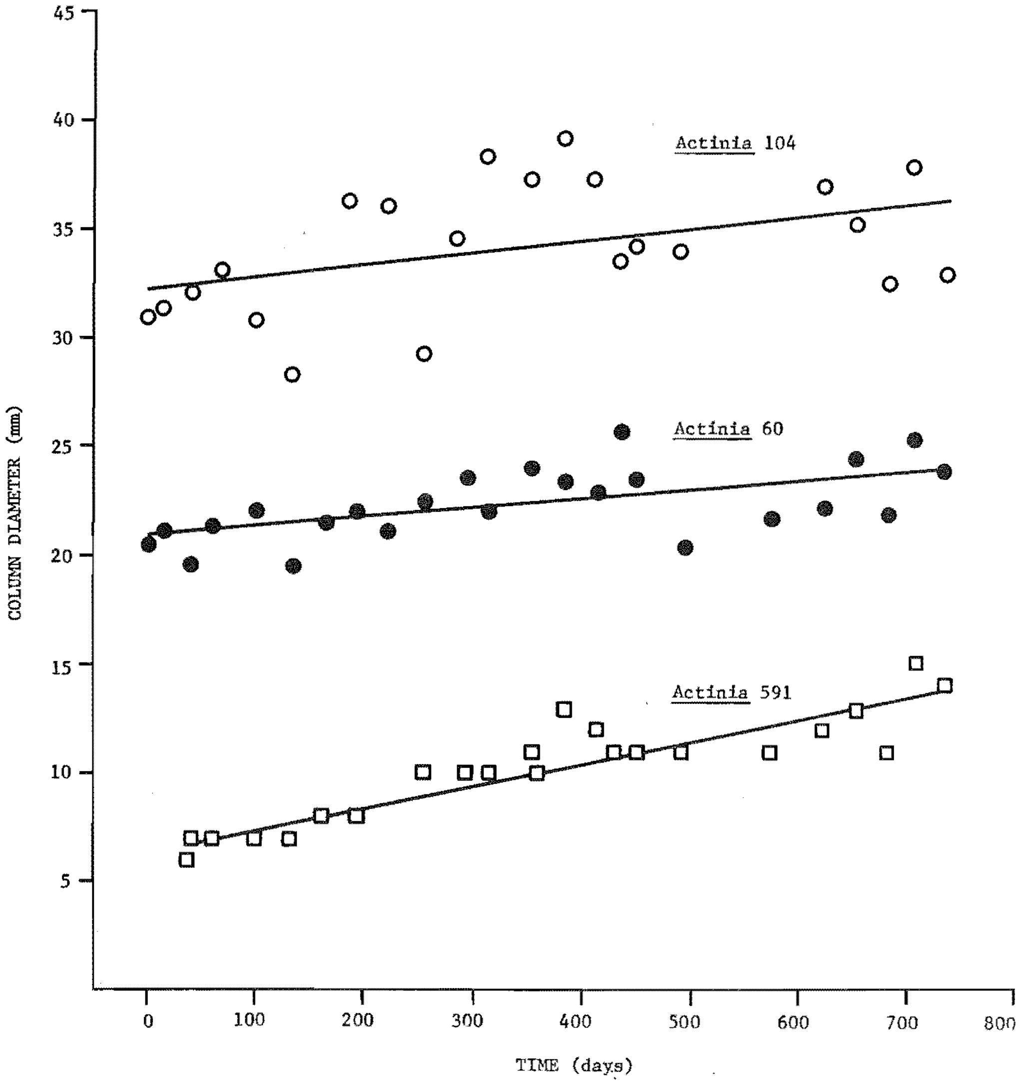
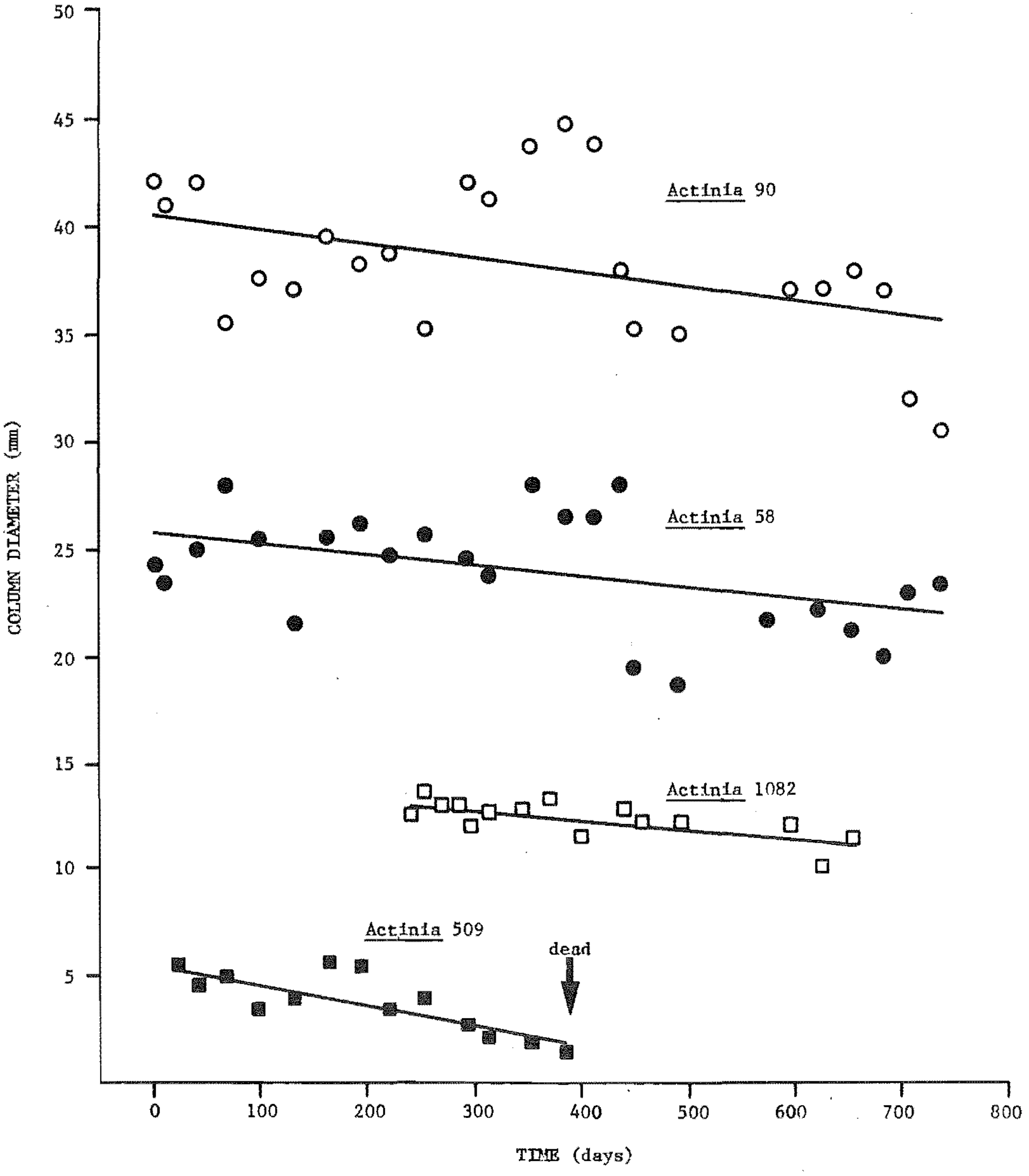

45
40
35
30
25
20
15
10
5
COLUMN DIAMETER (mm)
0
100
200
300
400
500
600
700
800
TIME (days)
Actinia 104
Actinia 60
Actinia 591

FIGURE 27: Representative examples of negative growth rates observed for *Actinia tenebrosa*. Graphs are derived from standard linear regression analyses of column diameter (mm) against time (days) from start of observations, 24 November 1973.


50
45
40
35
30
25
20
15
10
5
COLUMN DIAMETER (mm)
0
100
200
300
400
500
600
700
800
TIME (days)
Actinia 90
Actinia 58
Actinia 1082
Actinia 509
dead

increase in size about October to November, and then a decrease in size about January to March, after spawning (Chapter 2). This seasonal effect has been minimised to some extent in the calculations, however, because the mean annual growth increments for adults were calculated on the basis of measurements extending over 2 y.

Mean absolute growth increments were low for all class intervals considered. Calculated growth increments were in the range -4.25 to 6.2 mm (Table 11). Actinia in the size class 13 - 17.99 mm CD showed the greatest absolute mean increase in CD (1.6 $mm.y^{-1}$), while adults in the size class 28 to 32.99 mm CD showed the least absolute mean increase (-0.04 $mm.y^{-1}$). The smallest anemones, those in the class interval 3 to 7.99 mm CD, had the greatest mean relative increase in column diameter (mean absolute increase/mean size of class interval), of 24%, while the largest adults showed the least mean relative increase in size, of $-0.1\%.y^{-1}$. There were wide variations in mean annual growth increments in all six size classes (Figure 29). As a general statement, absolute and relative mean growth rates were low, and decreased as the anemones increased in size (Table 11).

5.4 LONGEVITY ESTIMATES FROM GROWTH DATA

Longevities can be calculated from both the pooled growth data discussed above and from the natural mortality rates observed on Colony #1 (Chapter 4).

For the purpose of the calculation from growth data, it will be assumed that juvenile Actinia settle at 5.5 mm CD, that Actinia develops gonads in the first summer following the time that it reaches 15 mm CD, and that the maximum possible size reached by Actinia is 40 mm CD.

FIGURE 28: An atypical growth pattern for Actinia tenebrosa on Colony #1. Specimen 1 appeared healthy until the end of August 1974. Following a storm in early September 1974, the anemone was highly contracted and showed severe impact injuries. It extruded mesenterial filaments through column ruptures for the next three months. By January 1975, all external injuries were apparently healed, and the anemone was again increasing in size; however, by November 1975, it was still considerably smaller than when first seen two years previously.

Graphs are derived from standard linear regression analyses of column diameter (mm) against time (days) for the three sets of data indicated.

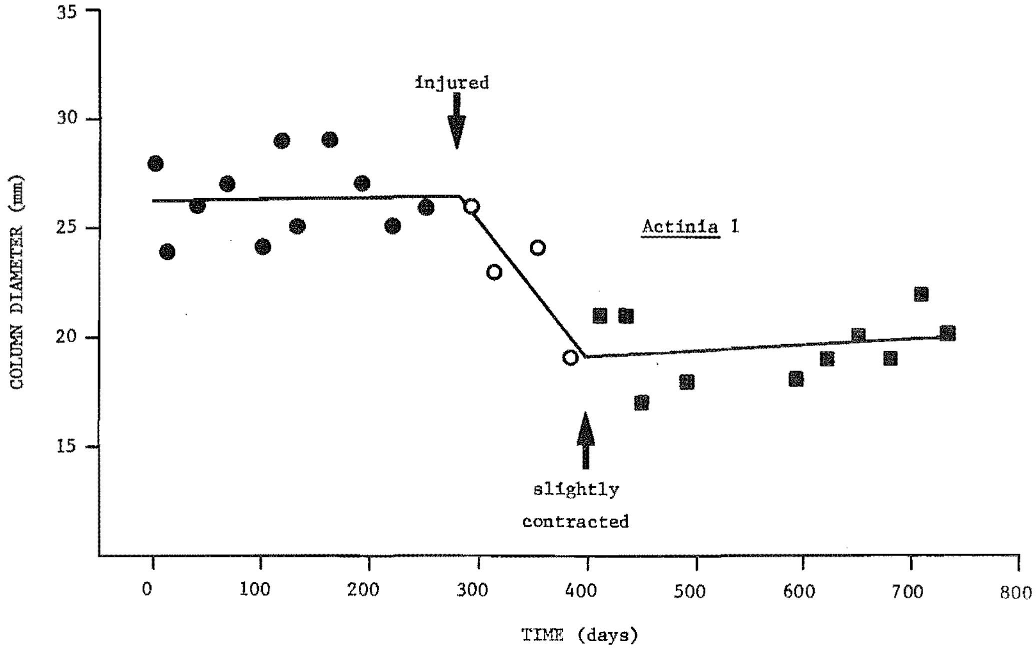

35
30
25
20
15
COLUMN DIAMETER (mm)
injured
Actinia 1
slightly
contracted
0
100
200
300
400
500
600
700
800
TIME (days)

FIGURE 29: Frequency histograms of annual growth increments for Actinia tenebrosa surviving longer than 350 days. A total of 297 specimens from Colonies #1 and #3, in the size range 3 to 32.99 mm CD, were considered.

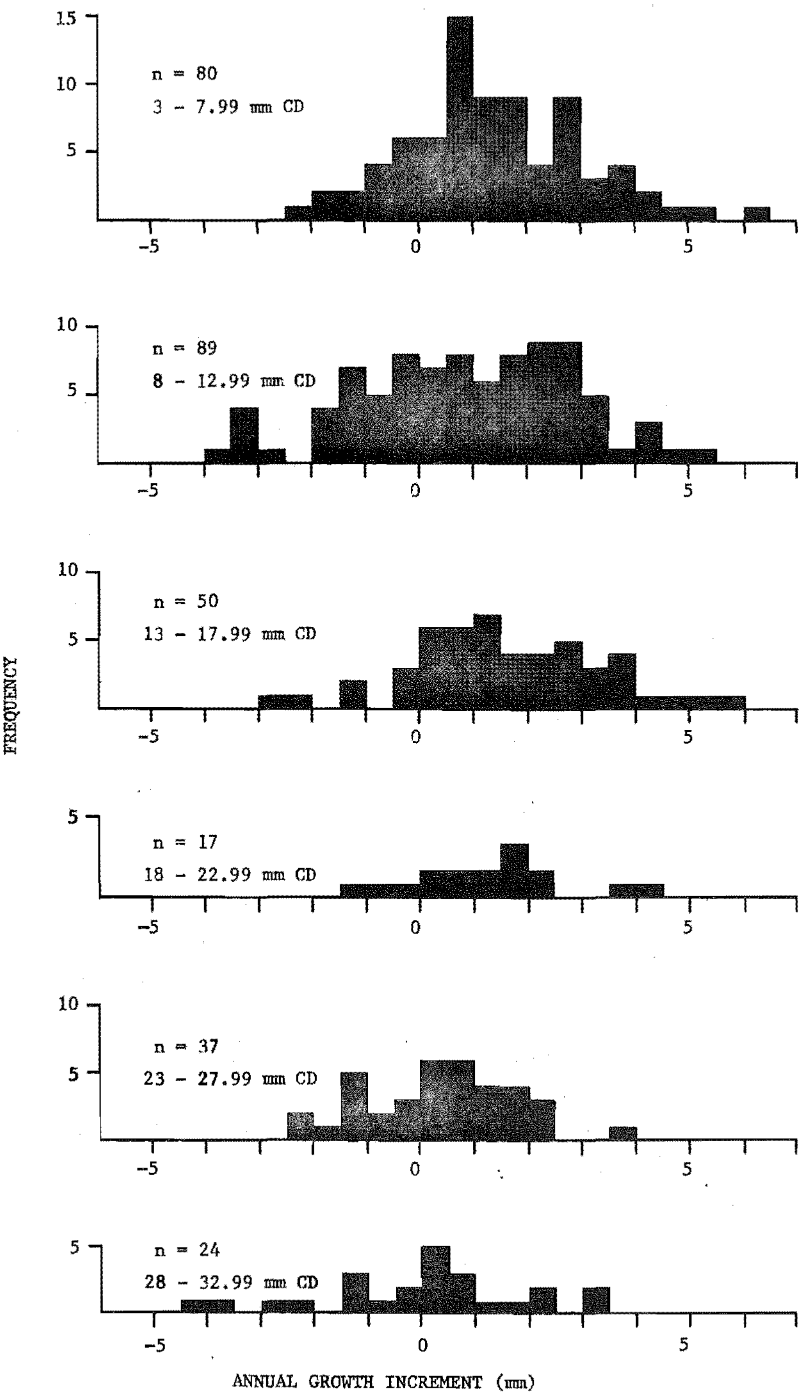

15
10
5
n = 80
3 - 7.99 mm CD
-5
0
5
10
5
n = 89
8 - 12.99 mm CD
-5
0
5
10
5
n = 50
13 - 17.99 mm CD
-5
0
5
FREQUENCY
5
n = 17
18 - 22.99 mm CD
-5
0
5
10
5
n = 37
23 - 27.99 mm CD
-5
0
5
5
n = 24
28 - 32.99 mm CD
-5
0
5
ANNUAL GROWTH INCREMENT (mm)

TABLE 11: Minimum, mean and maximum annual growth rates for _Actinia tenebrosa_ on Colonies #1 and #3. Only anemones surviving longer than 350 days are considered.

		Annual growth rates					
		Minimum		Mean		Maximum	
Size class (mm CD)	n*	absolute (mm)	relative (%)	absolute (mm)	relative (%)	absolute (mm)	relative (%)
3 - 7.99	80	-3.548	-64.5	1.399	24.4	6.216	113.0
8 - 12.99	89	-3.610	-34.4	0.941	9.0	6.143	58.5
13 - 17.99	50	-2.770	-17.9	1.611	10.4	5.796	37.4
18 - 22.99	17	-1.350	- 6.6	1.298	6.3	4.201	20.5
23 - 27.99	37	-2.486	- 9.5	0.331	1.1	3.584	14.1
28 - 32.99	24	-4.453	-14.6	-0.039	-0.1	3.329	10.9

* n = number of anemones considered in that particular size class.

Settling with a size of 5.5 mm CD and growing at a mean rate of 1.3 $\mathrm{mm.y^{-1}}$ (Table 11), an anemone would reach 8 mm CD after 1.9 y. Then, growing at a mean rate of 0.9 $\mathrm{mm.y^{-1}}$, it would reach 13 mm after 7.2 y. Continuing on this calculation, using the mean growth rates for the appropriate size classes (Table 11), anemones growing at the mean rate would reach maturity 8.4 y after settlement, and maximum size 65.5 y after settlement. Growing continuously at the maximum rate, Actinia would reach maturity after 1.6 y and maximum size after 8.3 y (Table 12). Thus, surviving anemones would probably first develop gonads 2 to 9 y after settlement.

5.5 LONGEVITY ESTIMATES FROM MORTALITY DATA

Juveniles

Considering the survival of the 233 juveniles which were first seen between November 1973 and April 1974 (Figure 30), inclusive, 50% died within 17 days of settlement. From observed mortality over the first 150 days after settlement,

$$M = -\ln(\frac{49}{233}).\ 0.411^{-1} \quad . \quad . \quad . \text{ from equation (2) above,}$$

$$= 3.794.y^{-1}$$

$$T = -\ln\ (\frac{N_T}{233}).\ 0.2636\ y \quad . \quad . \quad . \text{ from equation (3) above,}$$

therefore, the predicted time at which only one juvenile is left ($N_T = 1$) is

$$T = 1.437\ y$$

and $\bar{T} = 0.2636\ y$ . . . . from equation (4) above.

Hence, from the survivorship curve of the first 150 days, the mean longevity of those juveniles at the time of settlement was 14 weeks, and only one of those juveniles should be living 1.4 y after

TABLE 12: Calculated periods for Actinia tenebrosa to reach maximum size of class intervals shown, growing at the mean and maximum annual rates found for wild anemones.

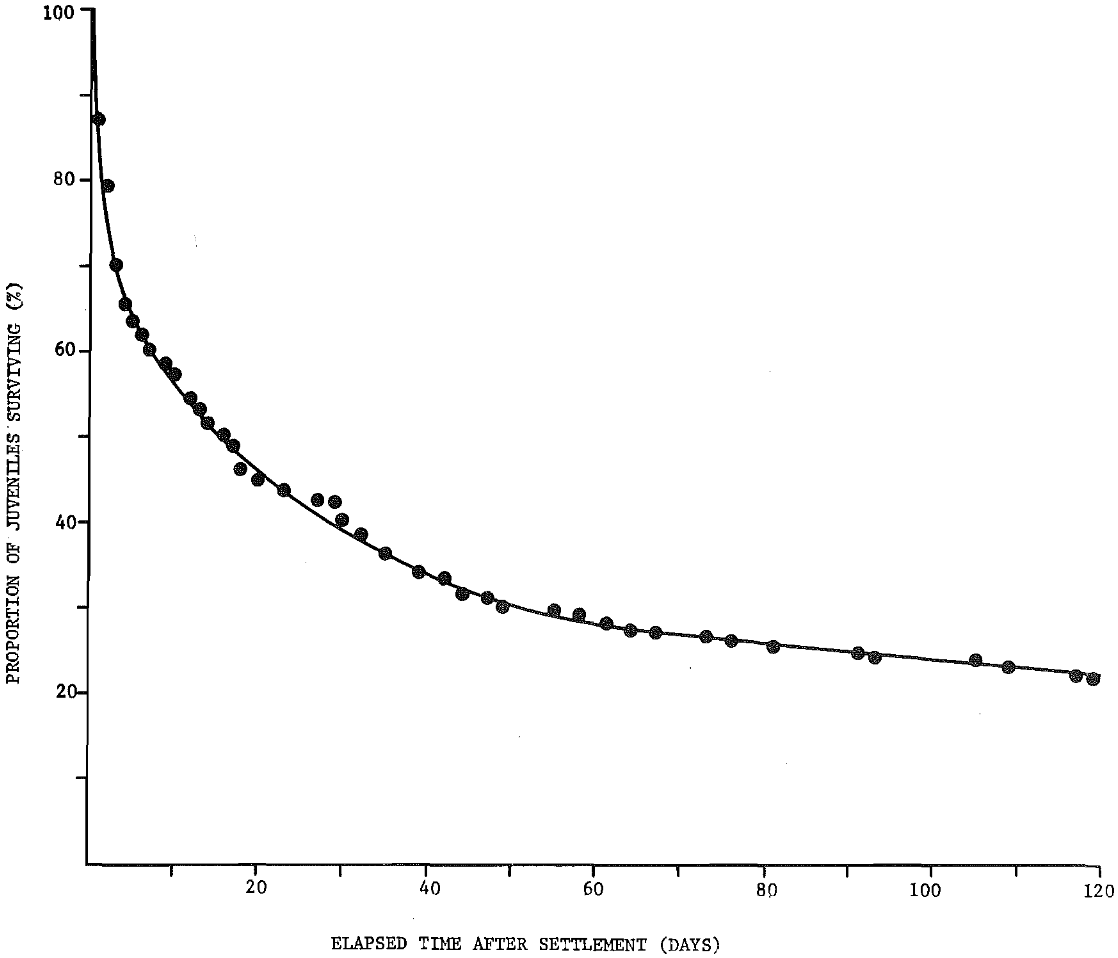
Size class (mm CD)	Period for growth (cumulative years after settlement)	
	at mean rate*	at maximum rate*
5.5 - 7.99	1.9	0.4
8.0 - 12.99	7.2	1.2
13.0 - 17.99	10.3	2.1
18.0 - 19.99	11.8	2.6
20.0 - 22.99	14.1	3.3
23.0 - 27.99	29.3	4.7
28.0 - 39.99	65.5+	8.3++

* Mean and maximum absolute growth rates are taken from Table 11.

\+ Mean absolute growth rate of 0.331 mm.y^{-1} is used for this calculation.

++ Maximum absolute growth rate of 3.329 mm.y^{-1} is used for this calculation.

FIGURE 30: Survivorship curve of juveniles which were first seen between November 1973 and April 1974 inclusive. The curve shown was fitted by eye. Only 49 juveniles, of the original 233, survived 150 days, but then 17 survived 525 days. This suggests that the instantaneous exponential mortality rate ($M = 3.7941.y^{-1}$ for 150 days) does not remain constant, but approaches closer to zero with time.


100
80
60
40
20
PROPORTION OF JUVENILES SURVIVING (%)
20
40
60
80
100
120
ELAPSED TIME AFTER SETTLEMENT (DAYS)

settlement. These predicted values were clearly low, however, because from direct observations, 17 of the original 233 were still living 1.4 y after settlement, and <u>at least</u> five lived 2 y (Chapter 4).

<u>Adults</u>

Over the three years of observations, five adults died, of the original 82. Hence,

$$M = -\ln(\tfrac{77}{82}).3\ y^{-1} \quad . \quad . \text{ from equation (2) above}$$

$$= 0.02097.y^{-1}$$

$$T = -\ln(\tfrac{N_T}{82}).0.02097^{-1}\ y \quad . \text{ from equation (3) above}$$

$$\bar{T} = 47.7\ y \quad . \quad . \text{ from equation (4) above.}$$

Therefore, 41 adults (50%) should live 33 y after the start of observations, 8 adults (10%) should live 110 years after the start, and 1 adult (1.2%) should live 210 y after the start.

Mean longevity of adults should be 48 y after the start of observations. As calculated previously (Chapter 5.3), a juvenile would take a minimum of 1.6 y, and probably about 8.4 y, to reach adult size. So, all adults of size 20 mm CD seen during the first period of observations would have been <u>at least</u> several years old then, to reach that size. Thus, 50% of the adults seen on Colony #1 should live to be at least 35 y, and the mean longevity should be in excess of 50 y.

5.6 DISCUSSION

Harenactis attenuata lives in an unstable environment, burrowing through unconsolidated sand, yet Fager (1968) found that the mean life expectancy of observed adults was still over 3.5 years.

Colony #1, although offering considerably harsher physical conditions, nevertheless provided a very stable substrate for Actinia, and the mean longevity of the observed adults was calculated to be in excess of 50 years. Since the period of observations included record extremes of wind, rainfall and high temperatures, as well as some of the most severe gales at Kaikoura for many years (Chapter 4), the observed mortality of adults may well have been higher than in "normal" years. Hence, I regard the predicted longevities as minimum estimates for the adults on Colony #1.

The longevities calculated for juveniles, from the observed rate of mortality in their first 150 days after settlement, were also low. The instantaneous exponential mortality rate indicated that only one juvenile should be living 1.4 years after settlement, whereas direct observations showed that 17 juveniles survived 1.4 years and at least 5 juveniles survived 2 years. It seems likely that the first year of the survivorship curve for settled juveniles may be best represented by the summation of three or more curves, rather than just one exponential relationship, in which the mortality rate successively decreases as the juveniles age and grow. As pointed out previously, the rate of mortality is to some extent dependent on size: large juveniles can not only withstand a degree of desiccation that would kill small juveniles (Ottaway 1973), but they can also resist the interference of grazing molluscs (Chapter 4). The mortality rate of settled juveniles on stable rock outcrops probably shows at least three significant decreases within the first 150 days after settlement, as particular mortality factors diminish in importance. Firstly, many juveniles are washed away within days of settlement because they do not attach firmly to a suitable substrate. Secondly, a high proportion of juveniles that successfully do settle die soon after, because of unfavourable physical conditions at low tide. In some instances, juveniles survived on exposed positions during cool, moist weather at low tides, but died during warm, dry periods which followed months after their settlement. To some extent, the latter mortality was correlated with size, but it was more a consequence of the particular site on which the juvenile chanced to settle. Similar size ranges of juveniles were seen to settle on the Colony area and away from it, yet none of those settling away from it survived a year. In all, over 50% of juveniles died within 20 days of settlement. Thirdly, throughout the year juveniles were susceptible to dislodgement or crushing by grazing molluscs. This accounted for only a small proportion of the total juvenile mortality, but the risk of fatal interference from molluscs became markedly less as the juvenile grew. Juveniles greater than 10 mm column diameter could resist all but the largest limpets, and even those molluscs had minimal effect on adult Actinia (Chapter 4).

Thus, the survival of juveniles on stable rock outcrops in the first 20 days after release is to a large extent independent of size, and is mainly dependent on a chance combination of many other factors associated with sea and weather conditions during and immediately following the time of release. Juveniles settling at column diameters of less than about 2 mm were markedly short-lived, and were killed by quite normal low-tide conditions. Survival rates for juveniles settling at the mean size (5.5 mm CD) and those settling at the largest size were not notably different. In terms of survival value for the species, there may well be an advantage here in releasing the greatest number of moderately-sized young. On the other hand, there is presumably a limitation on the mass of juveniles which can be supported in the coelenteron of a brooding adult, since apart from volume constraints the brooded juveniles are, in effect, parasitising the ingested food of their host.

On semi-stable boulder beaches, the greatest survival value would seem to lie with releasing fewer but larger juveniles than is optimal on stable rock outcrops. The chances of a juvenile successfully settling and surviving the first 20 days are probably quite high, perhaps even as much as 50%, but because of catastropic disturbances during most winters (Chapter 4), even adults would be unlikely to survive more than several years.

As noted above, however, juveniles less than 2 mm column diameter are very unlikely to survive on stable rock outcrops, and probably would also have a very high mortality rate on unstable boulder beaches even if they did successfully settle. Larger juveniles still have a low survival rate on stable rock outcrops, but they have a higher survival rate on unstable boulder beaches. Since it probably requires, on the part of a brooding adult, about equivalent energy expenditure to produce 250 juveniles of 2 mm column diameter, as 10 juveniles of 5.5 mm column diameter, as one juvenile of 13 mm column diameter, there may be some mechanism which allows environmental factors to determine the optimum mean size at which juveniles are released.

Annual mean growth rates were low for all size classes of Actinia considered, but the smallest juveniles, those between 3 mm and 8 mm column diameter, showed the greatest variation in annual relative growth increments, from -65% to 113%. Juveniles generally seem to grow faster while being brooded (Chapter 2) than when free-living (Chapter 4). As the free-living juveniles increased in size, their growth appeared to become less erratic, and after having been established for a year or so those juveniles over 10 mm column diameter had a high survival rate and were growing such that most would reach maturity within a few years. The particular growth rate of individuals is probably determined by the amount of food that individual captures, and although this aspect was not investigated it probably depends as much on the site on which the juvenile chanced to settle as on the annual and seasonal abundance of zooplankton.

What factors determine the maximum size to which *Actinia* may grow are not known. As the anemones increase in size the drag forces acting upon them, from waves passing over the shore, are also increasing (Wainwright & Koehl 1976; Koehl 1976). Possibly the very largest individuals may be exposed to a high risk of detachment by wave action, though on stable rock outcrops the mortality of *Actinia* between 15 mm and 40 mm column diameter seemed effectively independent of size (Chapter 4).

The factors determining the maximum age of *Actinia* are also unknown. There is no indication of a decline in reproductive capacity with size (Chapter 2), or of senescence, and the mortality data indicate that in those exceptionally rare circumstances where environmental conditions are suitable, some free-living *Actinia* live for over 210 years.

CHAPTER SIX

SUMMARY

1. The original name and description of the species *Actinia tenebrosa*, which were given by Farquhar (1898), are considered to be valid.

2. *A. tenebrosa* occurs intertidally, on stable and semi-stable rocky shores, around most of New Zealand and its offshore islands.

3. The population ecology of the species was studied at Kaikoura, with both field and laboratory work, from 1972 - 1976 inclusive.

4. It is suggested that the normal reproductive mode of the observed population may be cross-fertilising labile gonochorism, in which adults change from one sex to the other within the one breeding season. Brooding adults would be the maternal parents of their brooded embryos.

5. Up to 77% of the adult population developed gonads at any one time. The main period of gonad development, November to April inclusive, coincided with the warmest annual sea temperatures.

6. Throughout the year, females, males and adults without gonads may be found brooding embryos. Some 20% to 94% of adults were brooding at any one time.

7. Over 99.4% of brooded embryos dissected from collected specimens were tentaculate young, with a size range of 0.5 mm to 12.6 mm column diameter. The rest were planulae of diameters in the range 0.3 mm to 0.6 mm.

8. Tentaculate juveniles were released throughout the year. Peaks of juvenile release coincided with peaks of brooding in January,

February or March. In each season the peak of brooding followed about two months after the peak of gonad development.

9. There was no significant difference between the sizes of adults found to contain ovaries, and those found containing testes.

10. The extent of gonad development and the mean number of juveniles found per adult per month, by dissections, were quite variable over the three seasons studied. The peaks in mean numbers of juveniles brooded per adult were 13.6 for 1972 - 1973, 3.8 for 1973 - 1974, and 10.5 for 1974 - 1975.

11. With very few exceptions, only Actinia larger than 15 mm column diameter developed gonads and were found to be brooding. There was a wide variation in the number of juveniles brooded per adult (mean = 4.01, range = 0 - 98), but, generally, and considering all of the 1851 dissected adults, the mean number of juveniles brooded increased with increasing size of brooder.

12. Actinia showed very little pedal locomotion on a stable rock outcrop in a colony which was observed intensively over 738 days. Some 73% of the adults and juveniles moved less than 50 mm, and some anemones showed no discernible locomotion at all.

13. Large, directed movements of up to 1.6 m and 210 mm/day were sometimes associated with such external factors as impact injuries from moving rocks or logs, physical shocks, repeated desiccation, biological interference from molluscs, or wounding from intraspecific aggression.

14. Acrorhagi, or marginal spherules, are specialised structures containing atrichous nematocysts (Carlgren 1949, 1950a), which are used during intraspecific aggression. Acrorhagi usually develop only after a juvenile has been free-living for at least several months and has grown to more than 10 mm column diameter.

All examined Actinia larger than 15 mm column diameter possessed well-developed acrorhagi.

15. Contact of two adult Actinia did not always result in an aggressive conflict. Once initiated, an "acrorhagial response" was completed within five minutes, but acrorhagial wounds were apparent on the victim for up to 10 days afterwards.

16. After intraspecific aggression the wounded anemone always moved directly away from the aggressor. Pedal locomotion of 100 mm within 2 h of wounding was not uncommon in the laboratory experiments.

17. During 2 y of observations on the Actinia colony on a stable rock outcrop, some 44% of adults were involved in fights with other adults. None of these fights was fatal.

18. The number of juveniles in that colony fluctuated markedly from season to season, between 81% and 225% of the number first seen in November 1973. Some 8% of the juveniles first seen in that month survived at least 2 y. Between December 1973 and December 1975 the number of juveniles present showed a net increase of 21%.

19. The number of adults in that colony remained very stable. Some 94% of the adults first seen survived 3 y, and the number of adults present during that period showed a net decrease of 2.4%.

20. The mean size of released juveniles was 5.5 mm column diameter; the size range was 0.5 - 13.3 mm column diameter.

21. At least 60% of the released juveniles were washed away from their brooding adults without attaching. Of those that did attach, over 50% died or were washed away within 20 days of settlement.

22. The main causes of juvenile mortality were, in order of decreasing importance, failure to successfully attach, desiccation at low tides, dislodgement or crushing by grazing molluscs, impact injuries during gales, and exposure to a combination of excessive

desiccation and high temperatures at low tides.

23. The main cause of adult mortality was impact injuries, from moving rocks or logs during gales.

24. The rate of mortality of juveniles in their first 20 days after settlement is largely independent of their size. After that, the mortality rate is correlated with size until they exceed about 10 mm column diameter: the smaller juveniles are more susceptible to both desiccation at low tide and to fatal interference from grazing molluscs. Adult mortalities appeared to be independent of size, although very large Actinia, those exceeding 40 mm column diameter, may be more susceptible to being torn off the substratum by waves passing over the shore.

25. Annual growth increments were small, for all sizes of Actinia observed, and most increments were in the range -2 mm to +4 mm per year. The largest absolute increase in size was 6.2 mm in one year, which was also the largest relative increase, of 113%.

26. From growth data, Actinia first develop gonads 2 to 9 y after settlement, and would reach maximum size of about 40 mm column diameter 8 to 66 y after settlement.

27. From mortality data, the adults observed on the stable rock outcrop have a predicted mean longevity of at least 50 y, and a predicted maximum longevity of at least 210 y.

CHAPTER SEVEN

ACKNOWLEDGEMENTS

I especially thank Dr W.C. Clark for his guidance and patient supervision.

Thanks are also offered to all those friends and colleagues who have contributed to this thesis, in particular: Professor G.A. Knox, Mrs. F.R. Allison, Dr W.C. Clark, Dr J.M. Daly, I. Mannering, S.L. Bennington, R.M. Ogilvie, K. Sainsbury and J.C. Town. In addition, the late Dr E.J. Batham, Professor F.S. Chia, Dr D.F. Dunn, Professor C. Hand and Dr E.A. Robson have given their comments, which were very useful, on parts of my work. Mr A. Gall was meticulous in his expert construction of equipment used in the study.

Financial support from a New Zealand Commonwealth Postgraduate Award is gratefully acknowledged, as is the continued assistance of the Secretaries of the New Zealand University Grants Committee, Mr. W. Broad and Miss Dorothy Anderson. Finally, I record my gratitude to Patricia Miethke for her support during 1972 - 1974.

CHAPTER EIGHT

REFERENCES

Abel, E. F. (1954). Ein Beitrag zur Giftwirkung der Aktinien und Funktion der Randsäckchen. Zoologischer Anzeiger. 153, 259-268.

Andrewartha, H. G. and Birch, L. C. (1954). "The Distribution and Abundance of Animals". (University of Chicago Press: Chicago).

Appellöf, A. (1900). Studien über Actinien-Entwicklung. Bergens Museums Aarbog. 1, 3-99.

Ashworth, J. H. and Annandale, N. (1904). Observations on the some aged specimens of Sagartia troglodytes, and on the duration of life in Coelenterates. Proceedings of the Royal Society of Edinburgh. 25, 295-308.

Barnes, H. (1975). Reproductive rhythms and some marine invertebrates: an introduction. Pubblicazioni della Stazione Zoologica di Napoli. 39 (suppl.), 8-25.

Batham, E. J. (1958). Ecology of southern New Zealand exposed rocky shore at Little Papanui, Otago Peninsula. Transactions of the Royal Society of New Zealand. 85, 647-658.

Batham, E. J. (1965). The neural architecture of the sea anemone Mimetridium cryptum. American Zoologist. 5, 395-402.

Batham, E. J. and Pantin, C. F. A. (1950a). Muscular and hydrostatic action in the sea-anemone Metridium senile (L.). Journal of Experimental Biology. 27, 264-289.

Batham, E. J. and Pantin, C. F. A. (1950b). Inherent activity in the sea-anemone Metridium senile (L.). Journal of Experimental Biology 27, 290-301.

Batham, E. J. and Pantin, C. F. A. (1950c). Phases of activity in the sea-anemone *Metridium senile* (L.), and their relation to external stimuli. *Journal of Experimental Biology*. **27**, 377-399.

Bigger, G. H. (1976). The acrorhagial response in *Anthopleura krebsi*: intraspecific and interspecific recognition. Pp. 127-136 *in* "Coelenterate Ecology and Behavior". (Ed. G. O. Mackie.) (Plenum Press: New York.)

Black, J.H. (1971). Port Phillip Bay Survey Part 2: benthic communities. *Memoirs of the National Museum of Victoria*. **32**, 129-170.

Blackburn, M. (1937). Lady Julia Percy Island: Coelenterata. *Proceedings of the Royal Society of Victoria*. **49**, 364-371

Bonnin, J. P. (1964). Recherches sur la "réaction d'agression" et sur le fonctionnement des acrorrhages d'*Actinia equina* L. *Bulletin Biologique de la France et de la Belgique*. **98**, 225-250.

Cain, A. J. (1974). Breeding system of a sessile animal. *Nature*. **247**, 289-290.

Carlgren, O. (1900). Ostafrikanische Actinien. *Mitteilungen aus dem Naturhistorischen Museum, Hamburg*. **17**(2), 21-144.

Carlgren, O. (1924). Actiniaria from New Zealand and its subantarctic islands. Papers from Dr Th. Mortensen's Pacific Expedition 1914-1916, No. 21. *Videnskabelige Meddelelser fra Dansk naturhistorisk Forening i Kjøbenhavn*. **77**, 179-261.

Carlgren, O. (1949). A survey of the Ptychodactiaria, Corallimorpharia and Actiniaria. *Kungliga Svenska Vetenskapsakademien Handlingar (Fjärde serien)*. **1**,(1), 1-121.

Carlgren, O. (1950a). Corallimorpharia, Actiniaria and Zoantharia from New South Wales and South Queensland. *Arkiv för Zoologi, Kungliga Svenska Vetenskapsakademien*. **1**(10), 131-146.

Carlgren, O. (1950b). Actiniaria and Zoantharia from South Australia. Kungliga Fysiografiska Sällskapet i Lund Forhandlingar. 20(10), 121-135.

Carlgren, O. (1954). Actiniaria and Zoantharia from South and West Australia with comments upon some Actiniaria from New Zealand. Arkiv för Zoologi, Kungliga Svenska Vetenskapsakademien. 6 (34), 571-595.

Chia, F.S. (1976). Sea anemone reproduction: patterns and adaptive radiations. Pp. 261-270 in "Coelenterate Ecology and Behavior". (Ed. G. O. Mackie.) (Plenum Press: New York.)

Chia, F. S. and Rostron, M. A. (1970). Some aspects of the reproductive biology of Actinia equina (Cnidaria: Anthozoa). Journal of the Marine Biological Association of the United Kingdom. 50, 253-264.

Chia, F. S. and Spaulding, J.G. (1972). Development and juvenile growth of the sea anemone, Tealia crassicornis. Biological Bulletin of the Marine Biological Laboratory, Woods Hole. 142, 206-218.

Cleland, J. B. and Southcott, R. V. (1965). Injuries to Man from marine invertebrates in the Australian region. National Health and Medical Research Council. Special Report Series No. 12.

Clubb, J. A. (1908). Coelenterata. IV. Actiniae. In "National Antarctic Expedition 1901-1904. Natural History, 4, Zoology". Pp. 1-12. (British Museum: London.)

Comfort, A. (1964). "Ageing: the Biology of Senescence". (Routledge and Kegan Paul: London.)

Connell, J. H. (1961). Effect of competition, predation by Thais lapillus, and other factors on natural populations of the barnacle Balanus balanoides. Ecological Monographs. 31, 61-104.

Cotte, J. (1922). Études sur le comportment et les réactions des actinies. Bulletin de l'Institut Océanographique. 410, 1-44.

Crisp, D. J. (1964). North-west Ireland. Pp. 197-198 in "The effects of the severe winter of 1962-1963 on marine life in Britain". (Ed. D. J. Crisp.) Journal of Animal Ecology. 33, 165-210.

Crisp, D. J., Moyse, J. and Nelson-Smith, A. (1964). General conclusions. Pp. 202-207 in "The effects of the severe winter of 1962-1963 on marine life in Britain". (Ed. D.J. Crisp.) Journal of Animal Ecology. 33, 165-210.

Crisp, D. J. and Southward, A. J. (1964). South and south-west coast. Pp. 179-183 in "The effects of the severe winter of 1962-1963 on marine life in Britain". (Ed. D. J. Crisp.) Journal of Animal Ecology. 33, 165-210.

Dakin, W. J. (1952). "Australian Seashores". (Angus & Robertson: Sydney.)

Dakin, W. J., Bennett, I., and Pope, E. (1948). A study of certain aspects of the ecology of the intertidal zone of the New South Wales coast. Australian Journal of Scientific Research. B 1, 176-230.

Dalyell, J. G. (1848). "Rare and Remarkable Animals of Scotland, Represented from Living Subjects; with Practical Observations on their Nature". Vol. 2. (Van Voorst: London.)

Dana, J. D. (1856). "United States Exploring Expedition During the Years 1838-1842: Atlas: Zoophytes". (Sherman: Philadelphia.)

Dayton, P. K. (1971). Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecological Monographs. 41, 351-389.

Dellow, V. (1955). Marine algal ecology of the Hauraki Gulf, New Zealand. *Transactions of the Royal Society of New Zealand*. **83**, 1-91.

Dellow, V. and Cassie, R. M. (1955). Littoral zonation in two caves in the Auckland district. *Transactions of the Royal Society of New Zealand*. **83**, 321-331.

Dicquemare, L'Abbé. (1773). Mémoire pour fervir à l'hiftoire des anemones de mer. *Philosophical Transactions of the Royal Society (London)*. **63**, 361-403.

Dicquemare, L'Abbé. (1775). Second mémoire pour fervir à l'hiftoire des anemones de mer. *Philosophical Transactions of the Royal Society (London)*. **65**, 207-248.

Dicquemare, L.'Abbé. (1777). Troifieme mémoire pour fervir à l'hiftoire des anemones de mer. *Philosophical Transactions of the Royal Society (London)*. **67**, 56-84.

Dix, T. G. (1970). Biology of *Evichinus chloroticus* (Echinoidea: Echinometridae) from different localities. 1. General. *New Zealand Journal of Marine and Freshwater Research*. **4**, 91-116.

Drayton, J. (1848). Actinidae. Pp. 122-154 *in* "United States Exploring Expedition During the Years 1838-1842: Zoophytes". (Ed. J. D. Dana.) (Lea and Blanchard: Philadelphia.)

Dunn, D. F. (1975a). Gynodioecy in an animal. *Nature*, *London*. **253**, 528-529.

Dunn, D. F. (1975b). Reproduction of the externally brooding sea anemone *Epiactis prolifera* Verrill, 1869. *Biological Bulletin of the Marine Biological Laboratory*, *Woods Hole*. **148**, 199-218.

Dunn, D. F. (1977a). Dynamics of external brooding in the sea anemone *Epiactis prolifera*. *Marine Biology*. **39**, 41-49.

Dunn, D. F. (1977b). Locomotion by Epiactis prolifera (Coelenterata: Actiniaria). Marine Biology. 39, 67-70.

Dunn, D. F. (1977c). Variability of Epiactis prolifera (Coelenterata: Actiniaria) in the intertidal zone near Bodega Bay, California. Journal of Natural History. 11, 457-463.

Edmunds, M., Potts, G. W., Swinfen, R. C., and Waters, V. L. (1976). Defensive behaviour of sea anemones in response to predation by the opisthobranch mollusc Aeolidia papillosa (L.). Journal of the Marine Biological Association of the United Kingdom. 56, 65-83.

Elmhirst, R. (1915). Notes on anemones from the Millport Marine Biological Station. Zoologist (London). 19, 21-24.

Fager, E. W. (1968). A sand-bottom epifaunal community of invertebrates in shallow water. Limnology and Oceanography. 13, 448-464.

Farquhar, H. (1898). Preliminary account of some New Zealand Actiniaria. Journal of the Linnean Society of London (Zoology). 26, 527-536.

Fleure, H. J. and Walton, C. L. (1907). Notes on the habits of some sea anemones. Zoologischer Anzeiger. 31, 212-220.

Ford, C. E. (1964). Reproduction in the aggregating sea anemone, Anthopleura elegantissima. Pacific Science. 18, 138-145.

Foster, B. A. (1971). Desiccation as a factor in the intertidal zonation of barnacles. Marine Biology. 8, 12-29.

Fox, H. M. (1964). Longevity in a polychaete and a coelenterate. Nature. 198, 1222-1223.

Francis, L. (1973a). Clone specific segregation in the sea anemone Anthopleura elegantissima. Biological Bulletin of the Marine Biological Laboratory, Woods Hole. 144, 64-72.

Francis, L. (1973b). Intraspecific aggression and its effect on the distribution of *Anthopleura elegantissima* and some related sea anemones. *Biological Bulletin of the Marine Biological Laboratory*, *Woods Hole*. **144**, 73-92.

Francis, L. (1976). Social organization within clones of the sea anemone *Anthopleura elegantissima*. *Biological Bulletin of the Marine Biological Laboratory*, *Woods Hole*. **150**, 361-376.

Gemmill, J. F. (1920). The development of the sea-anemones *Metridium dianthus* (Ellis) and *Adamsia palliata* (Bohad). *Philosophical Transactions of the Royal Society (London)*. *Series B*. **209**, 351-375.

Gillespie, A. S. (1931). Notes on the breeding habits of *Actinia equina* (Linnaeus). *Proceedings of the South Western Naturalists' Union (Bristol)*. **2**, 111-112.

Gosse, P. H. (1860). "A History of the British Sea-Anemones and Corals". (Van Voorst: London.)

Gravier, C. J. (1916). Sur l'incubation chez l'*Actinia equina* L. à l'Île de San Thomé (golf de Guinée). *Comptes Rendus Hebdomaires des Séances de l'Académie des Sciences*. **162**, 986-988.

Guiler, E. R. (1950). The intertidal ecology of Tasmania. *Papers and Proceedings of the Royal Society of Tasmania*. For **1949**, 135-201.

Guiler, E. R. (1954). The recolonization of rock surfaces and the problem of succession. *Papers and Proceedings of the Royal Society of Tasmania*. **88**, 49-66.

Hand, C. (1955). The sea anemones of central California. Part II. The endomyarian and mesomyarian anemones. *Wasmann Journal of Biology*. **13**, 37-99.

Hargitt, C. W. (1907). Notes on the behavior of sea-anemones. Biological Bulletin of the Marine Biological Laboratory, Woods Hole. 12, 274-284.

Hartog, J. C. den. (1954). Notities over Actinia equina. Het Zeepaard. 14, 19-20.

Hartog, J. C. den. (1961). Enige aantekeningen over Actinia equina (L.) de gewone zeeanemoon. De Levende Natuur. 64, 280-285.

Hatton, H. (1938). Essais de bionomie explicative sur quelques espèces intercotidales d'algues et d'animaux. Annales de l'Institut océanographique (Monaco). 17, 241-348.

Heath, E. and Dell, R. K. (1971). "Seashore Life of New Zealand". (Reed: Wellington.)

Hedley, C. (1915). An ecological sketch of the Sydney beaches. Proceedings of the Royal Society of New South Wales. 49, 15-77.

Hodgkin, E. P. (1959). Catastropic destruction of the littoral fauna and flora near Fremantle, January 1959. The Western Australian Naturalist. 7, 6-11.

Howe, N. R. and Sheikh, M. Y. (1975). Anthopleurine: a sea anemone alarm pheromone. Science. 189, 386-389.

Hutton, F. W. (1904). Phylum Coelenterata. Pp. 314-321 in "Index Faunae Novae Zealandiae". (Ed. F. W. Hutton.) (Dulau: London.)

Hyman, L. H. (1940). "The Invertebrates: Protozoa through Ctenophora". (McGraw-Hill: New York.)

Jennings, H. S. (1905). Modifiability in behavior. I. Behavior of sea anemones. Journal of Experimental Zoology. 2, 447-472.

Johnston, G. (1846). "A History of British Zoophytes". (Van Voorst: London.)

Johnston, T. H. (1917). Ecological notes on the littoral fauna and flora of Caloundra, Queensland. The Queensland Naturalist. 2, 53-63.

Johnson, L.L. and Shick, J. M. (1977). Effects of fluctuating temperature and immersion on asexual reproduction in the intertidal sea anemone Haliplanella luciae (Verrill) in laboratory culture. Journal of Experimental Marine Biology and Ecology. 28, 141-149.

Kensler, C. B. (1967). Desiccation resistance of intertidal crevice species as a factor in their zonation. Journal of Animal Ecology. 36, 391-406.

Kinne, O. (1970). Temperature: animals: invertebrates. Pp. 407-514 in "Marine Ecology". Vol. I. (Ed. O. Kinne.) (Wiley-Interscience: London.)

Kinne, O. (1971). Salinity: animals: invertebrates. Pp. 821-995 in "Marine Ecology". Vol. I. (Ed. O. Kinne.) (Wiley-Interscience: London.)

Kirk, R. M. (1975). Statistical summary of sea state observations in New Zealand, 1974. Unpublished Report from the Department of Geography, University of Canterbury.

Kirk, R. M. (1976). Tidal observations at the Edward Percival Marine Laboratory, Kaikoura. October 1967 to October 1972. Unpublished Report from the Department of Geography, University of Canterbury.

Knox, G. A. (1960). Littoral ecology and biogeography of the southern oceans. Proceedings of the Royal Society. B 152, 557-624.

Knox, G. A. (1963). The biogeography and intertidal ecology of the Australasian coasts. Oceanography and Marine Biology Annual Review. 1, 341-404.

Knox, G. A. (1969). The plants and animals of the rocky shores. Pp. 536-552 in "The Natural History of Canterbury". (Ed. G. A. Knox.) (Reed: Wellington.)

Koehl, M. A. R. (1976). Mechanical design in sea anemones. Pp. 23-31 *in* "Coelenterate Ecology and Behavior". (Ed. G. O. Mackie.) (Plenum Press: New York.)

Landauer, W. (1924). Laceration, Knospung und Heteromorphose bei *Actinia equina*, L. *Zeitschrift für Morphologie und Ökologie der Tiere (Berlin)*. **3**, 177-187.

Lewis, J. R. (1954). Observations on a high-level population of limpets. *Journal of Animal Ecology*. **23**, 85-100.

Lewis, J. R. (1964). "The Ecology of Rocky Shores". (English University Press: London.)

Lewis, J. R. (1968). Water movements and their role in rocky shore ecology. *Sarsia*. **34**, 13-36.

Livingstone, A. A. (1928). Sea anemones and their associates. *The Australian Museum Magazine*. **3**, 229-232.

Mackie, G. O. (1964). Locomotion, flotation and dispersal. Pp. 313-357 *in* "Coelenterate Biology". (Eds. L. Muscatine and H. M. Lenhoff.) Academic Press: New York.)

Mariscal, R. N. (1974). Nematocysts. Pp. 129-178 *in* "Coelenterate Biology". (Eds. L. Muscatine and H. M. Lenhoff.) (Academic Press: New York.)

M'Bain, J. (1878). Notes on *Actinia mesembryanthemum*, taken from a rock pool at North Berwick by the late Sir John Graham Dalyell in August 1828. *Proceedings of the Royal Society (Edinburgh)*. **4**, 280-288.

McMurrich, J. P. (1890). Contributions on the morphology of the Actinozoa. II. On the development of the Hexactiniae. *Journal of Morphology*. **4**, 303-330.

Meadows, P. S. and Campbell, J. I. (1972a). Habitat selection by aquatic invertebrates. *Advances in Marine Biology*. **10**, 271-282.

Meadows, P. S. and Campbell, J. I. (1972b). Habitat selection and animal distribution in the sea: the evolution of a concept. *Proceedings of the Royal Society of Edinburgh*. **B**, **73**, 145-157.

Milia, A. Di, and Geppetti, L. (1964). On the expansion-contraction rhythm of the sea anemone, *Actinia equina* L. *Experientia*. **20**, 571-572.

Milne-Edwards, H. (1857). "Histoire Naturelle des Coralliaires ou Polypes Proprement Dits". Vol. I. (Roret: Paris.)

Moore, P. G. (1975). The role of habitat selection in determining the local distribution of animals in the sea. *Marine Behaviour and Physiology*. **3**, 97-100.

Morgans, J. F. C. (1967a). The macrofauna of an excellently sorted isolated beach at Kaikoura: and certain tidal observations. *Transactions of the Royal Society of New Zealand*. **9**, 157-167.

Morgans, J. F. C. (1967b). Records of breeding activity of marine invertebrates at Kaikoura. *Transactions of the Royal Society of New Zealand*. **9**, 169-174.

Morton, J. E. and Miller, M. (1968). "The New Zealand Seashore". (Collins: London.)

Moyse, J. and Nelson-Smith, A. (1964). Effects of the severe cold of 1962-1963 upon shore animals in South Wales. Pp. 183-190 *in* "The effects of the severe winter of 1962-1963 on marine life in Britain". (Ed. D. J. Crisp.) *Journal of Animal Ecology*. **33**, 165-210.

Nyholm, K. G. (1943). Zur Entwicklung und Entwicklungsbiologie der Ceriantharien und Aktinien. *Zoologiska bidrag fran Uppsala*. **22**, 87-248.

Oliver, W. R. B. (1923). Marine littoral plant and animal communities in New Zealand. *Transactions of the New Zealand Institute*. **54**, 496-545.

Osburn, R. C. (1914). Movements of sea anemones. Bulletin of the New York Zoological Society. 17, 1163-1166.

Ottaway, J. R. (1973). Some effects of temperature, desiccation, and light on the intertidal anemone *Actinia tenebrosa* Farquhar (Cnidaria: Anthozoa). Australian Journal of Marine and Freshwater Research. 24, 103-126.

Ottaway, J. R. (1974). Resistance of juvenile *Actinia tenebrosa* (Cnidaria: Anthozoa) to digestive enzymes. Mauri Ora. 2, 73-83.

Ottaway, J. R. (1975a). Review of *Actinia*, *Isactinia* and *Cnidopus* (Cnidaria: Anthozoa) in New Zealand. New Zealand Journal of Marine and Freshwater Research. 9, 53-61.

Ottaway, J. R. (1975b). Tidal tank system in operation at the Edward Percival Marine Laboratory, Kaikoura. Mauri Ora. 3, 31-36.

Ottaway, J. R. (1975c). *Epiactis thompsoni* (Coughtrey, 1875) and *E. mortenseni* Carlgren, 1924 (Cnidaria: Anthozoa) (Note). New Zealand Journal of Marine and Freshwater Research. 9: 253-255.

Ottaway, J. R. (1976). Inshore sea temperatures at Kaikoura, New Zealand, 1973-1975. Mauri Ora. 4, 69-73.

Ottaway, J. R. (1977a). Predators of sea anemones. Tuatara. 22, 213-221.

Ottaway, J. R. (1977b). *Pleurobranchaea novaezelandiae* preying on *Actinia tenebrosa*. New Zealand Journal of Marine and Freshwater Research. 11, 125-130.

Ottaway, J. R. and Kirby, G. C. (1975). Genetic relationships between brooding and brooded *Actinia tenebrosa*. Nature. 255, 221-223.

Ottaway, J. R. and Thomas, I. M. (1971). Movement and zonation of the intertidal anemone *Actinia tenebrosa* Farqu. (Cnidaria: Anthozoa) under experimental conditions. *Australian Journal of Marine and Freshwater Research*. **22**, 63-78.

Pantin, C. F. A. (1952). The elementary nervous system. *Proceedings of the Royal Society*. **B**, **140**, 147-168.

Pantin, C. F. A. (1965). Capabilities of the coelenterate behaviour machine. *American Zoologist*. **5**, 581-589.

Parker, G. H. (1915). The locomotion of actinians. *Science*. **41**, 471.

Parker, G. H. (1917a). Pedal locomotion in actinians. *Journal of Experimental Zoology*. **22**, 111-124.

Parker, G. H. (1917b). Actinian behavior. *Journal of Experimental Zoology*. **22**, 193-229.

Parker, G. H. (1919). "The Elementary Nervous System". (Lippincott: Philadelphia.)

Parry, G. (1951). The Actiniaria of New Zealand. Part I. *Records of the Canterbury Museum*. **6**, 83-119.

Poore, G. C. B. (1973). Ecology of New Zealand abalones, *Haliotis* species (Mollusca, Gastropoda). *New Zealand Journal of Marine and Freshwater Research*. **7**, 67-84.

Pope, E. C. (1943). Animal and plant communities of the coastal rock platform at Long Reef, N.S.W. *Proceedings of the Linnean Society of N.S.W.* **68**, 221-254.

Ramsay, J. A. (1935). Methods of measuring the evaporation of water from animals. *Journal of Experimental Biology*. **12**, 355-372.

Reidl, R. (1971). Water movement: animals. Pp. 1123-1149 *in* "Marine Ecology". Vol. I. (Ed. O. Kinne.) (Wiley-Interscience: London.)

Robson, E. A. (1964). Adaptive changes in Cnidaria. Pp. 54-59 in "Learning and Associated Phenomena in Invertebrates". (Eds. W. H. Thorpe and D. Davenport.) (Bailliere, Tindall and Cassell: London.)

Robson, E. A. (1976). Locomotion in sea anemones: the pedal disk. Pp. 479-490 in "Coelenterate Ecology and Behavior". (Ed. G. O. Mackie.) (Plenum Press: New York.)

Ross, D. M. (1964). The behaviour of sessile coelenterates in relation to some conditioning experiments. Pp. 43-52 in "Learning and Associated Phenomena in Invertebrates". (Eds. W. H. Thorpe and D. Davenport.) (Bailliere, Tindall and Cassell: London.)

Ross, D. M. (1974). Behavior patterns in associations and interactions with other animals. Pp. 281-312 in "Coelenterate Biology". (Eds. L. Muscatine and H. M. Lenhoff.) (Academic Press: New York.)

Rossi, L. (1971). Thelytochus parthenogenesis in Cereus pedunculatus (Actiniaria). Experientia. 27, 349-351.

Rossi, L. (1975). Sexual races in Cereus pedunculatus (Boad.). Pubblicazioni della Stazione Zoologica di Napoli. 39, (Suppl.), 471-479.

Russell, F. S. and Yonge, C. M. (1936). "The Seas". (Warne: London.)

Saies, A. B., Beever, S. E., Hay, J. R., and Woods, R. G. (1972). The intertidal life of Red Mercury Island. Tane. 18, 43-55.

Sebens, K. P. (1976). Utilization of space on a coral reef. Pp. 67-77 in "Coelenterate Ecology and Behavior". (Ed. G. O. Mackie.) (Plenum Press: New York.)

Segal, E. (1970). Light: animals: invertebrates. Pp. 159-211 "Marine Ecology". Vol. I. (Ed. O. Kinne). (Wiley-Interscience: New York.)

Shick, J. M. (1976). Ecological physiology and genetics of the colonizing actinian *Haliplanella luciae*. Pp. 137-146 *in* "Coelenterate Ecology and Behavior". (Ed. G. O. Mackie.) (Plenum Press: New York.)

Siebert, A. E. (1973). A description of the sea anemone *Stomphia didemon* sp. nov. and its development. *Pacific Science*. **27**, 363-373.

Siebert, A. E. (1974). A description of the embryology, larval development and feeding of the sea anemones *Anthopleura elegantissima* and *Anthopleura xanthogrammica*. *Canadian Journal of Zoology*. **52**, 1383-1388.

Siebert, A. E. and Spaulding, J. G. (1976). The taxonomy, development and brooding behavior of the anemone, *Cribrinopsis fernaldi* sp. nov. *Biological Bulletin of the Marine Biological Laboratory, Woods Hole*. **150**, 128-138.

Sokal, R. R. and Rohlf, F. J. (1969). "Biometry". (Freeman: San Francisco.)

Southward, A. J. (1956). The population balance between limpets and seaweeds on wave-beaten rocky shores. *Reports of the Marine Biological Station, Port Erin*. **68**, 20-29.

Stephenson, T. A. (1922). On the classification of Actiniaria. III. Definitions connected with the forms dealt with in Part II. *Quarterly Journal of Microscopical Science*. **66**, 247-319.

Stephenson, T. A. (1928). "The British Sea Anemones". Vol. I. (Ray Society: London.)

Stephenson, T. A. (1935). "The British Sea Anemones". Vol. 2. (Ray Society: London.)

Stimpson, J. (1970). Territorial behavior of the owl limpet, *Lottia gigantea*. *Ecology*. **51**, 113-118.

Stock, J. H. (1951). Anemonen-notities. *Het Zeepaard*. **11**, 7-9.

Stuckey, F. G. A. (1909). A review of the New Zealand Actiniaria known to science, together with a description of twelve new species. *Transactions of the New Zealand Institute*. **41**, 374-398.

Stuckey, F. G. A. (1914). Description of a collection of Actinians from the Kermadec Islands. *Transactions of the New Zealand Institute*. **46**, 132-134.

Stuckey, F. G. A. and Walton, C. L. (1910). Notes on a collection of sea-anemones. *Transactions of the New Zealand Institute*. **42**, 541-543.

Tardent, P. (1975). Sex and sex determination in coelenterates. Pp. 1-13 *in* "Intersexuality in the Animal Kingdom". (Ed. R. Reinboth.) (Springer-Verlag: Berlin.)

Torelli, B. (1938). Istologia e senescenza in *Cerianthus*. *Pubblicazioni della Stazione Zoologica di Napoli*. **17**, 1-19.

Tugwell, G. (1856). "A Manual of the Sea-Anemones". (Van Voorst: London.)

Urk, J. M. van. (1952). Voorkomen en leefwijze van de gewone zeeanemoon langs onze kust. *De Levende Natuur*. **55**, 97-100.

Urk, J. M. van. (1953). De merkwaardige verspreiding van *Actinia equina* (gewone zeeanemoon). *Het Zeepaard*. **13**, 55-57.

Wainwright, S. A. and Koehl, M. A. R. (1976). The nature of flow and the reaction of benthic cnidaria to it. Pp. 5-21 *in* "Coelenterate Ecology and Behavior". (Ed. G. O. Mackie.) (Plenum Press: New York.)

Walton, A. C. (1918). Longitudinal fission in *Actinia*. *Journal of Morphology*. **31**, 43-52.

Wilber, C. G. (1971). Turbidity: animals. Pp. 1181-1189 *in* "Marine Ecology". Vol. I. (Ed. O. Kinne.) (Wiley-Interscience: New York.)

Williams, R. B. (1975). Catch-tentacles in sea-anemones: occurrence in *Haliplanella luciae* (Verrill) and a review of current knowledge. *Journal of Natural History*. **9**, 241-248.

Wolcott, T. G. (1973). Physiological ecology and intertidal zonation in limpets (*Acmaea*): a critical look at "limiting factors". *Biological Bulletin of the Marine Biological Laboratory, Woods Hole*. **145**, 389-422.

Zahl, P. A. and McLaughlin, J. J. A. (1959). Studies in marine biology. IV. On the role of algal cells in the tissues of marine invertebrates. *Journal of Protozoology*. **6**, 344-352.