Declaration.

I declare that the research reported in this thesis is my own, and that no part of it has been previously submitted for any other degree. The research was conducted in the Gatty Marine Laboratory, University of St Andrews, under the direction of Dr. C.D.Todd.

signed.

(Candidate)

Certificate.

I certify that Dominic Counsell has fulfilled the conditions laid down under Ordinance General Number 51, and Resolution of the University Court, 1974, Number 2; and that he is qualified to submit the accompanying thesis for the degree of Master of Science.

signed..

(Supervisor)

Copyright Declaration.

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Population dynamics and aspects of the feeding ecology of the starfish *Asterias rubens* (L.) at St Andrews.

by

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being a thesis submitted to the University of St Andrews
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ABSTRACT

The *A.rubens* populations at four fixed locations in St Andrews Bay were studied by periodic sampling using benthic trawls. Starfish densities, size-frequency distributions and organ index cycles were followed, and have been interpreted in terms of larval settlement, stochastic abiotic mortality factors, and the availability of benthic infauna.

A comparative study was made of littoral *A.rubens* from the southern edge of St Andrews Bay. A capture-recapture study indicated that there may be considerable interchange between littoral and sublittoral starfish. The two populations are therefore not discrete, in spite of differences in their size-structure and reproductive capacities.

A laboratory study of *A.rubens* foraging behaviour when presented with dispersed *Mytilus edulis* (L.) of a range of sizes revealed a preference for mussels smaller than the energetically-determined "optimal" size. When mussels were allowed to aggregate the mean size consumed was larger and more closely approximated the "optimal" size, but a reduced rate of consumption suggested foraging behaviour was constrained. The implications of an "optimal" prey size for *A.rubens* have been discussed in the context of periodic invasions of littoral mussel beds by this starfish.

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Chapter 1.

INTRODUCTION.

Asterias rubens (L.) is a widely distributed forcipulate asteroid ranging from the White Sea to the Senegal coast, from the low intertidal to a depth of at least 650m (Mortensen, 1927). Recent reports (*e.g.* Barker and Nichols, 1983) indicate that *A.rubens* may be conspecific with *A.vulgaris* (Verrill) on the Atlantic coast of North America. It is an opportunist predator, specialising on bivalves but capable of surviving on a wide range of foodstuffs (Sloan, 1980). It appears to be an "r-selected" species (*sensu* MacArthur and Wilson, 1967) whose planktotrophic life history and plasticity of growth permit it to exploit a wide variety of intertidal and subtidal habitats.

The biology of asteroids has received greater attention than that of other echinoderm classes, perhaps with the exception of echinoids, and the feeding biology in particular has recently been extensively studied (see Feder and Christensen, 1966; Sloan, 1980; Jangoux, 1982 for reviews). The genus *Asterias* has been implicated as a competitor with commercial fisheries over much of its range, either by direct consumption of shellfish or by competing with demersal fish for benthic infauna (Forbes, 1840; Galtsoff and Loosanoff, 1939; Smith, 1940; Nauen, 1978; Ventilla, 1982; Dare, 1982). Scallops, however, seem to possess an adequate escape response and even on commercial beds do not appear to be typical prey for A.rubens (Briggs, 1983).

Menge (1982) reviewed the literature concerning the effects of asteroid predation in intertidal and subtidal habitats around the world. He concluded that asteroid predation has been an intense and chronic selective force in marine benthic communities over evolutionary time. In temperate and polar regions at least, asteroids occupy a dominant predatory role both above and below the low water mark. In the tropics they are less important, and the role of top predator tends to be occupied by fish. In spite of the recent publicity given to the tropical crown-of-thorns starfish Acanthaster planci (L.) it appears that outbreaks of this starfish are sporadic. It has been suggested (Birkeland and Randall, 1979, in Menge, 1982) that these "plagues" are related to periods of unusually heavy rainfall during the A.planci breeding season, and that the high nutrient terrestrial runoff stimulates phytoplankton blooms which promote higher larval survival.

Temperate asteroids play different roles in both intertidal and subtidal habitats. In the former they occupy only the top trophic level, in the latter they may occupy at least the top two (Menge, 1982). Where mussels are present on the shore they are the superior competitors for space there. Since many intertidal starfish feed preferentially on mussels, the starfish play an important role in the structuring of this community. Paine (1969) coined the term "keystone" species to describe Pisaster ochraceus (Brandt) on

North-East Pacific shores. *P.ochraceus* feeds preferentially on *Mytilus californianus*, the competitive dominant for primary space there, and when excluded (Paine, 1966, 1974) the lower limit of *M.californianus* rapidly moved downshore and the species richness decreased as mussels took over. The ecological relationships of the New Zealand rocky intertidal appear to be similar to those of the Pacific coast of the USA, and exclusion of the asteroid *Stichaster australis* (Verrill) there had similar effects (Paine, 1971).

The niches occupied by *P.ochraceus* and *S.australis* in their respective habitats have no exact parallel in Great Britain. *Asterias rubens* is found in greatest numbers sublittorally, and on the shore occupies only the low shore (as opposed to mid- and low-shore occupied by *P.ochraceus*). Periodically, however, intertidal beds of *Mytilus edulis* (L.) are invaded by aggregations of *A.rubens* (*e.g.* Vinberg, 1967; Seed, 1969; Dare, 1982). For a period of several weeks the line of starfish advances five to seven metres a day (Dare, 1982). *M.edulis* are mostly (>95%) removed, up to an environmentally-imposed predation line (P.J.Dare, pers.comm.), and the starfish subsequently return to the subtidal in the autumn.

As a predator of bivalves *A.rubens* is almost certainly a "keystone" species also, and the aims of this study were to qualify and quantify aspects of the populaton dynamics of intertidal and subtidal *A.rubens* in St Andrews. In addition, laboratory experiments were designed to shed light on the foraging behaviour of *A.rubens*, particularly with regard to reports of indiscriminate mussel removal during invasions (C.Todd, pers.comm.). Optimal Foraging Theory predicts that natural selection favours an animal that gathers its food efficiently, thereby maximising its genetic contribution to the next generation (see Krebs, 1978). The currency normally considered to be maximised is that of energy.

Most studies testing this "energy maximisation hypothesis" (Schoener, 1971) have attempted to determine which of two prey species is more valuable to a predator, and in what circumstances and in what proportions less valuable prey should be included in the diet. Elner and Hughes (1978) performed size-specific predation experiments using the crab Carcinus maenas (L.) foraging on Mytilus edulis. Each mussel was envisaged to confer an associated cost in terms of time and effort required to overcome it, and a benefit in terms of gross caloric yield. C.maenas chooses that size of prey providing it with the highest net energy intake per unit time. These types of experiment were here repeated with A.rubens, a specialist bivalve predator but an animal whose nervous organisation is poorly understood, and an animal whose foraging patterns are likely to be important in determining the structure of some benthic communities in Great Britain.

Chapter 2.

SUBLITTORAL A.RUBENS POPULATIONS IN ST.ANDREWS BAY

2.1. Introduction.

Asterias rubens is a wide-ranging predator, well adapted for both hard and soft substrata. As a sand-dweller it may be less of a threat to commercial bivalve species than was once thought (Briggs, 1983); but by consuming the same food items it has been shown to compete with commercially-important demersal fish species (Galtsoff and Loosanoff, 1939; Anger *et al*, 1977; Nauen, 1978; Allen, 1983). As a generalist predator and a facultative scavenger it thrives on a wide variety of marine invertebrates and can also feed microphagously. One of the salient features of the biology of asteroids is their plasticity of growth. In the absence of food *A.rubens* has been shown to survive 17 months in the sea, and with superabundant food can attain an arm-length of eight or nine cm in its first year (Vevers, 1949).

St Andrews Bay is an apparently homogeneous shallow sandy habitat supporting large numbers of *A.rubens*. Studies both on *A.rubens* (Hulbert, 1980; Barker and Nichols, 1983) and on other asteroids (Pearse, 1965; Paine, 1969; Crump, 1971) have demonstrated clear differences in both size structure and reproductive potential in separated populations, attributable to differences in food quality and quantity. In these circumstances the reproductive and food storage capacities are therefore valid criteria for assessing trophic suitability and carrying capacity of the habitat (Scheibling, 1980b).

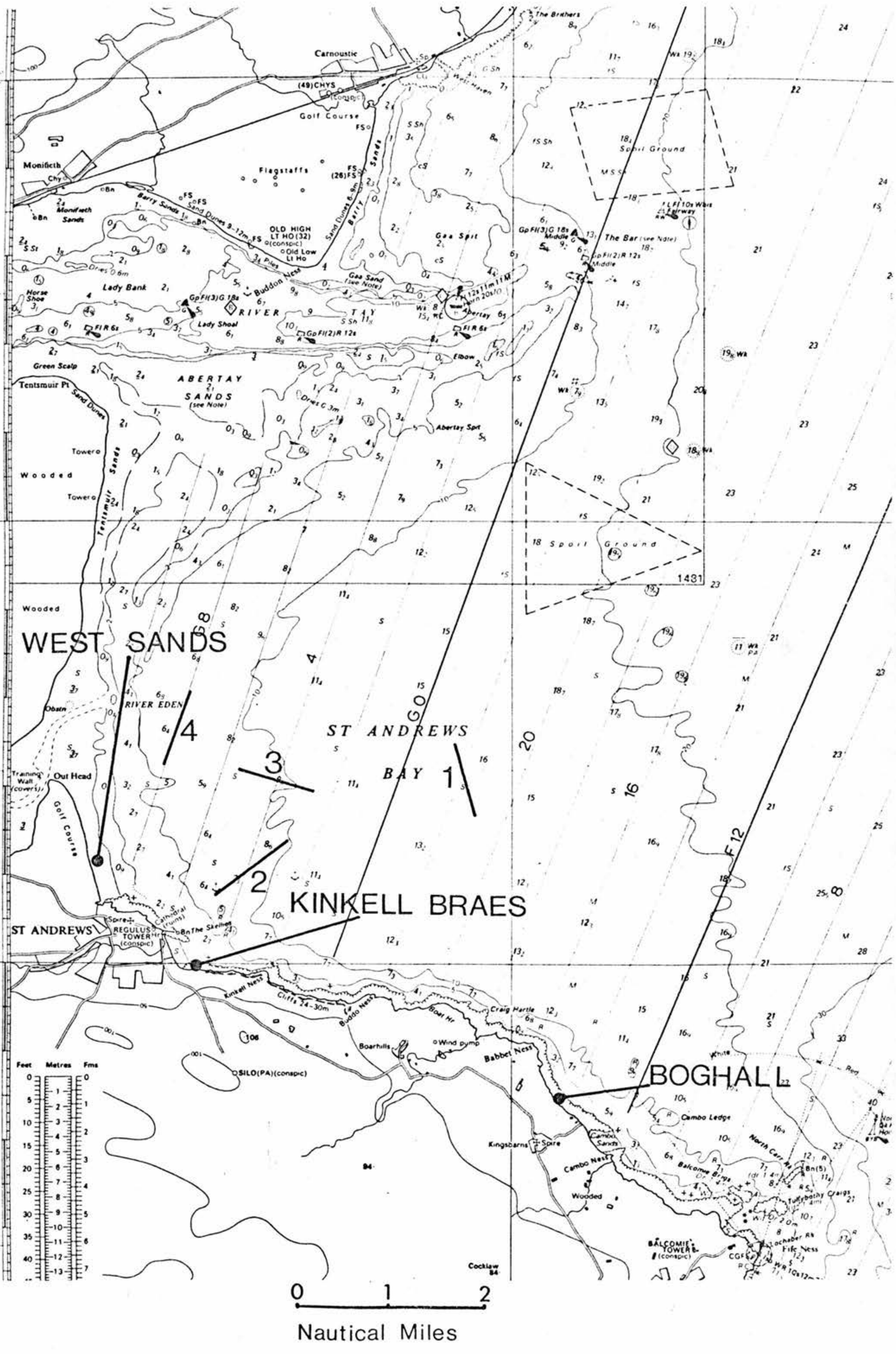
In the present study A.rubens from four areas of St Andrews Bay were compared for various population parameters, and these discussed with reference to larval settlement and the availability of benthic infauna.

2.2. Description of trawl sites.

A section of Admiralty chart number 190, showing St Andrews Bay and the four trawl transects is illustrated in Figure 1. St Andrews Bay is a shallowly shelving expanse of sand, lying between the outfall of the river Tay and the Firth of Forth, into which the river Eden drains. Prevailing winds come from the West/South-West, and there is an anticlockwise tidal gyre throughout the bay generated by the outflow of the river Tay. The trawl transects (denoted 1 to 4) were chosen to cover a wide area of St Andrews Bay and yet be within operating distance of St Andrews harbour for the R.V."Homarus". Trawl 1 is in deeper water (15-16m) about four nautical miles from St Andrews, while trawls 2,3 and 4 cover the inshore areas from St Andrews to the estuary of the Eden. These three are shallow (6-9m). Rather than make each transect a precise distance the lines started and finished on points distinguishable by the alignment of distinctive landmarks on the shore. The precise positions of the trawls, the

FIGURE 1

A section of Admiralty Chart 190, showing the four St. Andrews Bay trawls and other study areas.


WEST SANDS
KINKELL BRAES
BOGHALL
1
2
3
4
ST ANDREWS BAY
ST ANDREWS
Carnoustie
Monifieth
Barry Sands
Buddon Ness
RIVER TAY
ABERTAY SANDS
Tentsmuir Pt
Tentsmuir Sands
RIVER EDEN
Out Head
Golf Course
Kinkell Ness
Boarhills
Babbet Ness
Kingsbarns
Cambo Ness
Cambo Ledge
BALCOMIE TOWER
Fife Ness
Spoil Ground
The Bar
1481
Feet
Metres
Fms
0
1
2
Nautical Miles

distance covered and the depth, are shown in Table 1.

2.3. Benthic infauna in St Andrews Bay.

2.3.(i). Introduction.

In their review of feeding in asteroids Feder and Christensen (1966) recorded that A.rubens eats "primarily bivalves, but also gastropods, echinoderms (often A.rubens), echinoids, ophiuroids, and crustaceans (especially barnacles)". Sloan (1980) records a predominantly molluscan diet. Hulbert (1980), working on A.vulgaris (=A.rubens? Barker and Nichols, 1983), suggested that a series of prey specialisations on increasingly larger prey items seemed to be required for the species to grow larger, and Sloan (1980) commented that this sort of dietary partition limits intraspecific competition for food. On hard substrata post-metamorph A.rubens are capable of immediate carnivorous feeding on prey species such as barnacles and tubeworms (Barker and Nichols, 1983); on soft subtrata small A.rubens have long been "assumed to eat detritus and meiofauna" (Nauen, 1978). Hulbert (1980) showed the components of "substrate feeding" in A.vulgaris to be largely diatoms, foraminifera, radiolaria, ectoprocts and hydrozoans.

TABLE 1

Precise locations of the St. Andrews Bay trawls.

			DEPTH	Distance
TRAWL No. 1	FROM:	LAT. 56° 22.5'N LONG. 2° 41.2'W	19.5m(64')	.85 Nautical miles 1575m
	TO:	LAT. 56° 21.65'N LONG. 2° 40.67'W	19.5m(64')	
TRAWL No. 2	FROM:	LAT. 56° 20.8'N LONG. 2° 45.9'W	11.6m(38')	1.02 Nautical miles 1890m
	TO:	LAT. 56° 21.4'N LONG. 2° 44.4'W	15.2m(50')	
TRAWL No. 3	FROM:	LAT. 56° 21.95'N LONG. 2° 44'W	15.8m(52')	.82 Nautical miles 1520m
	TO:	LAT. 56° 22.25'N LONG. 2° 45.4'W	11.9m(39')	
TRAWL No. 4	FROM:	LAT. 56° 22.25'N LONG. 2° 46.9'W	10.4m(34')	.86 Nautical miles 1590m
	TO:	LAT. 56° 23.05'N LONG. 2° 46.4'W	12.5m(41')	

A study of benthic infauna in St Andrews Bay was undertaken in order to determine the abundance of potential prey species in different areas of the bay. This has been related to aspects of population dynamics and reproductive output, (e.g. Vevers, 1949; Pearse, 1965; Crump, 1971; Scheibling 1981b).

2.3.(ii). Materials and methods.

Samples of the benthos were collected using a Petersen grab at the North end (N), the South end (S), and the middle (M), of each trawl transect. Samples were not all collected on the same dates; sampling procedure for each station was as follows:

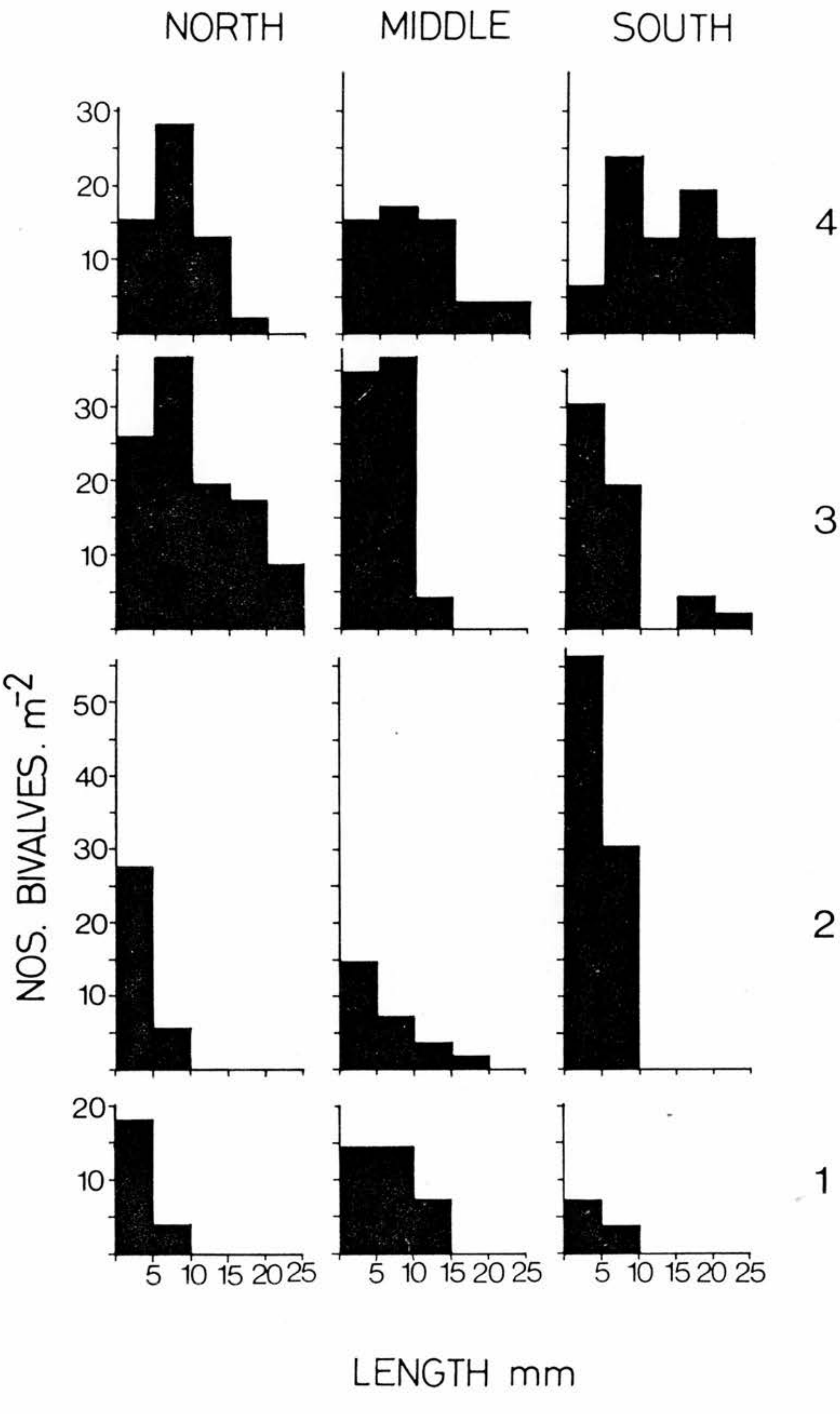
Trawl 1(N,M,S): 3 bites with .0924m^2 grab (June 1983). (=.2772m^2 sampled)

Trawl 2(N): 3 bites with .0924m^2 grab (June 1983), and 20 bites with .0225m^2 grab (Oct 1983). (=.7272m^2 sampled)

Trawl 2(M): 25 bites with .0225m^2 grab (Oct 1983). (=.5625m^2 sampled)

FIGURE 2

Bivalve size-frequency distributions and a histogram of the mean polychaete biomass recorded from the four trawl locations.


NORTH
MIDDLE
SOUTH
NOS. BIVALVES. m-2
30
20
10
4
30
20
10
3
50
40
30
20
10
2
20
10
1
5 10 15 20 25
5 10 15 20 25
5 10 15 20 25
LENGTH mm

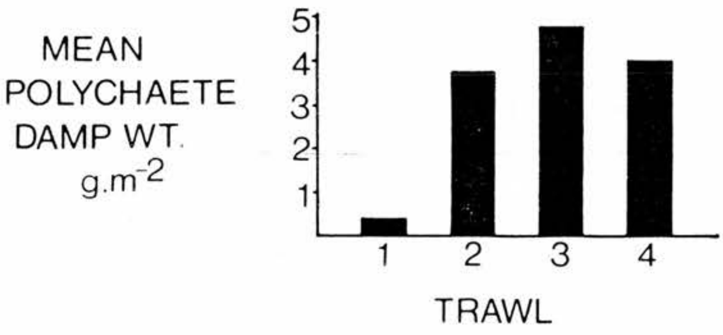

MEAN
POLYCHAETE
DAMP WT.
g.m-2
5
4
3
2
1
1
2
3
4
TRAWL

TABLE 2

Faunistic data for St. Andrews Bay. Numbers refers to mean abundance per m^2; a dot merely records the presence of an individual.

	TRAWL 1			TRAWL 2			TRAWL 3			TRAWL 4		
Area sampled, m^2	N .277	M .277	S .277	N .727	M .563	S .462	N .462	M .462	S .462	N .462	M .462	S .46
BIVALVES:												
Tellina sp.		10.8	3.6	9.6	16	65	28.1	47.6	21.6	28.1	17.3	23.
Venus striatula		10.8	3.6	5.5	3.5	2.2	30.3	4.3		25.2	13	13
Donax vittatus			3.6		1.8		23.8	6.5		6.5	23.8	39
Nucula sp.	7.2	10.8		4.1	7	4.3		8.7	39			
Ensis sp.				1.4	1.8	2.2			2.2			
Montacuta ferruginosa	3.6			1.4				39	7.2			
Spisula sp.					1.8	2.2				2.2		
Dosinia sp.					1.8	2.2						
Mytilus edulis		3.6										
Lutraria sp.	1.8				1.8							
Unidentified bivalves	10.8			24.8		4.3	6.5		4.3	2.2	2.2	
Natica sp.		3.6		1.4					4.3	4.3		
POLYCHAETES:												
0–10mm	29	7.2	21.6	73	66	481	288	286	273	208	227	11
11–20mm	3.6	7.2	3.6	33	85	134	87	143	143	47.6	43.3	47.
21–30mm				2.8	3.6	6.5	21.6	15.2	6.5	8.7	2.2	2.
30+ mm				1.4	1.8		2.2		2.2			
Worm damp wt(g) (where recorded)	.351	.201	.557	1.65		5.85			4.77	3.64	3.56	4.8
O. amphipoda	7.2	14.4	7.2	6.9	10.7	10.8	21.6	26	19.5	8.7	6.5	8.7
O. cumacea		3.6		3.6	25.2	64.9	10.8			2.2	2.2	2.2
O. ophiura sp.		2		8.3	7			6.5	13			
Echinocardium cordatum		3.6	3.6	2.2	142	4.3	10.8	21.6	8.7			4.3
O. isopoda (F. janiridae)					●●							
Decapoda (F.palaemonidae)					●							
Pagurus sp.					●							
Liocarcinus sp.				●	●							
Corystes cassivelaunus						●						
Amphiura sp.						● ●						
Asterias rubens						●						
FISH:												
Pogge (Agonus cataphractus)								●				

Trawl 2(S), Trawls 3(N,M,S) and 4(N,M,S): 5 bites with $.0924m^2$ grab (June 1983). ($=.462m^2$ sampled)

After sieving through a 2mm plastic screen, samples were preserved in 4% formalin until examination. Table 2 shows the infauna present. Organisms occurring frequently are shown as $number.m^{-2}$, the occurrence of less abundant species is indicated by a dot. Polychaetes have not been subdivided taxonomically, being grouped by size and, where recorded, by damp weight.

Starfish size was recorded as the parameter "R", the distance from the anus to the tip of the longest arm.

2.3.(iii). Results.

Bivalves are the predominant available food for <u>A.rubens</u> (Table 2). Figure 2 presents size-frequency distributions of total $bivalves.m^{-2}$ recorded from each station and the density is recorded in table 2. Trawl 2 (N and S) and Trawl 3 (N,M and S) produced appreciable numbers of small bivalves; but only from trawl 4 and 3 (N), were appreciable densities of bivalves >10mm recovered. The mean density of bivalves >15mm is $2.m^{-2}$ (trawl 2), $33.m^{-2}$ (trawl 3) and $26.m^{-2}$ (trawl 4). Trawl 1 produced no bivalves of this size. The mean polychaete $biomass.m^{-2}$ is illustrated in Figure 2; that from trawl 1 is less than one tenth that from any other trawl.

There are few apparent qualitative differences in the fauna in different areas of the bay.

2.3.(iv). Discussion.

The major feature of Table 2 and Figure 2 is the much-reduced biota from trawl 1. Qualitatively the infauna here is not much different to areas closer inshore, but organisms are present in fewer total numbers and as smaller individuals. It is shown in chapter 4 that adult A.rubens will not feed on Mytilus edulis 5mm long even in the absence of other prey. It is not clear whether this is because they are "suboptimal" on account of their small size and would be included in the diet after a period of starvation. Possibly A.rubens' chemosensory abilities are not sensitive to bivalves of this size. In either case, the prediction from obervations of size-specific bivalve predation by A.rubens is that "optimally" sized food items for starfish with R>20mm are in short supply in St Andrews Bay. The figures for bivalves >15-20mm (Table 2) are probably exaggerated by the inclusion of species such as Ensis which are not usually available as food for A.rubens.

The extent to which Echinocardium cordatum (Pennant) is included in the diet of A.rubens in St Andrews is uncertain. A.rubens is capable of consuming Echinocardium and does so in the laboratory (pers.obs). The fact that these urchins are caught, frequently undamaged, in the grab indicates that they are close to the sediment surface. This concurs with Buchanan's (1966) findings in Northumberland that offshore populations of E.cordatum were buried about two cm. deep, compared with 15 cm in littoral individuals. Recruitment in this species is sporadic; Buchanan (1966) observed no new settlement of E.cordatum during a seven year study period. In St Andrews Bay only one E.cordatum was found between 10 and 30mm in length. Buchanan's (1966) figures for growth in E.cordatum were three $mm.year^{-1}$ for offshore populations, eight $mm.year^{-1}$ closer inshore. Even allowing for the more generous figure, recruitment of this animal in St Andrews Bay must be as sporadic and unpredictable as in Northumberland. A single 14mm individual was recovered from Trawl 1. In the light of the impoverished biota from this area of the bay it is likely that this individual settled at the same time as the larger urchins of more inshore populations, and that its growth was stunted as a consequence of food shortage.

The absence of a consistent pattern in the three inshore trawls indicates that it is not purely because of distance from an area of presumed high primary production (i.e. River Eden outfall) that trawl 1 is faunistically poor.

2.4. A.rubens populations in St Andrews Bay.

2.4.(i). Introduction.

Initial studies on starfish populations were all carried out by means of trawls, dredges, or other indirect sampling techniques. (Galtsoff and Loosanoff, 1939; Vevers, 1949; Hancock, 1955, 1958; Hatanaka and Kosaka, 1958). In recent years the advent of scuba diving has enabled comprehensive _in situ_ studies (Larsson, 1968, Mauzey _et al_, 1968; Burla _et al_, 1972; Dayton _et al_, 1974; Nauen, 1978; Nojima, 1979; Scheibling, 1980a,b,c,d, 1981a; Briggs, 1983), and saturation diving from an underwater laboratory enabled prolonged observation of _A.rubens_ on soft sediment by Anger _et al_ (1977). Underwater TV can play a part in the study of certain aspects of echinoderm ecology (Wilson _et al_, 1977), but requires availability of considerable resources, and is therefore not always practical.

Continued monitoring of a sublittoral area to study aspects of population dynamics has been undertaken on a number of occasions (_e.g._ Pearse, 1965; Nauen, 1978; Nojima, 1979; Briggs, 1983), but Brun (1968) warned that long-term studies at fixed stations are always subject to error, particularly concerning growth measurements, because different populations are studied in that time. A migration offshore in colder weather has been observed for _Asterias_ species (Vinberg, 1967; Annala, 1968) and for _Pisaster ochraceus_ (Mauzey, 1966; Paine, 1969), and a mass movement onshore to feed on littoral bivalve aggregations is also common in _Asterias_ (Smith, 1940; Seed, 1969, Sloan and Aldridge, 1981; Dare, 1982; and see Chap.4.4.). However, the degree to which sublittoral asteroid populations are discrete, and the extent of migration and disperal, has received little attention.

Verrill (1914, in Sloan, 1980) "was convinced asteroids migrated to areas of amenable temperature and feeding conditions"; and in the light of laboratory experiments conclusively demonstrating a well-defined chemosenory ability in several temperate asteroid species (Castilla, 1972a and b; Zafirou et al, 1972; Valentincic, 1973; Castilla and Crisp, 1976), this is a likely basis for mass starfish migrations. However, Anger et al. (1977) and Ernst (1967) reported the movement of large numbers of Asterias by water currents, and Ernst (1967) described an adaptation in A.forbesi (Desor) to prevent damage to the starfish while this was occurring. Thus dispersal in post-metamorph asteroids is likely to be due in part to water movements.

Growth rate calculations based on size-class distributions are not reliable for A.rubens for the reason that different nutritional and other environmental factors cause wide variations in body size in starfish of the same age (e.g. Mead, 1900; Bull, 1934; Galtsoff and Loosanoff, 1939; Vevers, 1949; Hancock, 1958; Paine, 1976a). However, in spite of this, modal analysis of size-frequency data for A.rubens has been attempted by Guillou (1980) in the littoral and Nauen (1978) sublittorally in Kiel Bay.

The presence in greater numbers of small A.rubens in shallow water has been noted by several authors (Anger et al, 1977; Nauen, 1978; Briggs, 1983), and Anger et al (1977) reported that direct settlement on soft bottoms must be discounted because of the absence there of the youngest benthic stage, presumably due to the inability of the brachiolaria to attach. Loosanoff (1964) however, found settlement in A.forbesi in Long Island Sound at all depths down to 31m, although he was observing settlement on oyster shells lowered onto the bottom at each depth.

The disruption of sand-dwelling asteroid populations by storms has been recorded by Sieling (1960) and Nojima (1979); Anger et al (1977) reported large numbers of A.rubens being carried along on mobile algal carpets drifting over the bottom.

On the 15th October 1982 a large number of A.rubens were washed up on the West Sands beach (Fig. 1), St Andrews, after a storm. The preceding two days had been distinguished by winds that came uncharacteristically from the North-East and East. In his study of coexistence between the two sympatric asteroid species Asterias forbesi and A.vulgaris in New England, Menge (1979) concluded that the primary controlling agents for both populations were, in order of importance: storms, disease, competition and prey patchiness, and predation. Other work on the Pacific coast of North America concerning the coexistence of Leptasterias hexactis (Stimpson) and Pisaster ochraceus in the rocky intertidal (Menge, 1972a, 1974, 1975; Menge and Menge, 1974; Paine, 1976) show that these two species compete intensively for food and are affected little by storms, disease or predation. Menge (1979) suggested that the differences in population stability between these two pairs of starfish reflect differences in environmental stability and predictability: the patterns of environmental variation in New England may be both too wide and too unpredictable to permit the evolution of wide tolerance ranges or environmental tracking mechanisms.

St Andrews Bay is a shallow expanse of sand probably supporting an A.rubens population throughout much of its extent. It is an area commercially important for the recruitment of plaice, a species with which A.rubens has been shown to compete for food (Allen, 1983). The population dynamics of A.rubens in separate areas of the bay were examined over a period of 17 months to investigate the degree of heterogeneity in the St Andrews Bay A.rubens population, and the extent to which population characteristics reflect food availability.

In the estuary of the River Tay there is a submerged mussel bed, the Horseshoe Bank, about one kilometre downstream of the Tay Bridge. In the past the Horseshoe Bank has been the location of abundant A.rubens (W. Ireland, pers. comm.). It was decided to compare aspects of the population dynamics of A.rubens from this food-rich environment with those from St Andrews Bay. However, on first sampling the mussel bed in April 1982 with a naturalists' dredge it was found that starfish were absent. A.rubens were therefore collected from the adjacent shipping channel.

2.4.(ii).(a). Materials and methods, St Andrews Bay trawls.

A beam trawl 2.74m (nine feet) wide was collected from each transect (Fig. 1) on an approximately monthly basis, but none were collected between June and September 1982. Along the bottom of the main net (mesh 32mm) was attached net of mesh 11mm. Trawl contents were transferred to buckets, from which all starfish were subsequently removed and counted. "R", the longest arm, was recorded for 300 A.rubens or the whole trawl, whichever was the smaller.

2.4.(ii).(b). A.rubens from the Horseshoe Bank.

Owing to logistical difficulties, and the distance from St Andrews, only two samples were collected, on 21st April 1982 and 12th April 1983. Starfish were collected using a naturalists' dredge. The longest arm of each starfish was measured and a size-frequency distribution constructed.

2.4.(ii). (c). A.rubens mortality after a storm.

An area $40m^2$ was demarcated at the South end of the West Sands beach on 15th October 1982, from which all A.rubens were collected, counted, and measured.

2.4.(iii).(a). Results, St Andrews Bay trawls.

The numbers of A.rubens collected in the trawls are shown in Table 3, and size-frequency distributions of those caught are shown in Figs. 3-6. No starfish were found with R<9mm, smaller ones were presumably lost through the trawl mesh. The density of starfish at each transect is illustrated in Fig. 7 and the mean size caught in Fig. 8.

Trawl One: This offshore location produced a population of A.rubens with a very high proportion of small individuals (R:15-25mm), and the smallest mean size. The population is skewed to the left (Fig. 3), suggesting that smaller starfish were present but were not being caught. Very few A.rubens were found here with R>65mm.

Trawl Two: A.rubens were present up to R=100mm, with a peak of small starfish usually present (Fig. 4). The mean size increased markedly between September and October 1982 (Fig. 8); the size-frequency distribution shows this to be caused by a drop in the number of small individuals.

The density of starfish in Trawls 1 and 2 followed very similar patterns throughout the study period. Both populations rose sharply in April 1982, and fell from then until December 1982 (Fig 7). Likewise a short-lived increase in density was present in both populations in January 1983.

TABLE 3

St. Andrews Bay trawls

TRAWL 1		No. in trawl	No. per 100 m^2	No. measured for S.F.D.	Mean Arm length $\bar{x}$	Standard error
1982	JAN.	690	16.0			
	FEB.	392	9.1	300	22.9	.77
	MAR.	625	14.5	300	23.0	.65
	APR.	431	10.0	300	21.7	.6
	MAY	965	22.4	300	25.3	.99
	SEPT.	620	14.4	300	19.7	.85
	NOV.	353	8.2	300	23.4	1.8
	NOV.	210	4.9	210	24.6	1.14
1983	JAN.	467	10.8	300	24.7	.88
	MAR.	236	5.5	236	22.6	1.85
	MAY	317	7.3	280	22.6	.82
TRAWL 2						
1982	JAN.	251	4.9			
	FEB.	190	3.7	190	43.5	1.68
	MAR.	223	4.3	223	40.3	1.6
	APR.	495	9.6	300	40.4	1.3
	MAY	850	16.4	300	37.7	1.4
	SEPT.	545	10.5	300	33.5	1.22
	OCT.	260	5.02	260	54.0	2.26
	NOV.	157	3.0	157	39.0	2.3
1983	JAN.	474	9.2	300	41.2	1.62
	MAR.	262	5.1	262	45.6	2.38
	MAY	616	11.9	300	27.6	1.23
TRAWL 3						
1982	JAN.	211	5.0			
	MAR.	15	.4	15	48.9	6.97
	MAR.	172	1.7	72	45.8	2.8
	APR.	297	7.1	297	45.2	1.35
	SEPT.	780	18.7	300	47.2	1.4
	OCT.	164	3.9	164	51.5	2.15
	NOV.	151	3.6	151	53.0	2.1
1983	JAN.	208	5.0	208	41.3	1.59
	MAR.	143	3.4	143	52.5	2.64
	MAY	353	8.5	300	37.3	1.23
TRAWL 4						
1982	JAN.	48	1.1			
	MAR.	3	.07	3	70.6	13.2
	MAR.	36	.8	36	74.6	2.83
	APR.	39	.9	39	67.0	3.1
	SEPT.	26	.6	26	86.7	4.9
	NOV.	62	1.4	62	83.9	4.62
	NOV.	26	.6	26	97.6	2.3
1983	JAN.	16	.4	16	97.2	6.03
	MAR.	7	.2	7	88.9	7.1
	MAY	9	.2	9	103.8	4.6

<u>FIGURE 3</u>

Size-frequency distributions of *A. rubens* from trawl one, February 1982 - May 1983.

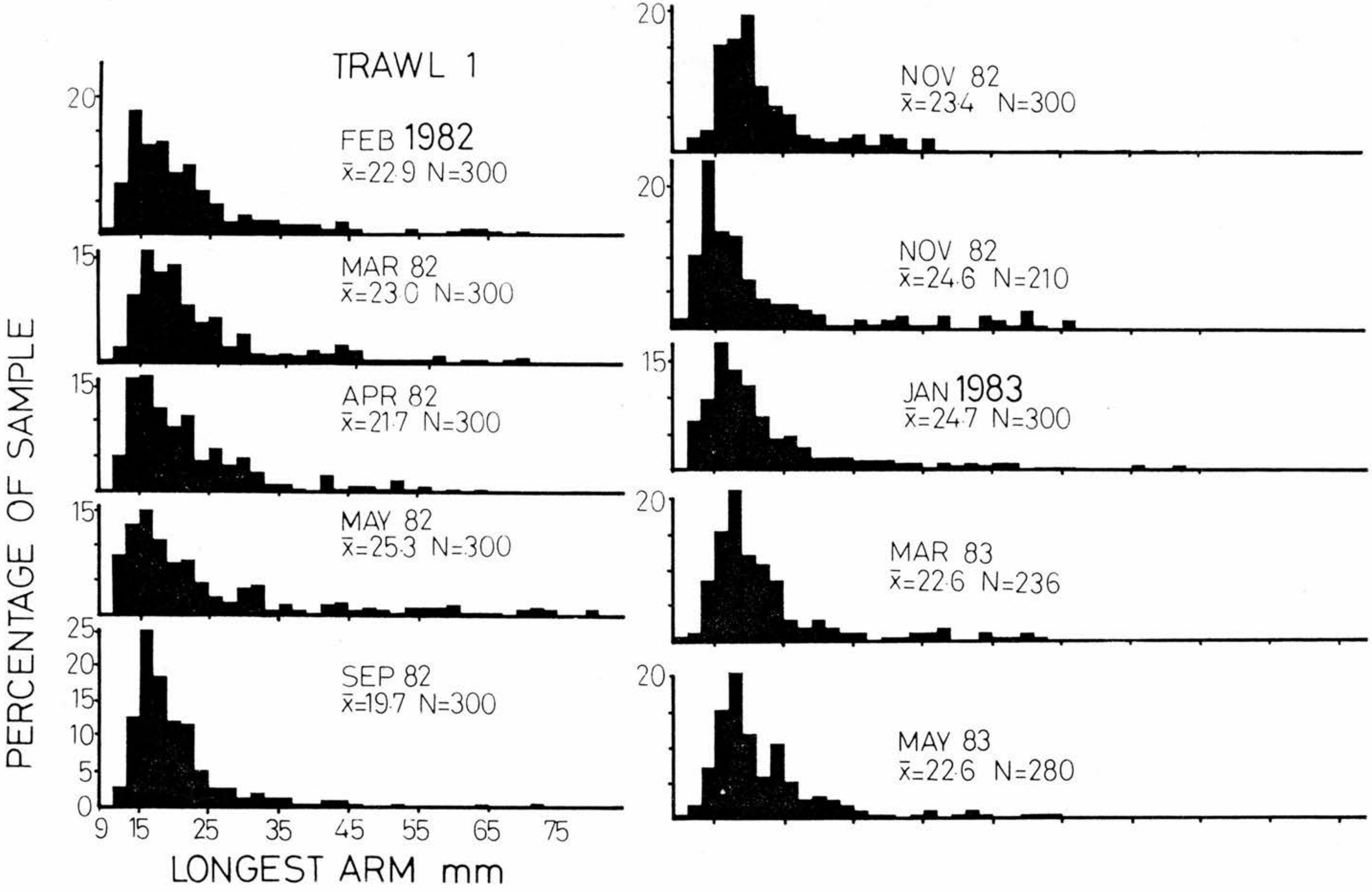

TRAWL 1
FEB 1982
x̄=22·9 N=300
MAR 82
x̄=23·0 N=300
APR 82
x̄=21·7 N=300
MAY 82
x̄=25·3 N=300
SEP 82
x̄=19·7 N=300
NOV 82
x̄=23·4 N=300
NOV 82
x̄=24·6 N=210
JAN 1983
x̄=24·7 N=300
MAR 83
x̄=22·6 N=236
MAY 83
x̄=22·6 N=280
PERCENTAGE OF SAMPLE
20
15
15
15
25
20
15
10
5
0
20
20
15
20
20
9
15
25
35
45
55
65
75
LONGEST ARM mm

FIGURE 4

Size-frequency distributions of *A. rubens* from trawl two, February 1982 - May 1983.

TRAWL 2

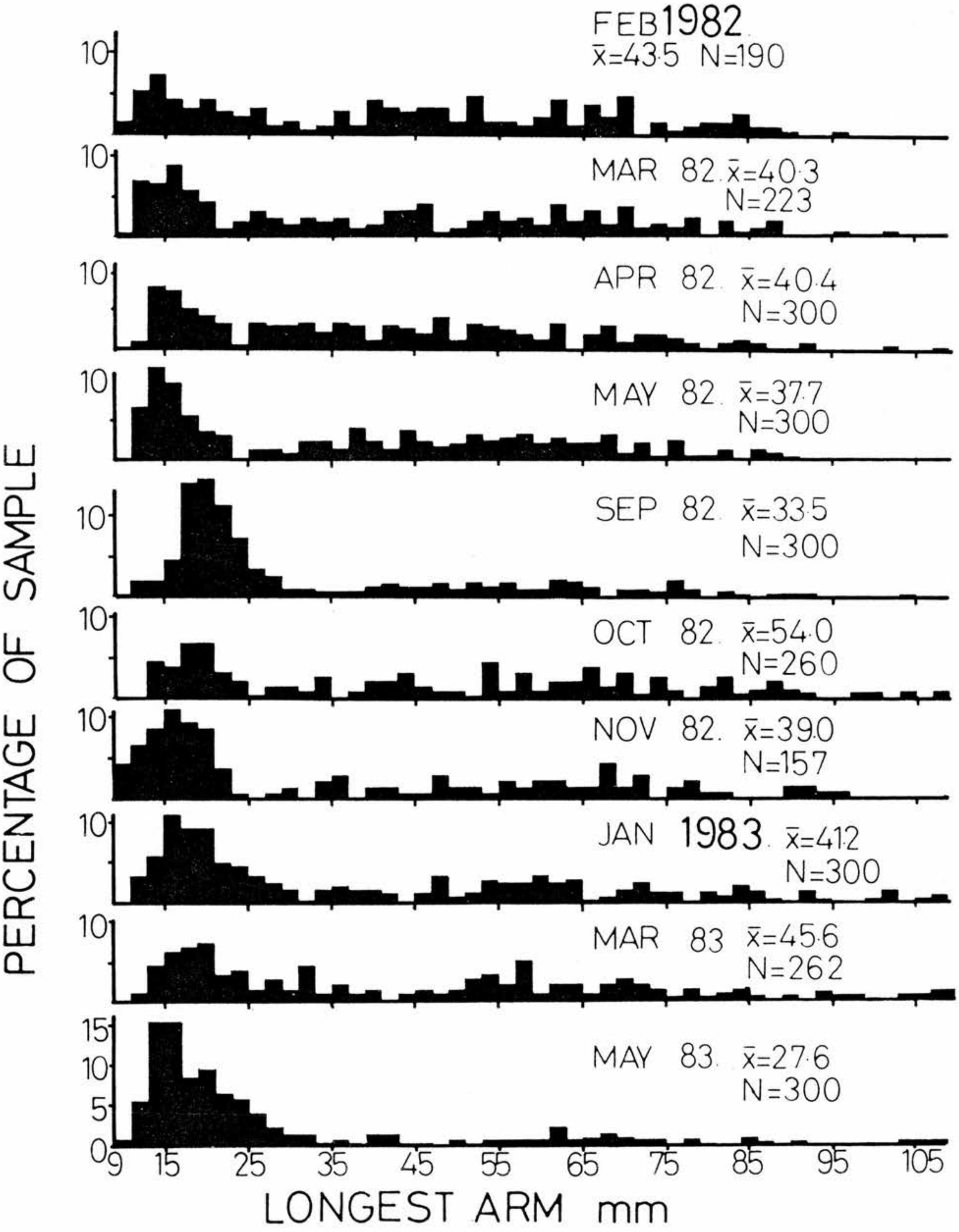

FEB 1982. x̄=43·5 N=190
MAR 82. x̄=40·3 N=223
APR 82. x̄=40·4 N=300
MAY 82. x̄=37·7 N=300
SEP 82. x̄=33·5 N=300
OCT 82. x̄=54·0 N=260
NOV 82. x̄=39·0 N=157
JAN 1983. x̄=41·2 N=300
MAR 83 x̄=45·6 N=262
MAY 83. x̄=27·6 N=300
10
15
5
0
9
15
25
35
45
55
65
75
85
95
105
PERCENTAGE OF SAMPLE
LONGEST ARM mm

FIGURE 5

Size-frequency distributions of A. rubens from trawl three, March 1982 - May 1983.

TRAWL 3

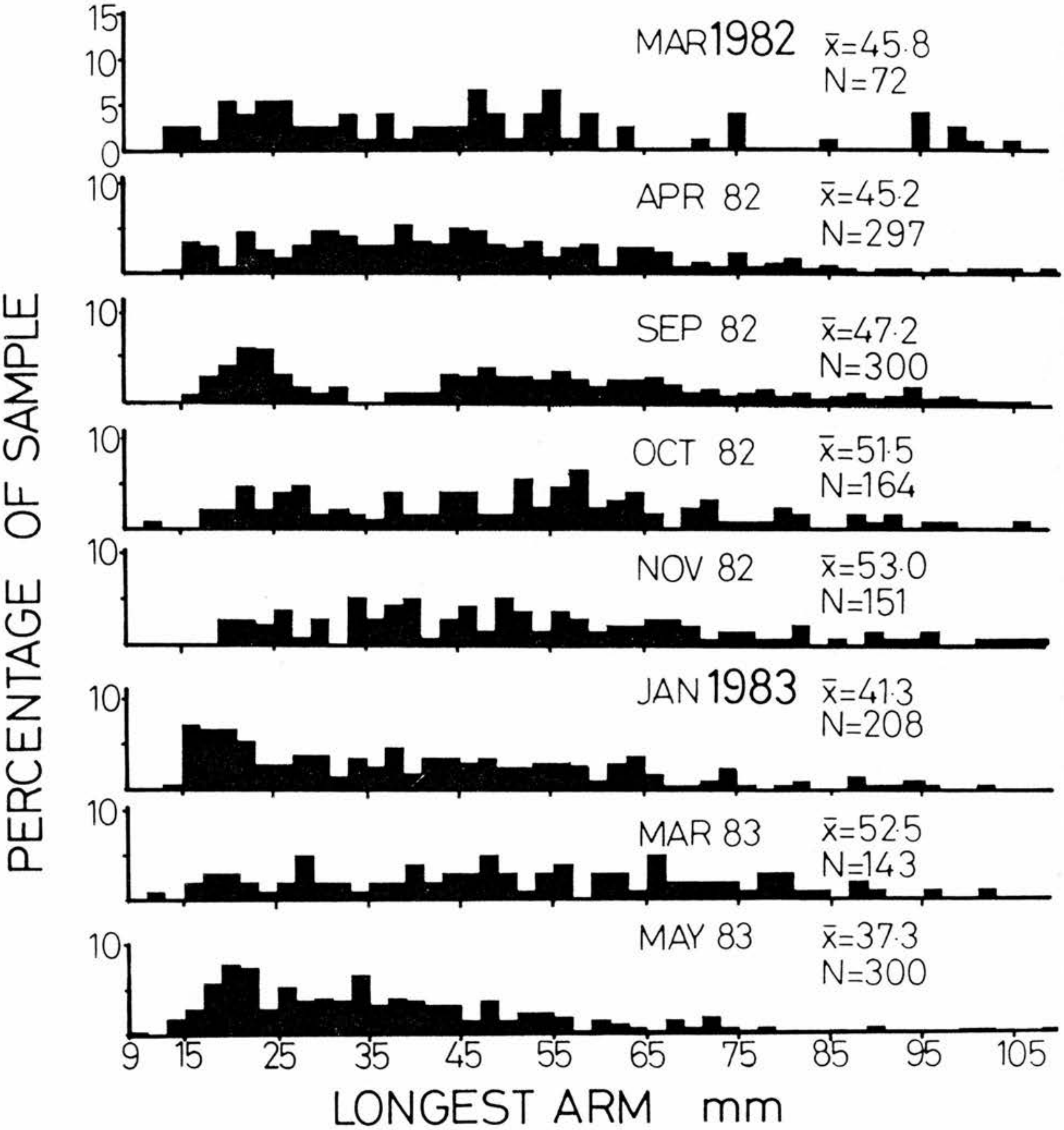

PERCENTAGE OF SAMPLE
15
10
5
0
MAR 1982 x̄=45·8 N=72
10
APR 82 x̄=45·2 N=297
10
SEP 82 x̄=47·2 N=300
10
OCT 82 x̄=51·5 N=164
10
NOV 82 x̄=53·0 N=151
10
JAN 1983 x̄=41·3 N=208
10
MAR 83 x̄=52·5 N=143
10
MAY 83 x̄=37·3 N=300
9
15
25
35
45
55
65
75
85
95
105
LONGEST ARM mm

FIGURE 6

Size-frequency distributions of A. rubens from trawl four, on those occasions when more than 25 starfish were collected. March - November 1982.

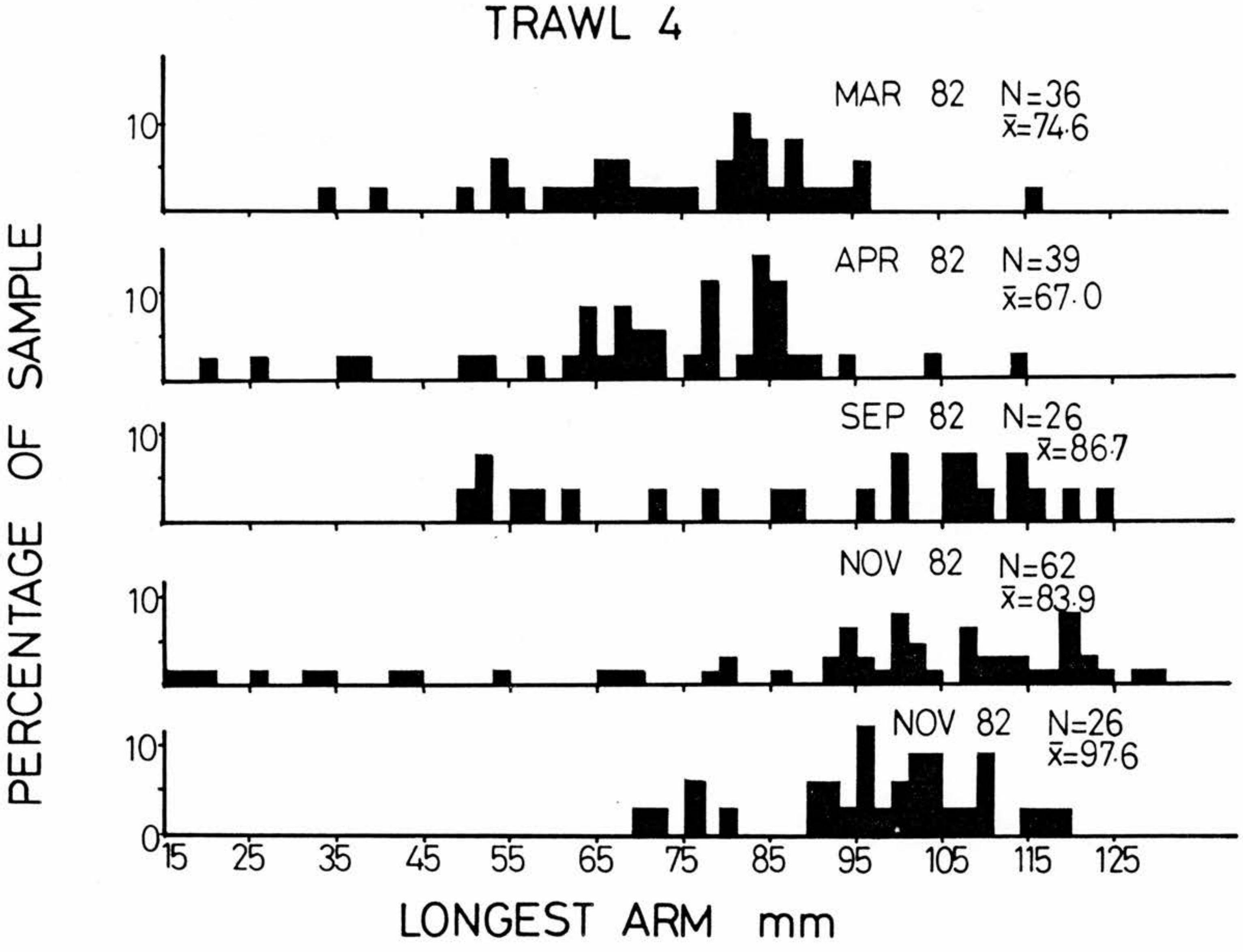

TRAWL 4
MAR 82 N=36
x̄=74·6
APR 82 N=39
x̄=67·0
SEP 82 N=26
x̄=86·7
NOV 82 N=62
x̄=83·9
NOV 82 N=26
x̄=97·6
10
0
15
25
35
45
55
65
75
85
95
105
115
125
PERCENTAGE OF SAMPLE
LONGEST ARM mm

FIGURE 7

The density of A. rubens at each trawl. Arrows represent occasions on which there was at least one hour in the day with a mean wind speed greater than 34 knots (Beaufort wind scale force eight, gale).

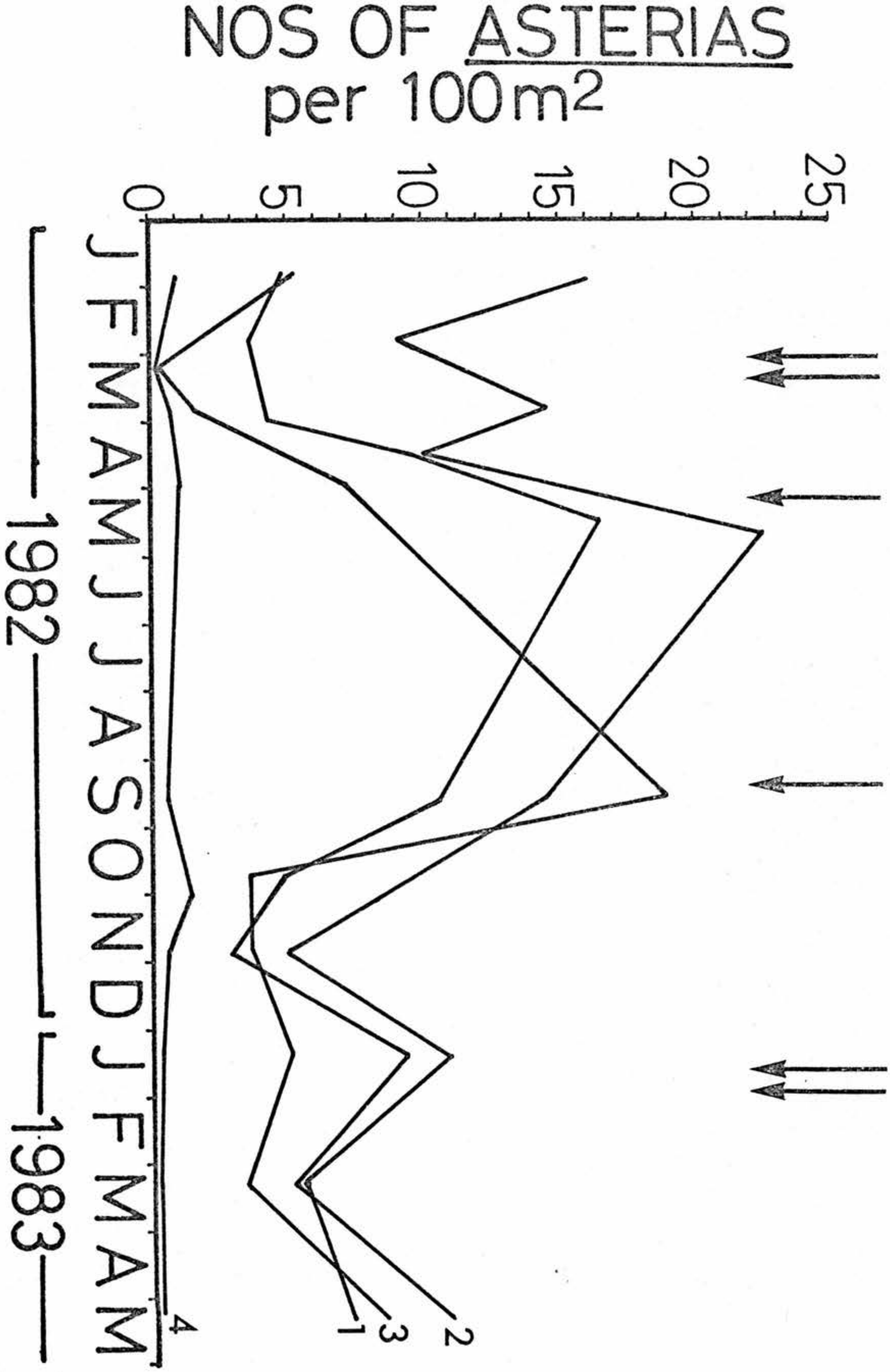
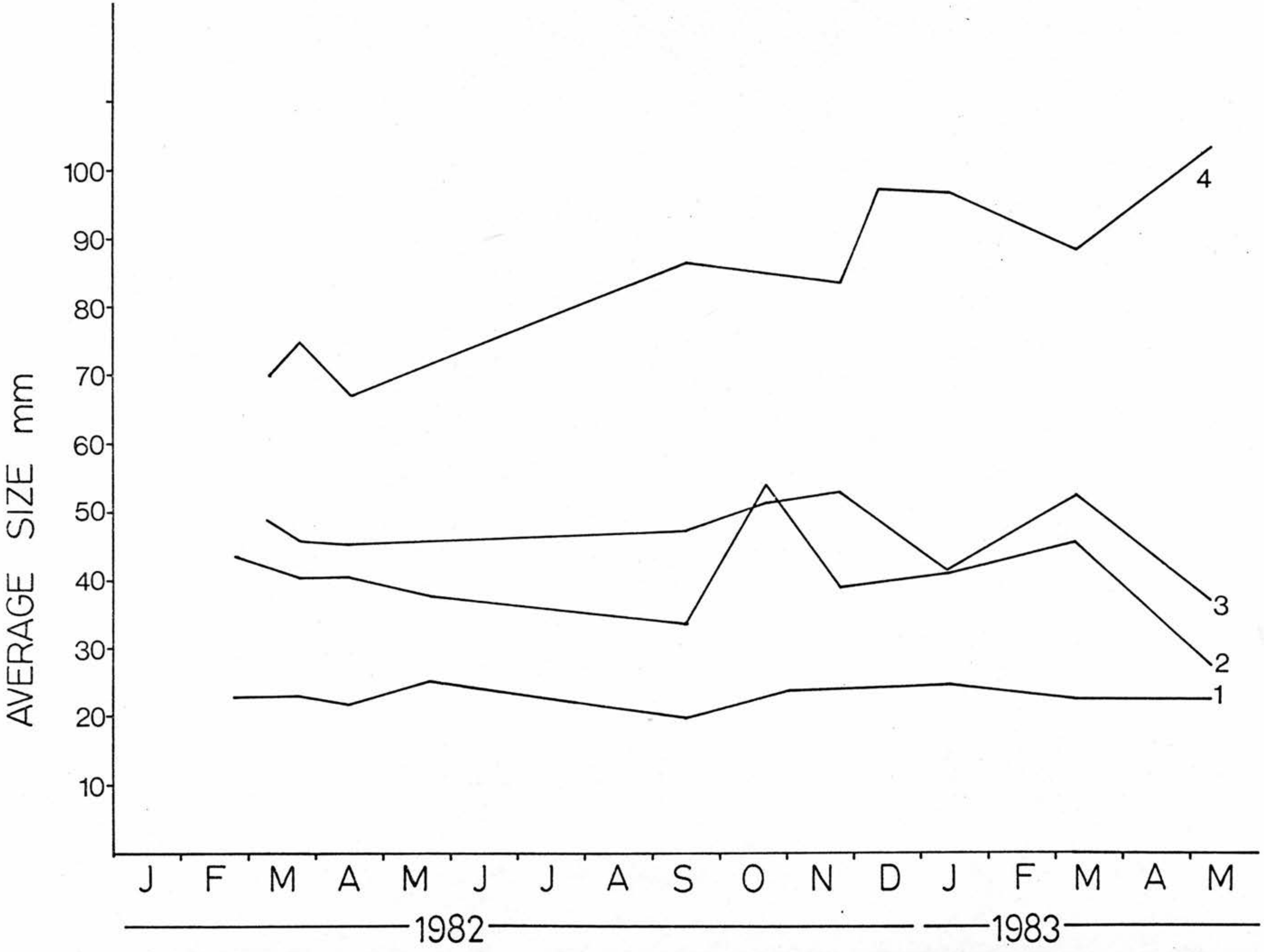

NOS OF ASTERIAS per 100m2
0
5
10
15
20
25
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
1982
1983
1
2
3
4

FIGURE 8

Mean A. rubens size (R) in each trawl.


AVERAGE SIZE mm
100
90
80
70
60
50
40
30
20
10
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
1982
1983
4
3
2
1

Trawl Three: A.rubens were present covering the same size range as Trawl 2, but without the peak of small individuals. Very few A.rubens were found here with R less than 15mm. The mean size was marginally larger than that of Trawl 2. Starfish density at this location fluctuated widely (Fig. 7), with population crashes in March 1982 and October 1982 after periods of high winds.

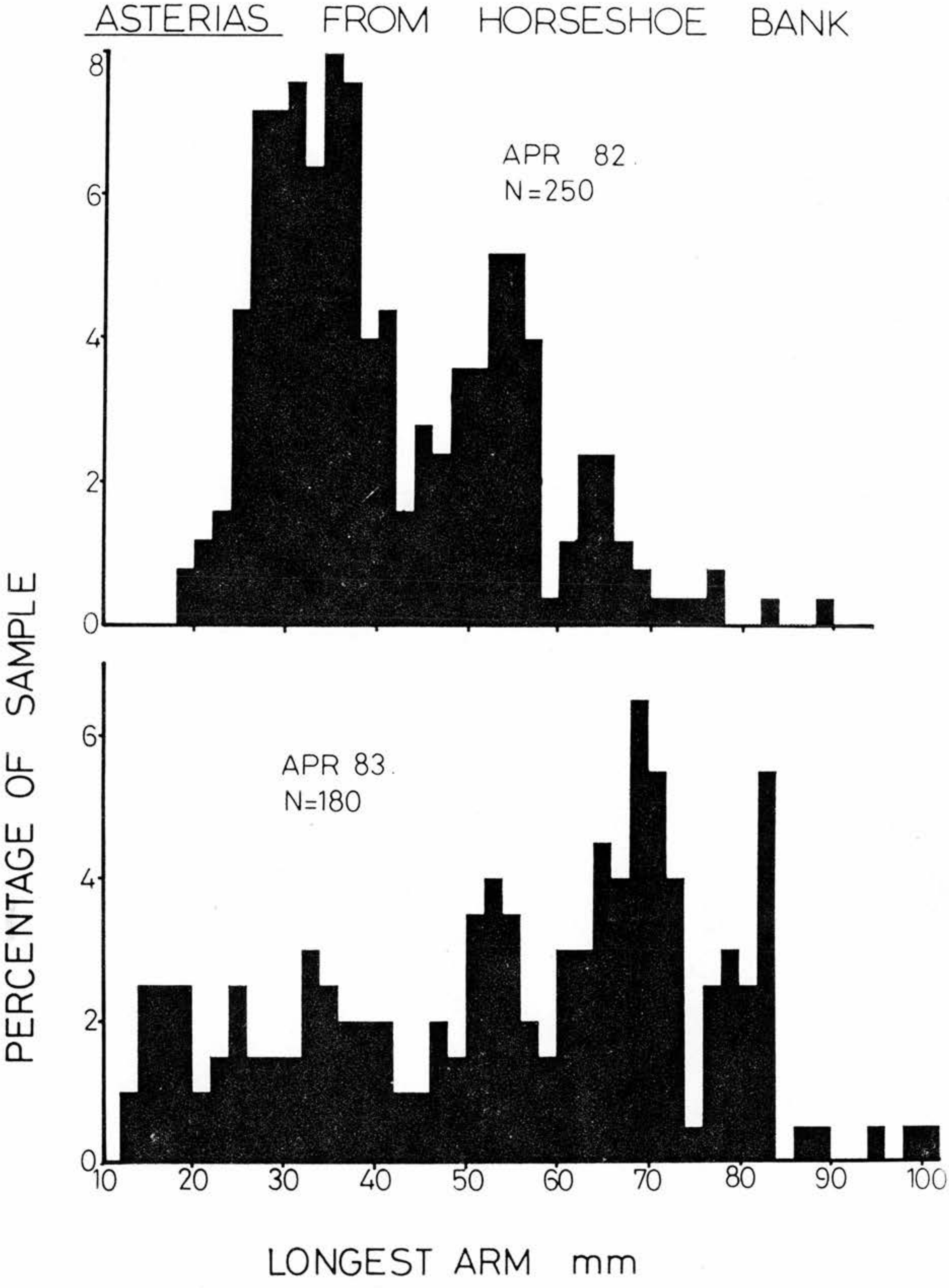
Trawl Four: The highest number of A.rubens collected from Trawl 4 numbered 62 (November 1982), giving a density for starfish in this area of the bay of only 1.4 per $100m^2$. Size-frequency distributions have been constructed for only five sampling occasions, when more than 25 were caught. These show virtually no starfish with $R<45mm$, a size rarely attained in Trawl 1. The mean size (Fig. 8) is much greater than that of starfish from elsewhere in the bay, and this increased steadily throughout the study period. The largest A.rubens found in St Andrews Bay came from this transect, with R up to 130mm.

2.4.(iii).(b). Results, A.rubens from the Horseshoe Bank.

Figure 9 shows size-frequency distributions of A.rubens collected adjacent to the Horseshoe Bank in April 1982 and 1983. A considerable change in the size structure of this population is apparent between the two sampling dates. The April 1982 sample appears to show a population composed of three distinct year-classes; the April 1983 sample, on the other hand, is dominated by large individuals and shows no such definition.

FIGURE 9

Size-frequency distributions of A. rubens collected from the shipping channel adjacent to the Horseshoe Bank.



ASTERIAS FROM HORSESHOE BANK

2.4.(iii).(c). A.rubens storm damage.

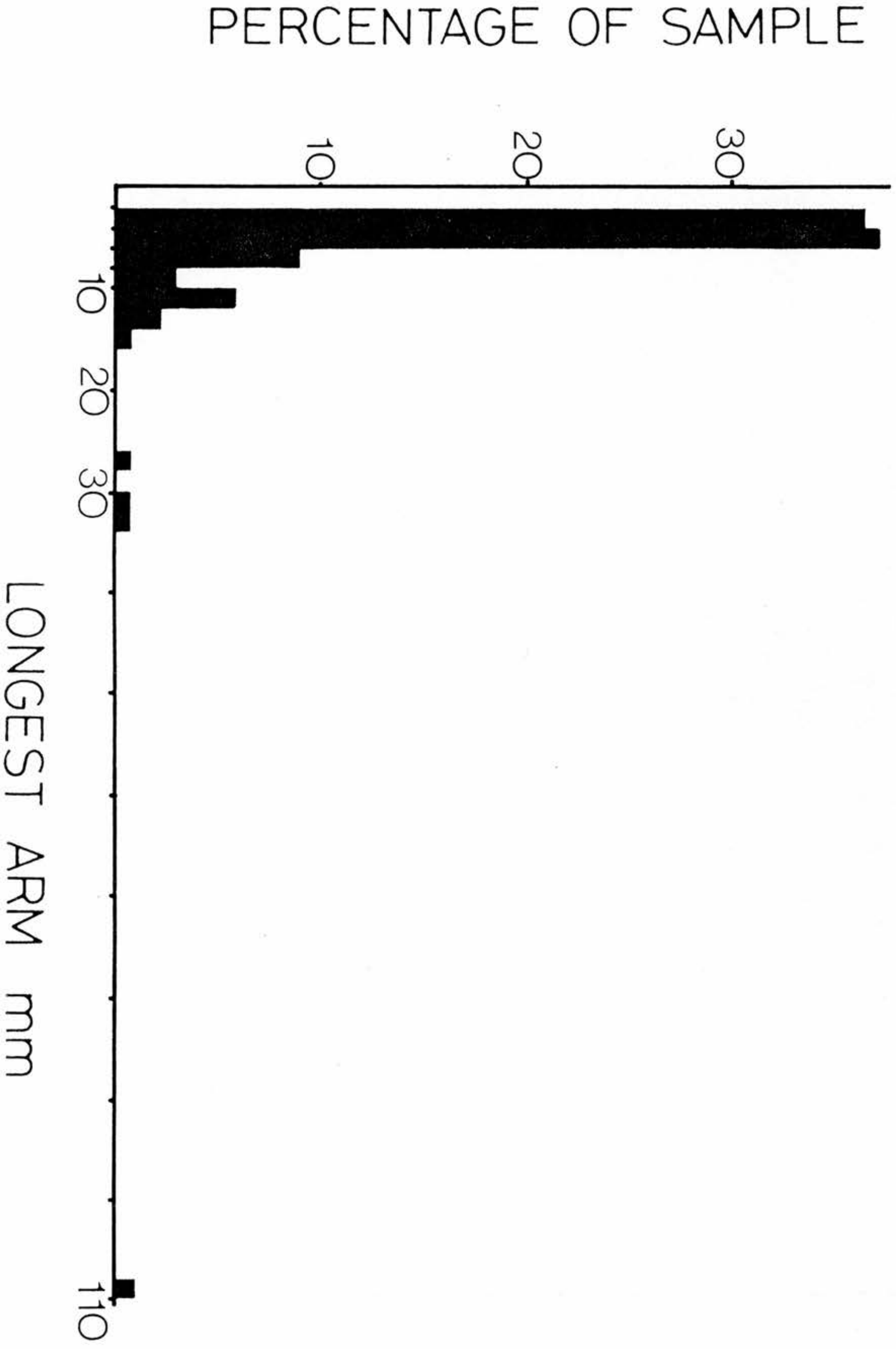
A size-frequency distribution of the A.rubens recovered from a $40m^2$ area of the West Sands, St Andrews is shown in Figure 10 (N=1905). Local water movements tend to congregate jetsam at this point and therefore the density is not representative of the beach as a whole. Lanice tubes, bivalves (e.g. Donax, Spisula, Venus, Lutraria, Arctica, Mactra), Echinocardium, crabs (Liocarcinus depurator, Corystes cassivelaunus (Pennant)), and anomurans (Pagurus spp.), were thrown up also, along with considerable quantities of kelp. A.rubens of all sizes were present, even if not included in Figure 10. The majority of small starfish were found within Laminaria holdfasts.

2.4.(iv). Discussion.

For the purposes of density estimates in the present study, the efficiency of the trawl has been taken as 100%. Hatanaka and Kosaka (1959) estimated their trawl efficiency as 50%, and Nauen (1978), by comparing numbers of A.rubens caught in a triangular dredge with numbers remaining in the path of the dredge (counted by scuba divers), derived correction factors for different sediment types. For sandy substrata she estimated that the dredge took $32.25 \pm 3.88\%$ of A.rubens

FIGURE 10

Size-frequency distributions of A. rubens from an area of $40m^2$ demarcated at the south end of the West Sands after a storm, 15th October 1982.


PERCENTAGE OF SAMPLE
10
20
30
LONGEST ARM mm
10
20
30
110

present. It is therefore likely that absolute densities in the present study are underestimated, although they serve for comparative purposes.

Thorson (1950) reported that A.rubens larvae are positively phototactic, and settle exclusively on hard bottoms and phytal in shallow water, prolonging planktonic existence if necessary until a suitable substratum is found. In general, the data from the inshore trawls bear this out. A rocky sublittoral is only found along the southern edge of St Andrews Bay, and personal observations of kelp holdfasts containing abundant juvenile A.rubens thrown onto the West Sands after a storm indicate that settlement is pronounced here.

If recruitment only occurs along the southern edge of the bay, the further an A.rubens population is from this area the larger will be its mean size, because of the time taken for the starfish to disperse from this point. Trawl 2, the southernmost trawl, shows a pronounced peak of juvenile starfish (Fig. 4). This peak is absent from Trawl 3, as are nearly all A.rubens with $R<15$mm. Trawl 4 contains no small A.rubens at all. However, Trawls 3 and 4 are roughly equidistant from St Andrews but possess very different population characteristics. It may be that since Trawl 4 is closer inshore, and 2-3m shallower (see Fig. 1), movements of the water surface disturb the substratum here, and that small A.rubens reaching this transect are dispersed elsewhere or washed onto the beach.

Settlement of A.rubens larvae only on hard bottoms around the coast does not explain the abundance of juvenile starfish in Trawl 1. In their experiments on the settlement of A.rubens larvae, Barker and Nichols (1983) found that larvae would attach to a variety of hard fragments provided an algal film was present. Since A.rubens is found to a depth of 650m (Mortensen, 1927), larval settlement is presumably not restricted exclusively to the shallow sublittoral, and may take place on rocks or shell fragments at greater depths.

The data from the grab samples (Chap.3.3.) and the absence of starfish with R>75mm in Trawl 1 both suggest that the A.rubens population in this area of the bay is food-limited. A.rubens may be considered an r-selected species (sensu MacArthur and Wilson, 1967) and populations are frequently encountered in conditions of suboptimal nutrient supply (Vevers, 1949; Hulbert, 1979; Barker and Nichols, 1983).

The four trawl locations produced characteristic and consistent size-frequency distributions throughout the 17-month study period. The consistency of these patterns is surprising since the density fluctuations imply considerable starfish rearrangement, and indicates a marked heterogeneity in the St Andrews A.rubens population.

Included on Fig. 7 are arrows showing the days on which there was an average wind speed of at least 34 knots (gale force eight) for at least one hour in the day. Changes in starfish numbers appear to coincide with strong winds on some occasions (March, September, 1982;

January, 1983), but not on others (April 1982). For two days preceding the 15th October 1982 stranding of A.rubens the wind came uncharacteristically from the North-East and East. Although never reaching force eight the water disturbance with the wind in this quarter appeared greater than at any time in the present study.

The similarity in the pattern of density in Trawls 1 and 2 is surprising considering the distance between them (Fig. 1). The number of starfish in both areas increased dramatically in April 1982, and declined over the summer of that year. A reciprocal increase in numbers over the summer was observed in Trawl 3. The storm on 15th October 1982 (that produced dramatic A.rubens mortality) was coincident with a sharp drop in starfish density in areas 1, 2, and 3, and a reduced proportion of starfish with R<25mm in Trawls 2 and 3 (Figs. 4 and 5). This disruption of the A.rubens population and removal of small individuals may explain the apparent increase in mean A.rubens size observed in Trawl 2 at this time (Fig. 8).

Studies by Seed (1969), Sloan and Aldridge (1981), and Dare (1982), attest to the fact that A.rubens populations are mobile and engage in periodic invasions of littoral mussel beds. The Horseshoe Bank is a shipping hazard over which run 6-7 knot currents at some states of the tide, but the absence of A.rubens cannot be attributed to water movements and remains inexplicable. The difference between the size-frequency distributions of starfish from the shipping channel adjacent to the Horseshoe Bank in successive years is not matched by any of the St Andrews Bay populations, and suggests that different populations have been sampled on each occasion.

The damage that can be inflicted on asteroid populations by abiotic factors was illustrated by the storms of 15th October 1982. In other locations such stochastic size-specific mortality may be important in controlling recruitment of juvenile asteroids into the adult population. In St Andrews Bay, however, the effect of the storms on the size-frequency composition of nearby populations was minimal, and local density alterations were short-lived.

2.5. Reproductive cycles in St Andrews Bay *A.rubens*.

2.5.(i). Introduction.

The presence of annual reproductive cycles in asteroids has been demonstrated in a number of studies (Farmanfarmaian *et al*, 1958, and Mauzey, 1966, for *Pisaster ochraceus*; Pearse, 1965, for *Odontaster validus* (Koehler); Jangoux and Vloebergh, 1973, for *A.rubens*; Chia, 1968, for *Leptasterias hexactis*; Crump, 1971, for *Patiriella regularis* (Verrill); and Scheibling, 1981, for *Oreaster reticulatus*) (L.). The Gonad Index -the ratio of gonad *volume* to eviscerated body wet weight (Pearse, 1965; Mauzey, 1966; Barker and Nichols, 1983), or the ratio of gonad *damp weight* to eviscerated body wet weight (Jangoux and Vloebergh, 1973; Scheibling, 1981)- is the usual measure of reproductive condition. Spawning is indicated by a sharp drop in the Gonad Index (henceforward called GI). A histological examination of the gonads in parallel with a study of the index cycle has been undertaken by Vevers (1949), Jangoux and Vloebergh (1973), Barker and Nichols (1983) for A.rubens; Mauzey (1966) for P.ochraceus; Pearse (1965) for Odontaster validus; and Crump (1971) for Patiriella regularis. An annual cycle in the pyloric caecae, the food storage organs (Anderson, 1966; Harrold and Pearse, 1980), is also present in several species. This is frequently reciprocal to that of the gonads, although this is not always the case (e.g. Pearse, 1965, for Odontaster validus; Farmanfarmaian et al, 1958, for Patiria miniata (Brandt) and Pisaster giganteus) (Stimpson).

The inverse relationship between the Pyloric Caecum Index (henceforward called PCI) and GI cycles has been interpreted as the diversion of reserves stored in the pyloric caecae to gamete production in the gonads (Farmanfarmaian et al, 1958; Mauzey, 1966; Crump, 1971; Jangoux and Vloebergh, 1973; Barker, 1979; Barker and Nichols, 1983). However, Harrold and Pearse (1980) urged caution on this point, concluding that "the relationship between pyloric caecum and gonad size is tenuous, and inverse relationships may be coincidental rather than causal".

Comparisons of reproductive effort in separated populations of asteroid species have been undertaken in tropical (e.g. Scheibling, 1981), temperate (Vevers, 1949; Crump, 1971; Briggs, 1983; Barker and Nichols, 1983), and polar waters (Pearse, 1965). The nutritional status of the habitat is reflected in the pyloric caecum size (Pearse, 1965; Crump, 1971; Barker and Nichols, 1983), gonad size (Pearse, 1965; Scheibling, 1981; Briggs, 1983; Barker and Nichols, 1983), and the proportion of starfish reaching breeding condition (Vevers, 1949). Pearse (1965) also noted a higher proportion of Odontaster with fewer than the usual ten gonads in a population limited by low levels of primary production.

2.5.(ii). Materials and methods.

Up to 30 A.rubens from each trawl transect, covering the full size range present, were dissected. Starfish were bissected along the abactinal midline, and the pyloric caecae and gonads removed. These two organs and the eviscerated body were dried to constant weight in a tissue freeze drier. Organ indices were defined as:

$$\frac{\text{Dry organ weight}}{\text{Dry weight eviscerated body}} \times 100\%$$

Since organ index is a function of R, and owing to the different size-frequency distributions in each trawl, the mean natural logarithm(organ index) was calculated to make allowance for the disparity in size of starfish dissected. For a comparison of PCIs and GIs (for A.rubens from different areas of the bay) with arm-length, the PCIs of A.rubens caught over the whole study period were grouped into 10mm arm-length size categories. GIs from all A.rubens caught on 12th January 1983; 8th March 1983; and 9th May 1983 (covering the 1983 gonad cycle) were grouped into 20mm arm-length size categories.

2.5.(iii). Results.

The mean PCIs and GIs of A.rubens from St Andrew Bay are shown in Fig. 11.

Pyloric Caecum index cycle: Trawls 2 and 3 show a low-amplitude annual cycle with a maximum PCI in October/November of about 20%, and a minimum in Febuary/April (1982) or May (1983) of 10-12%. The PCI cycle of A.rubens from Trawl 1 was poorly defined, and the peak was delayed until January. The PCI cycle for Trawl 4 was highly distinctive, rising to a maximum of 72% in Oct 1982. PCI and GI rise exponentially with R (Figs. 12 and 13); the amplitude of the Trawl 4 PCI cycle reflected the presence of large individuals in this area of the bay.

Gonad index cycle: Since no gonad indices were obtained between April and September 1982, Fig. 11 has been completed with a dotted line between these two dates, following the shape of the graph in 1983. Gonad indices show an annual cycle, with a peak in April/May falling almost to zero in June after spawning.

Since PCI and GI are a function of R, Fig. 11 reflects the size-frequency distribution of the A.rubens in each transect. It is therefore not an accurate representation of the PCI and GI cycles. However, a comparison between organ indices in A.rubens from different areas of St Andrews Bay can be made by plotting indices againt arm-length (Figs. 12 and 13). For $R<75$mm PCIs from all trawls are very similar. In the 75-85mm category the lowest PCI was found from Trawl 1, and the absence of any A.rubens larger than this from this

FIGURE 11

Plot of the mean gonad and pyloric caecum indices of A. rubens from St. Andrews Bay trawls.

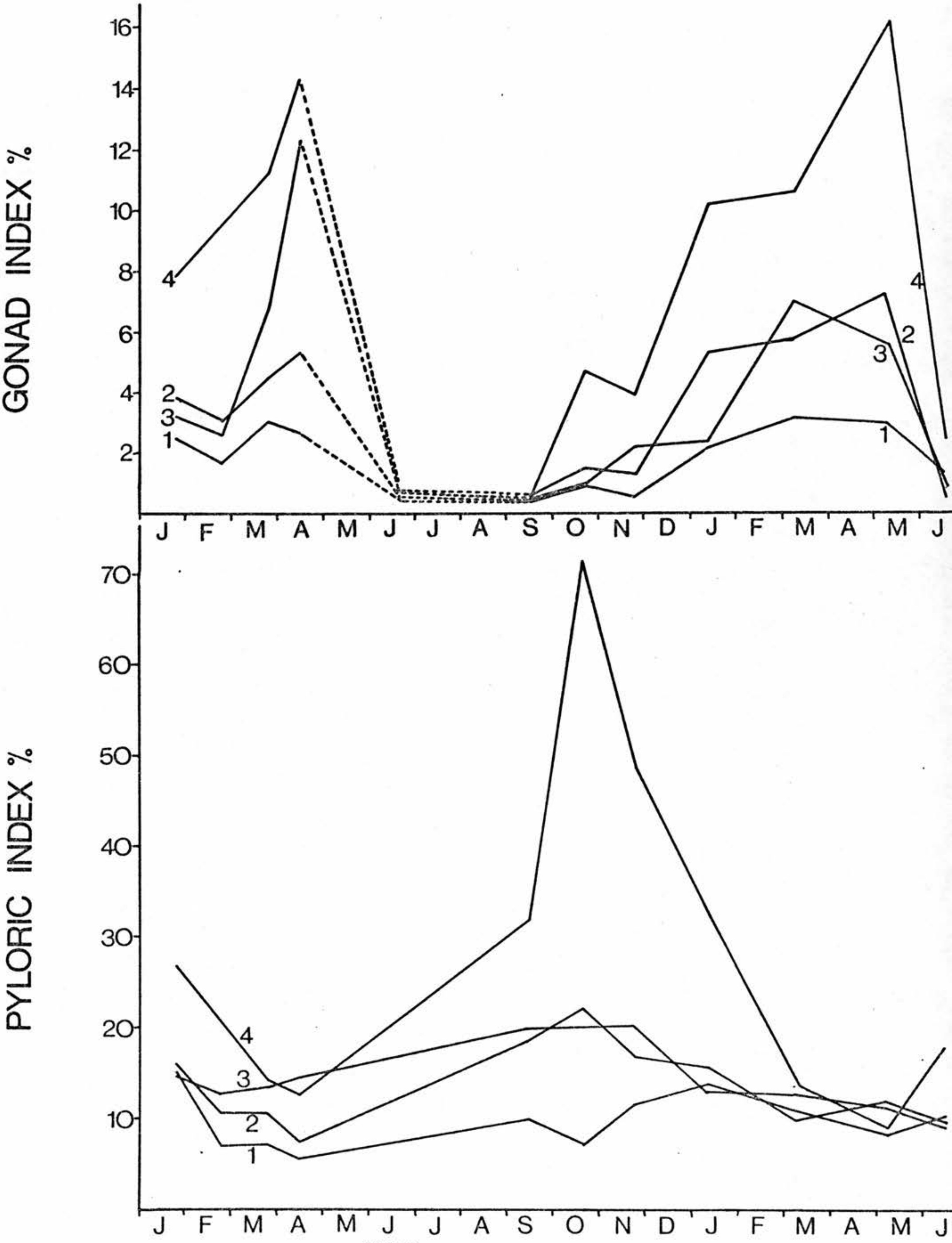

GONAD INDEX %
16
14
12
10
8
6
4
2
4
2
3
1
4
2
3
1
J F M A M J J A S O N D J F M A M J
PYLORIC INDEX %
70
60
50
40
30
20
10
4
3
2
1
J F M A M J J A S O N D J F M A M J
1982
1983

FIGURE 12

Plot of mean Pyloric Caecum Index (± 1 standard error) against *A. rubens* arm length for each trawl; calculated from all starfish collected during the study period.

The following key refers to the number of starfish from which each point was calculated:

* = 14
. = 15-29
Nothing = 30

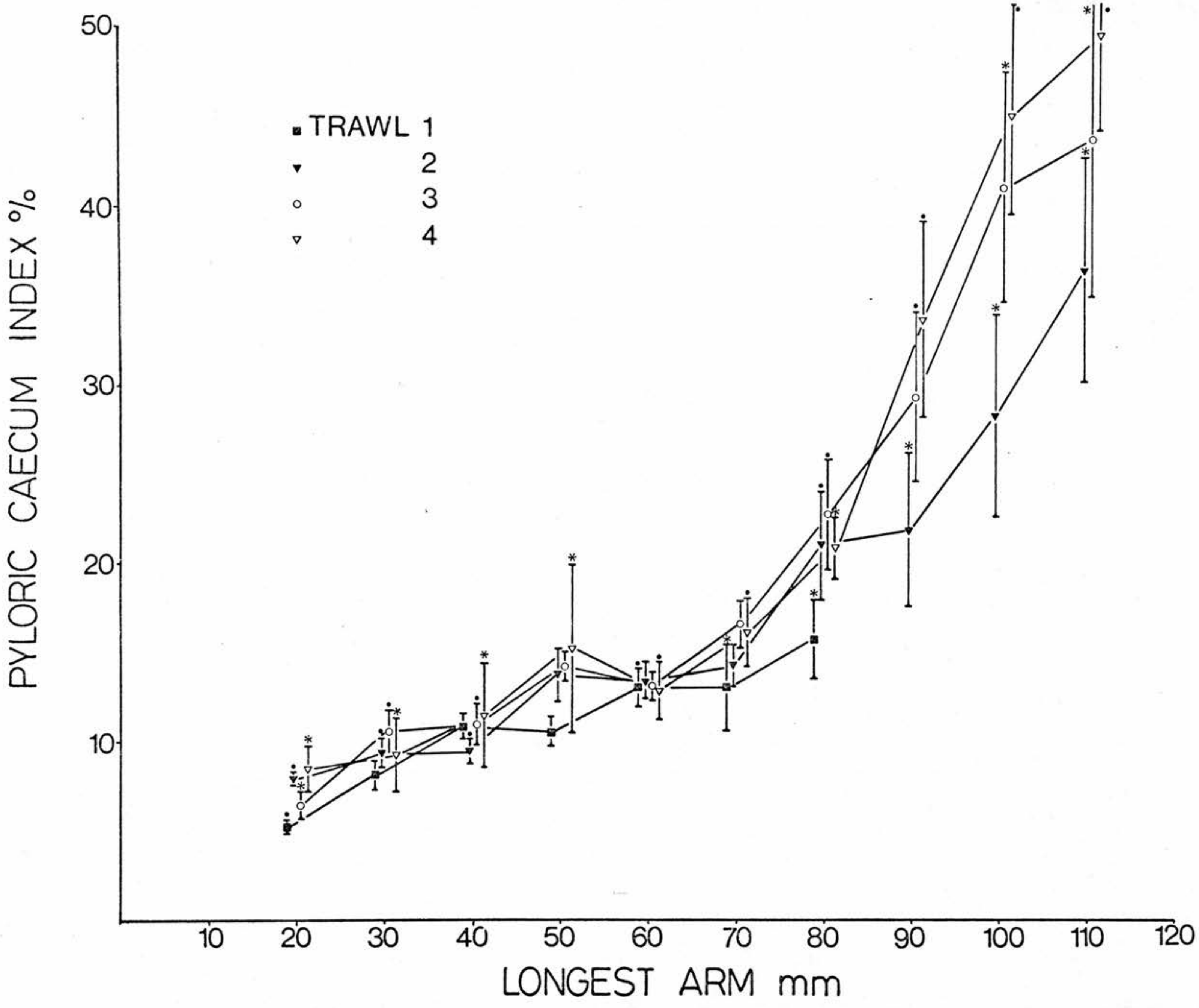

■ TRAWL 1
▼ 2
○ 3
▽ 4
PYLORIC CAECUM INDEX %
50
40
30
20
10
10
20
30
40
50
60
70
80
90
100
110
120
LONGEST ARM mm

FIGURE 13

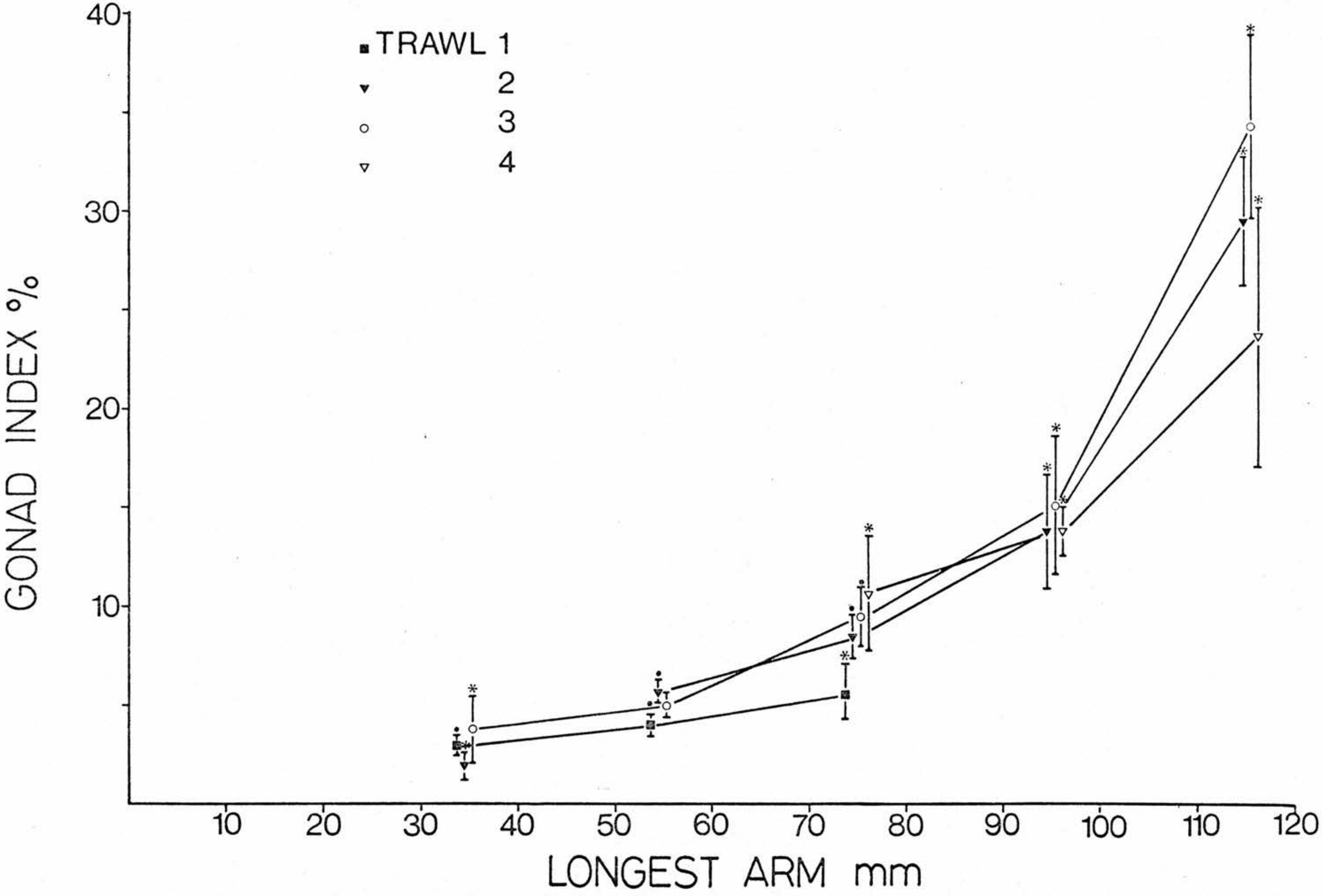
Plot of mean Gonad Index (± 1 standard error) against A. rubens arm length for each trawl; calculated from starfish collected on 12.1.83, 8.3.83 and 9.5.83 only.

The following key refers to the number of starfish from which each point was calculated:

* = 14

. = 15-29

Nothing = 30


■ TRAWL 1
▼ 2
○ 3
▽ 4
GONAD INDEX %
40
30
20
10
LONGEST ARM mm
10
20
30
40
50
60
70
80
90
100
110
120
*

trawl prevents extrapolation of the line beyond this point. A.rubens from Trawl 4 possess the highest mean PCIs, but they are not significantly different from those of any other trawl (Mann-Whitney U test. For example: testing Trawl 2 vs. Trawl 4 in the 96-105mm category, U=34.5, p=.085. Testing Trawl 1 vs. Trawl 4 in the 76-85mm category, U=26, p=.094.). The lowest GI comes again from Trawl 1, although not significantly different from any other trawl. In the largest starfish size category the lowest GI is from Trawl 4, the highest from Trawl 3.

2.5.(iv). Discussion.

Despite the low amplitude of the PCI cycle of A.rubens from Trawls 1, 2, and 3, an inverse relationship is apparent between PCI and GI cycles. This has previously been described in A.rubens by Jangoux and Vloebergh (1973), and is interpreted as a means of spreading the costs of reproduction over the entire year. The sexes of starfish dissected were not noted , previous work (Jangoux and Vloebergh, 1973) indicating that GIs are slightly higher in females than males.

In some asteroid species there is no correlation between GI and animal size (Crump, 1971), and the use of a GI eliminates animal size differences. In A.rubens, however, both pyloric and gonad indices increase exponentially with arm-length, so that a record of mean organ index is of value only if the sizes of starfish from which the samples were taken on each occasion are known and are constant. Otherwise the mean value reflects the size-distribution of starfish sampled as well as the stage of the organ cycle. In this study an attempt to overcome this difficulty by calculating the mean natural logarithm of the indices rather than the mean index itself, had limited success. The apparent highest mean GIs, from Trawl 4, are an artifact caused by the dissection of only large individuals from this area of the bay, and the disparity in PCIs between Trawl 4 and Trawls 1, 2, and 3 is exaggerated. A better criterion for comparison of inter-population differences in organ indices is a record of index against arm length (Figs. 12 and 13). GIs from Trawls 2, 3 and 4 were similar up to the largest size category, in which the highest indices were found from Trawl 3 (Fig. 13). PCIs from Trawls 2, 3 and 4 did not diverge until the 85-95mm category, the highest indices coming from Trawl 4. The use of dry tissue for the calculation of organ indices, in an attempt at a more empirical calculation of these cycles, has not been justified on account of the extra work involved and the inability to make comparisons with other authors.

2.6. General Discussion.

The abundance of macrofauna, particularly bivalves, is reflected in the size-structure and organ indices of starfish populations in St Andrews Bay. However, owing to A.rubens' ability to decimate burrowing bivalve populations (Warner, 1979), and its likely position as a "key species" (Paine, 1969) controlling faunal diversity, the infauna population is also a reflection of asteroid density. A.rubens from deeper water offshore on sediment from which no bivalves >15mm were recorded showed a restricted size distribution (no starfish with R>75mm), and consistently low values for both GIs and PCIs. The PCI cycle was poorly defined and the apparent maximum occurs three months after that of the other trawls. The requirement by asteroid populations for prey of different sizes is well established (Hulbert, 1979; Sloan, 1980), and asteroid populations whose restricted size-frequency distributions have been attributed to food shortage include Patiriella regularis (Crump, 1971); Asterias vulgaris (Hulbert, 1979); and A.rubens (Nauen, 1978).

Nauen (1978) suggested that small A.rubens in Kiel Bay may represent a "waiting stage" between the larval stage, serving propagation, and the growing stage, serving reproduction, in which starfish can remain for months waiting for a "free seat" in the ecological niche.

In St Andrews Bay the inshore trawls are consistent with a pattern of A.rubens recruitment only in the shallow rocky sublittoral along the south coast of St Andrews Bay. A peak of small animals from the southernmost of these trawls (2) is missing from number 3 in which few starfish are found with R<15mm. The difference in the minimum sizes of starfish from these two trawls is evidence that A.rubens from number 3 may have immigrated from the south. Trawl 4 produced a small number of large A.rubens showing an increase in arm length of over 2mm.month^{-1}. This compares with growth rates in the laboratory of 4.5mm.month^{-1} and on the shore of 1.5mm.month^{-1}.

Barker and Nichols (1983) found almost any hard substratum suitable for settlement by A.rubens brachiolariae, provided an algal film was present. The fact that conditions for settlement are apparently more suitable at Trawl 1 than at Trawls 3 and 4 cannot be explained.

Chapter 3.

LITTORAL POPULATIONS OF A.RUBENS AROUND ST.ANDREWS.

3.1. Introduction.

The four St Andrews Bay trawls studied showed characteristic and consistent population patterns. Nonetheless the illusion of separate populations is an artifact of the sampling procedure. In reality the sublittoral sandy habitat is largely homogeneous and A.rubens will be present over much of its area, the different "populations" merging into one another.

A.rubens are also found in the intertidal zone of rocky shores around the southern edge of St Andrews Bay. The aims of the present study were to determine the degree to which this intertidal population is discrete from sublittoral populations such as those described in chapter two, and to compare population dynamics and reproductive energetics of A.rubens in these different habitats.

3.2. Growth in intertidal A.rubens.

3.2.(i). Introduction.

Growth of asteroids has been examined by many workers both in the laboratory (Bull, 1934; Vevers, 1949; Feder, 1956, 1970; Yamaguchi,1974,1977), and in the field (Orton and Fraser, 1930; Barnes and Powell, 1951; Pearse, 1965; Dayton et al, 1974; Anger et al, 1977; Barker, 1979). The overriding impression is one of plasticity of growth depending on such factors as water temperature (Galtsoff and Loosanoff, 1939; Smith, 1940; Vevers, 1949; Hatanaka and Kosaka, 1959; Hancock, 1955, 1958; Mackenzie, 1970), quantity of food taken (Mead, 1900; Galtsoff and Loosanoff, 1939; Smith, 1940; Vevers, 1949; Hancock, 1958; Feder, 1963, 1970; Pearse, 1965; Menge, 1972b; Paine, 1976), and quality of food taken (Scheibling, 1981a).

A reduction in feeding rate is commonly observed either as a result of temperature or spawning. Asterias forbesi (USA) feeds little from January to the end of March and then increases to a maximum feeding rate in June/July. (Mackenzie, 1970). A.vulgaris in Eastern Canada feeds mostly in Spring and Autumn and relatively little in Winter (Needler, 1941). In both these species feeding rates are primarily controlled by water temperature, falling both when the water temperature is too low (Winter) and too high (Summer) (Mackenzie, 1970). Hancock (1958) reported that the feeding rate of A.rubens is greatest between 10 and 13°C, declining above and below this temperature. A lull in feeding prior to spawning has been reported for some asteroids (Hancock, 1955, 1958, for A.rubens) but not others (van Veldhuizen, 1977, for Pisaster brevispinus (Stimpson)). Laboratory experiments on A.rubens (see Chapter 4) showed that this starfish may cease feeding for up to a month after spawning. A.rubens can become sexually mature within its first year (Vevers, 1949), but Guillou (1979) reported that in the intertidal first maturity was seen for some individuals only in the second Winter.

A.rubens is reported as having a seasonal basis for its activity in the intertidal, with a migration offshore in colder Winter weather and a return inshore in warmer months (Vinberg, 1967; Annala, 1968; Rasmussen, 1973).

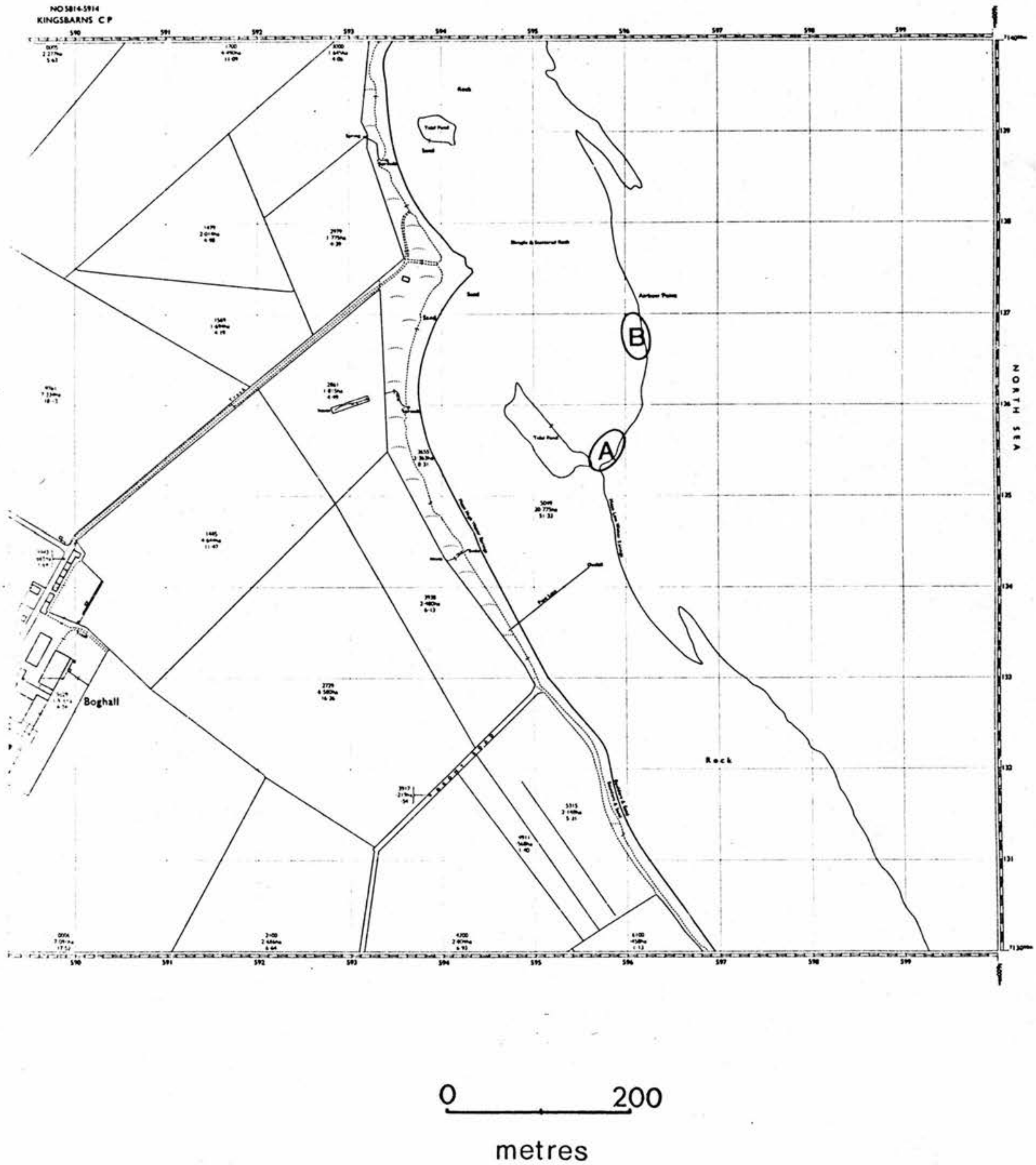
3.2.(ii). Materials and methods.

A.rubens were collected from Boghall area A (Fig. 14) on a monthly basis between February 1982 and August 1983. Collection continued until either 100 starfish had been found or one hour had elapsed. Starfish were weighed and measured in the laboratory, and returned to the shore the following day.

3.2.(iii). Results.

FIGURE 14

A section of Ordnance Survey $^{1}/25''$ map number 5813-5913, showing Boghall farm and sampling areas A and B.


NO 5814-5914
KINGSBARNS C P
590
591
592
593
594
595
596
597
598
599
Rock
Tidal Pond
Sand
Shingle & Scattered Rock
Airbow Point
B
A
Tidal Pond
NORTH SEA
Boghall
Rock
0
200
metres

From February to May 1982 mean A.rubens "R" increased from 33.5 to 41mm; an average of 2.2mm.month^{-1} (Fig. 15, Table 4). From June to October, however, the mean size decreased, and October saw the first appearance of a second year-class (Fig. 16, Table 5). The minimum arm-length of this cohort was 6mm.

Both cohorts increased in size from October to November, but this was followed by decreases in mean size over the Winter. From March to August 1983 the 0+ year class grew more quickly than the 1+ animals, and by the end of the sampling period the two peaks in the size-frequency distribution had begun to merge (Fig. 16). The 0+ cohort increased "R" at a mean rate of 3.5mm.month^{-1} over this period. The 1+ cohort increased in R at a rate of 1.6mm.month^{-1} between October 1982 and August 1983.

Numbers of A.rubens caught per hour fell markedly between July and September 1982, and appeared to be recovering slowly from this point until the end of the sampling period (Fig. 17, Table 6).

3.2.(iv). Discussion.

Increase in mean body size of the Boghall A.rubens population did not take place at a constant rate, and on occasions (e.g. November 1982 to January 1983) the mean size decreased. Guillou (1980) also found a decrease in the size of intertidal A.rubens on the coast of

TABLE 4, FIGURE 15

Size-frequency distributions of A. rubens collected from Boghall area A between February and September 1982.

MONTH	Arm length (mm)	N
February 1982	33.5	149
March	34.4	178
April	39.6	105
May	41.0	107
June	39.7	102
July	40.5	108
September	36.1	45

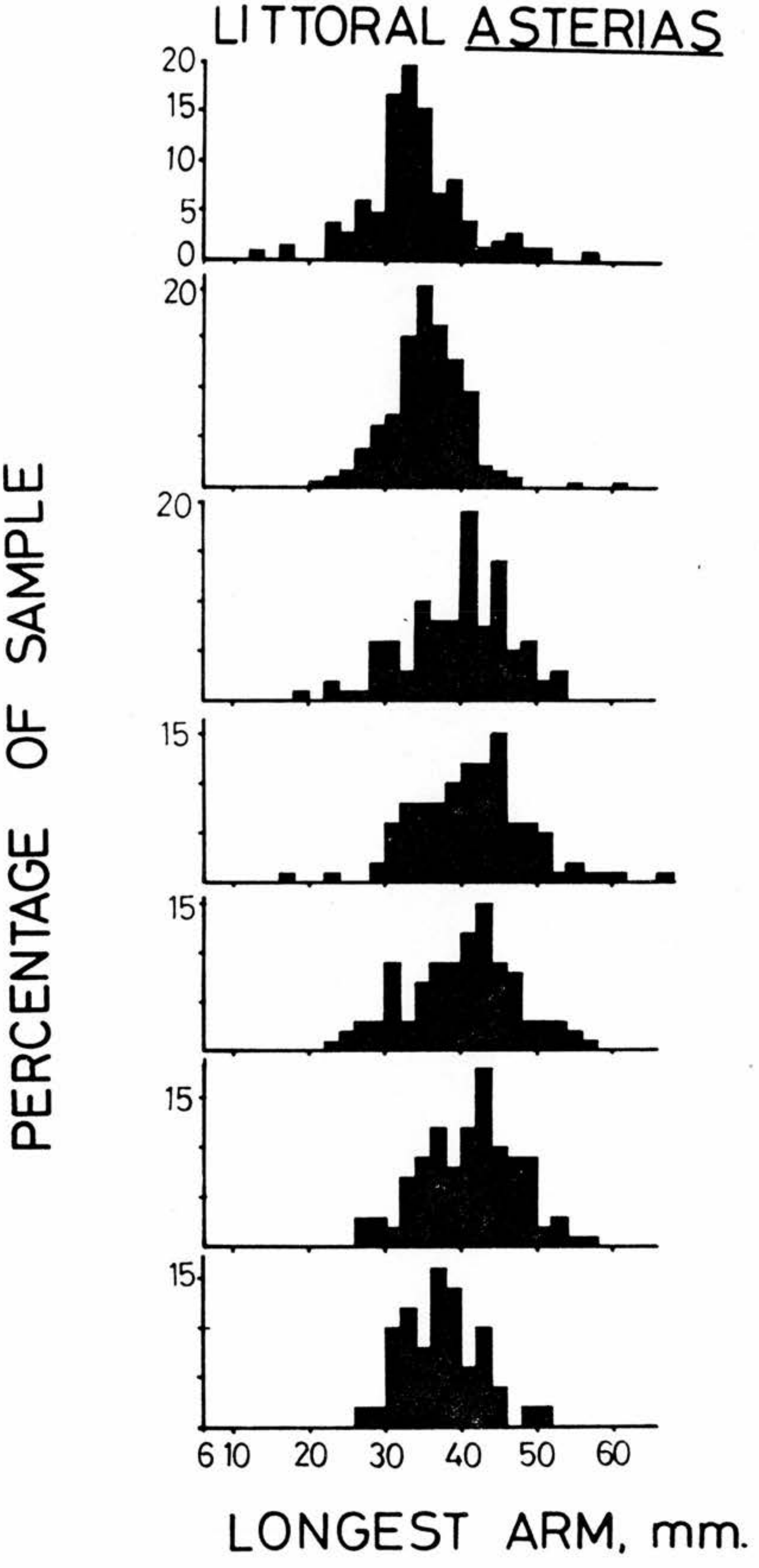

LITTORAL ASTERIAS
PERCENTAGE OF SAMPLE
20
15
10
5
0
20
20
15
15
15
15
6
10
20
30
40
50
60
LONGEST ARM, mm.

TABLE 5, FIGURE 16

Size-frequency distributions of A. rubens collected from Boghall Area A between October 1982 and August 1983.

MONTH	Arm length(mm) (mean of cohort 1)	Arm length(mm) (mean of cohort 2)	N
October 1982	11.1	33.4	48
November	14.9	41.8	59
January 1983	13.9	33.7	52
March	10.4	37.8	56
March	11.9	38.5	84
April	15.5	36.4	73
June	19.5	39.6	81
August	29.9	49.9	74

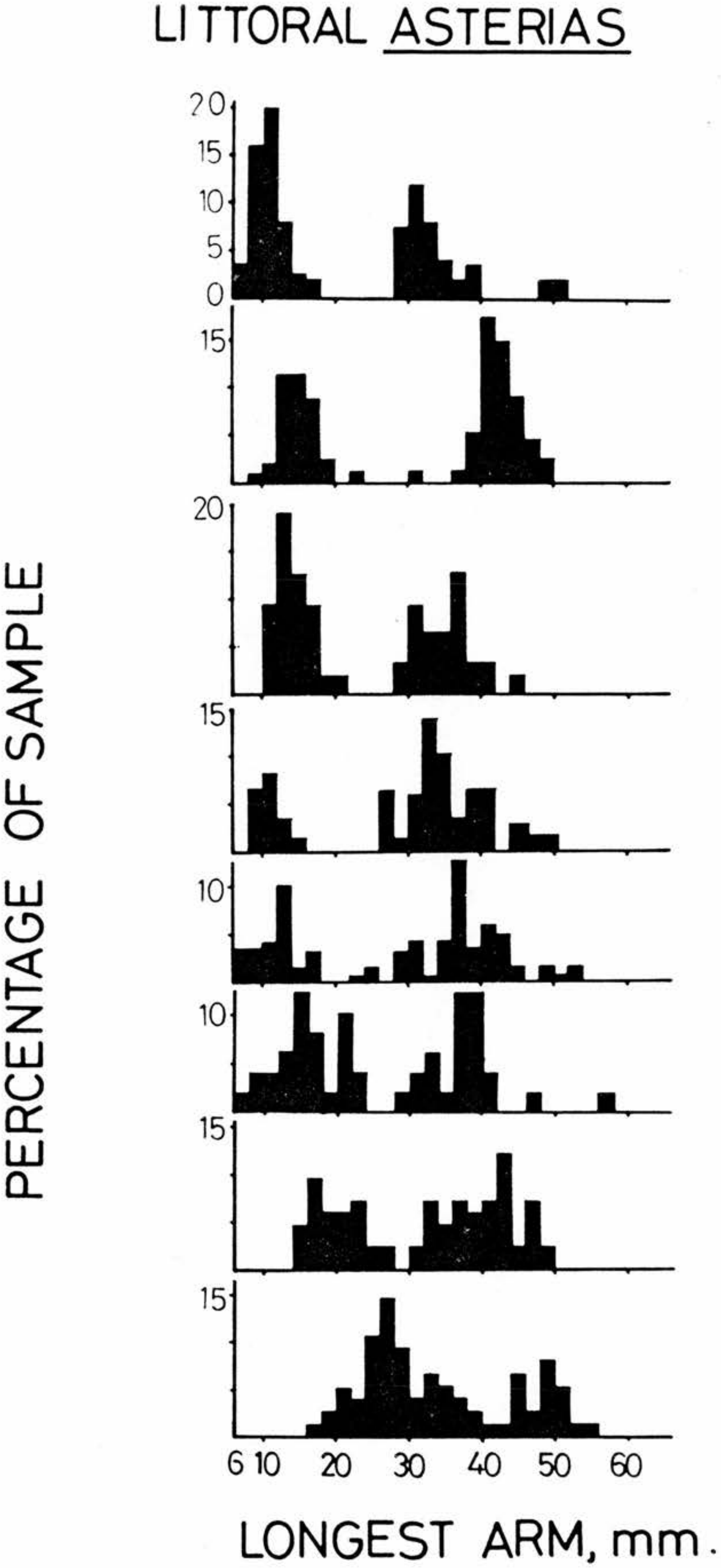

LITTORAL ASTERIAS
20
15
10
5
0
15
20
15
10
10
15
15
6 10 20 30 40 50 60
PERCENTAGE OF SAMPLE
LONGEST ARM, mm.

FIGURE 17

The abundance of A. rubens at Boghall area A, as numbers collected per hour.

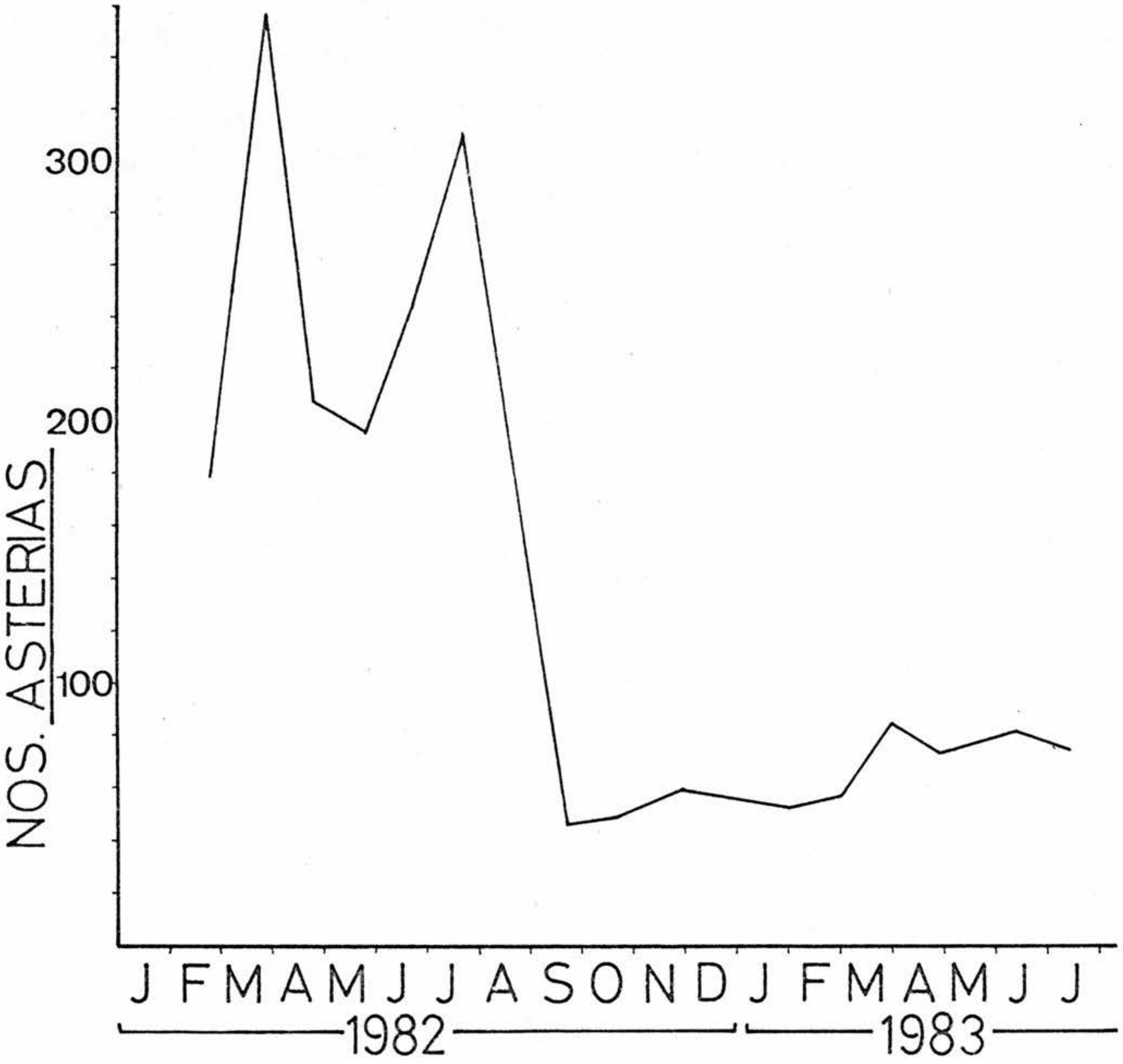

NOS. ASTERIAS
100
200
300
J F M A M J J A S O N D J F M A M J J
1982
1983

TABLE 6

Sampling regime at Boghall area A.

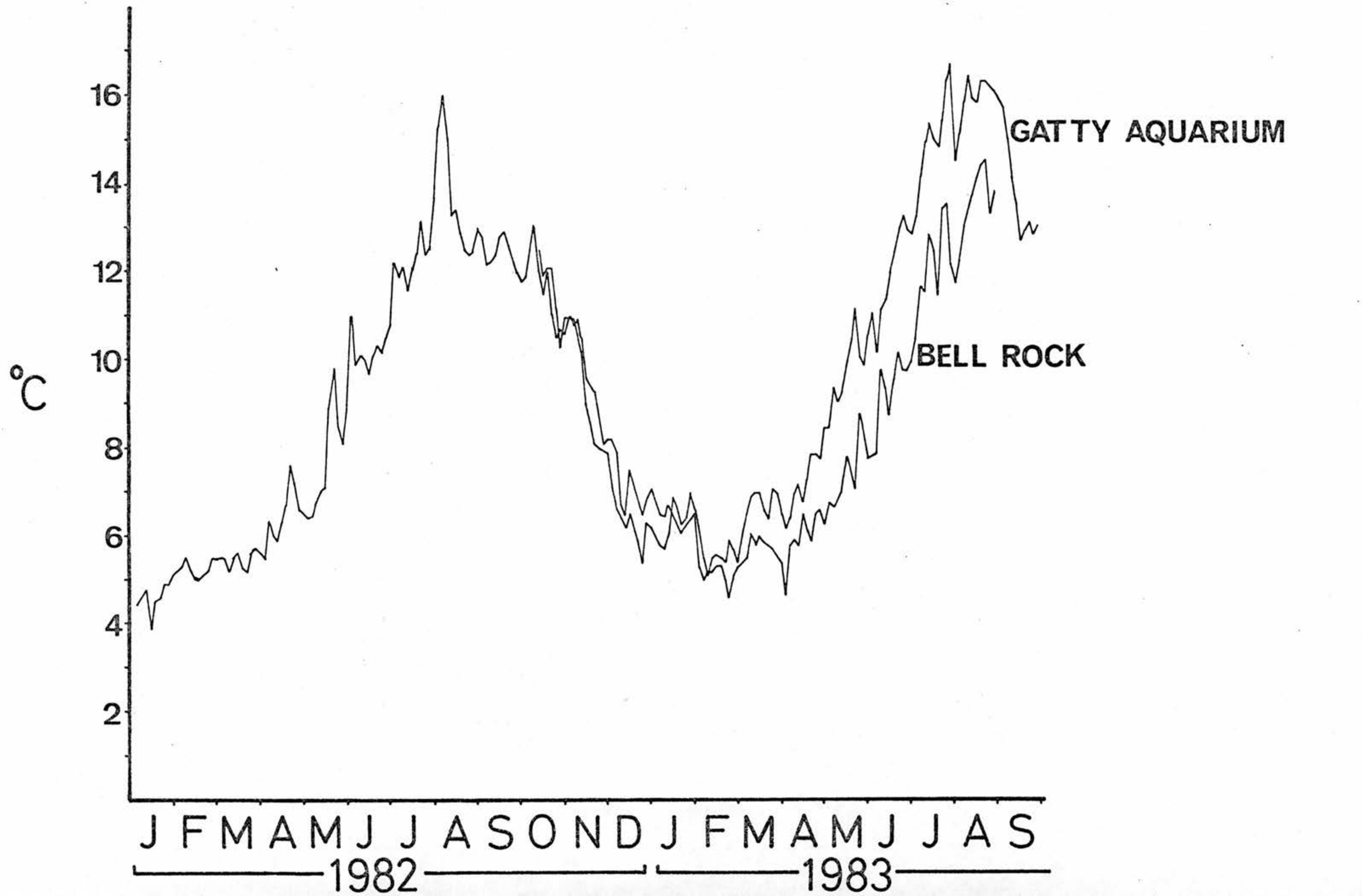
Date	Search Time, (mins)	No. Collected	No. Collected Corrected to One Hour (Fig. 17)
25. 2.82	50	149	179
26. 3.82	30	178	356
24. 4.82	30	105	208
24. 5.82	33	107	195
23. 6.82	25	102	245
21. 7.82	21	108	309
20. 9.82	60	45	45
18.10.82	60	48	48
31.11.82	60	59	59
31. 1.83	60	52	52
1. 3.83	60	56	56
31. 3.83	60	84	84
28. 4.83	60	73	73
13. 6.83	60	81	81
10. 8.83	60	74	74

Brittany between December and April every year. Both high and low water temperatures are reported as causing a reduction in feeding rate in *Asterias* species (Mackenzie, 1970). But examination of Figs. 15 and 16 show that decreases in mean body size did not coincide with extreme water temperatures (Fig. 18), and that while mean size decreased the minimum size remained constant at approximately 28mm, and thus the frequency distribution acquired a negative skew (Fig. 15). Additionally, no *A.rubens* were found at Boghall with R>60mm. Evidently, larger *A.rubens* were being "lost" from the population either through mortality or migration to the sublittoral. The profile of the number of *A.rubens* caught per hour (Fig. 17) shows that a population crash occurred in August/September 1982, and this is accompanied by a fall in mean size from 40.5 to 36.1mm (Table 4). Movement of larger starfish offshore has been suggested for species where the near-shore population is juvenile to represent a partitioning of resources and reduction of competition (Menge and Menge, 1974; Town, 1980). *A.rubens* have previously been reported as retreating from the littoral in Winter (Vinberg, 1967; Rasmussen, 1973), but this pattern is not reflected in the present study , and does not explain the observed decrease in mean size observed over the Summer of 1982.

Reports in the literature of offshore migrations as a result of temperature or stormy weather (Mauzey, 1966; Vinberg, 1967; Annala, 1968; Paine, 1969; Rasmussen, 1973; Pabst and Vincentini, 1978; Davis and van Blaricom, 1978; Scheibling, 1980c) refer to shifts in the whole population rather than in particular size categories.

FIGURE 18

Profile of sea water temperatures for the Gatty aquarium and for the Bell Rock Lighthouse. The latter is 14 nautical miles ENE of St. Andrews.


°C
16
14
12
10
8
6
4
2
GATTY AQUARIUM
BELL ROCK
J F M A M J J A S O N D J F M A M J J A S
1982
1983

The limit to Pisaster size in the intertidal is environmentally imposed (Paine, 1976). Paine concluded that a starfish growing in a particular area must either emigrate to better areas as its energy needs surpass those of the immediate environment, or growth must be adjusted to local resources. In his study Paine (1976) favoured the latter strategy. It may be that the asymptotic size for A.rubens at Boghall is reached when R=50-60mm, and to grow larger the starfish must emigrate.

The faster growth rate of younger asteroids is well documented (e.g. Bull, 1934; Vevers, 1949) and in this case probably reflects an abundance of food for newly settled starfish. Hulbert (1979) commented of A.rubens that "a series of prey specialiations on increasingly larger prey items seem to be required for this species to grow larger".

The smallest starfish found intertidally had R=6mm. Presumably all settlement occurs below ELWS (Extreme Low Water of Spring Tides) since careful searching never exposed any starfish smaller than this. Although there are a number of studies describing the reproductive cycles of adult starfish there is little known concerning the recruitment of juveniles into the adult populations. This is largely due to the infrequency with which starfish at this early stage of development are encountered on the shore (Feder, 1970; Barker, 1979).

From February to September 1982 there is only one peak in the size-frequency histogram. From October 1982 onwards there are two. This suggests that recruitment of juveniles did not occur in the autumn of 1981. Sporadic recruitment is common in echinoids (e.g. Buchanan, 1966), as well as asteroids (Feder, 1970; Kenchington, 1977). Towards the end of the present sampling programme, however, the two cohorts were beginning to merge. This suggest that although recruitment may not have taken place in 1981, the single peak in the size-frequency distribution during 1982 may not represent A.rubens of only one age-class. Indeed, Guillou (1980) separated his data on littoral A.rubens in Brittany into five age-classes. If recruitment in the intertidal A.rubens population in Fife only occurs every few years and if there is an asymptotic size for starfish on the shore then the size-frequency histogram will tend towards the shape encountered at the beginning of the study period: here the single peak would consist of starfish of more than one age-class. For this reason estimates of asteroid growth rates in the field by means of the modal analysis of size-frequency distributions cannot be used reliably.

3.3. Reproductive cycles in littoral A.rubens.

3.3.(i). Introduction.

Intertidal asteroid species have been the basis of several studies on predation (Paine, 1969, 1971, 1974, 1976; Menge, 1972, 1976, 1978) and competition (Menge and Menge, 1974; Menge, 1975, 1979; Menge and Sutherland, 1976), but study of their reproductive capacities has gone relatively ignored compared with work on sublittoral populations.

Certain asteroid species (*e.g. Pisaster ochraceus*) are particularly adapted to life on the shore and are found sublittorally only rarely. More commonly an intertidal asteroid population seems to be an extension of the sublittoral population, and a smaller size range of starfish is found there (*e.g.* Marsh, 1968; and see Chapter 2.3). In *P.ochraceus* recently recruited individuals have been found in special "nursery areas", for example in the San Juan Islands (Menge and Menge, 1974). However, these "nursery areas" are not found in exposed coastline communities. In the latter recruitment occurs seldomly, but great longevity and low mortality rates mean that starfish density remains surprisingly constant over long time intervals (Paine, 1976).

Farmanfarmaian *et al.* (1958) have compared organ index cycles of four Pacific asteroid species, three of which had been collected intertidally. However, the only study comparing reproductive cycles in the same species from both littoral and sublittoral habitats is that of Barker and Nichols (1983). Studying *A.rubens* at Plymouth, Barker and Nichols (1983) found that an offshore population had a lower mean Gonad Index (GI) than an intertidal population, and that there was little annual variation in the Pyloric Caecum Index (PCI) of offshore starfish. The sublittoral area sampled was close to one whose A.rubens population Vevers (1949) considered to be food-limited. Barker and Nichols (1983) calculated organ indices from dissection of ten "adult" A.rubens, but size-frequency histograms of the whole population are not included, and no criteria for adulthood mentioned.

In the present study organ indices of littoral A.rubens from Kinkell Braes (see Fig. 1) are compared with those of starfish from St Andrews Bay (see Chapter 2). A size-frequency distribution of the Kinkell Braes A.rubens population would be similar to that shown in Figs. 15 and 16 of the Boghall A population, in which few starfish were found with R>50mm.

3.3.(ii). Materials and methods.

A.rubens were collected intermittently between October 1982 and June 1983 from Kinkell Braes beach (Fig. 1). The method by which indices were calculated was the same as for sublittoral A.rubens and is described in Chapter 2.5.

3.3.(iii). Results.

The mean GI of Kinkell Braes A.rubens rose from 0.5% in October 1982 to 3.7% in June 1983 (Fig. 19, Table 7). PCI was at a high value of 10-12% in October 1982 and June 1983, and fell to 3.3% between these dates.

3.3.(iv). Discussion.

The low number of data points in figure 19 renders interpretation difficult. The mean PCI rose sharply between March and June 1983. This does not correspond with any similar rise in the PCI of sublittoral A.rubens (Chapter 2.5, see Fig. 11). Peak values for GI and PCI, and the months in which they occurred, cannot be determined. Nonetheless, values obtained were lower than those from most sublittoral A.rubens. With regards to PCI values, the Kinkell Braes population was most similar to Trawl 1, a population severely food-limited. The Kinkell Braes mean GI rose marginally higher than that of Trawl 1. All sublittoral populations, however, had spawned by June 1983. Barker and Nichols (1983) also found a difference in reproductive periodicity between intertidal and sublittoral A.rubens. They found that in 1981 spawning in the offshore population occurred in April/May, and in the littoral population in July/August. The previous year, however, spawning in the two populations had been coincident.

FIGURE 19

Plot of the mean Gonad and Pyloric Caecum Indices (± 1 standard error) of Littoral A. rubens collected from Kinkell Braes, October 1982 - June 1983.

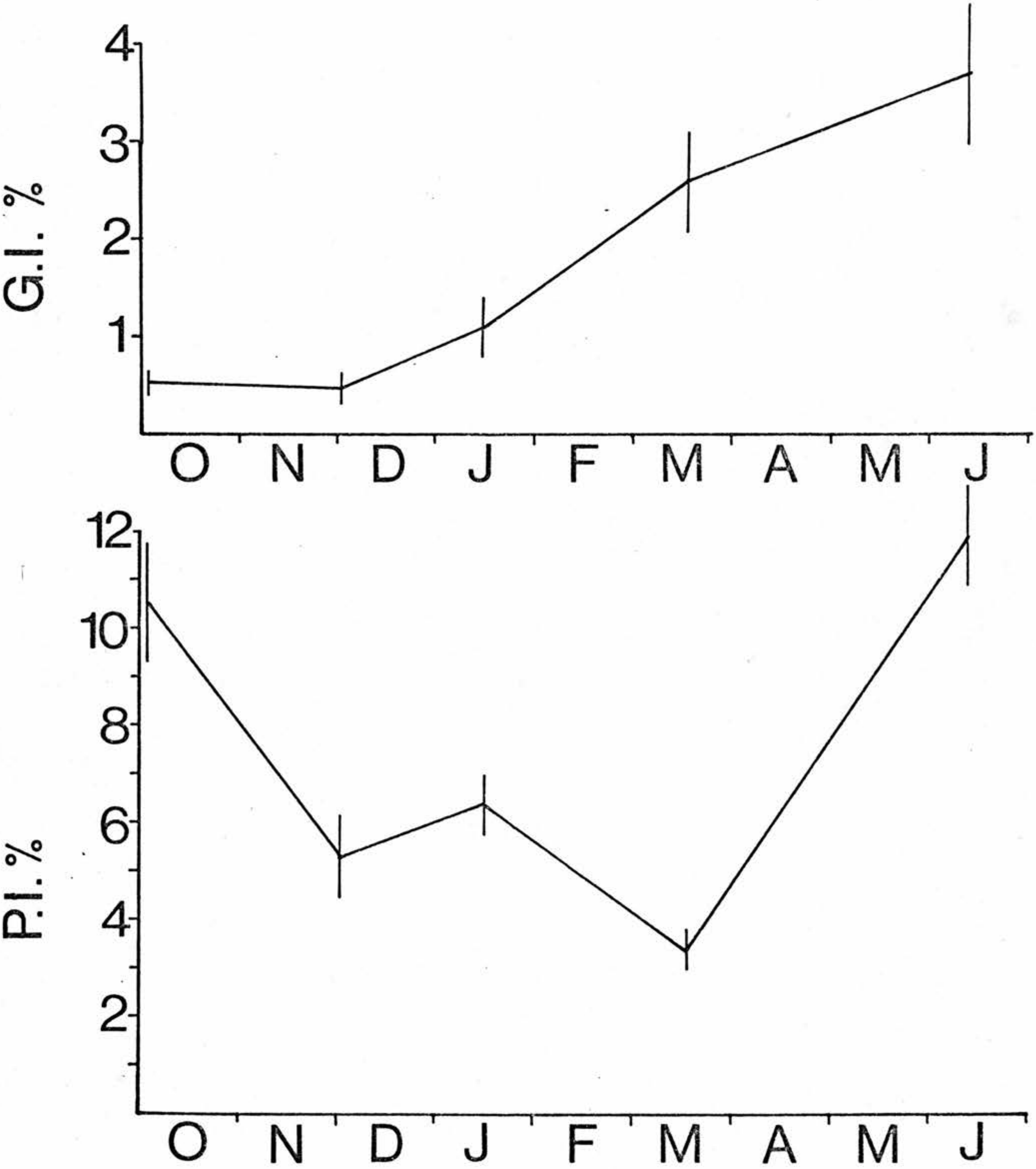

G.I. %
4
3
2
1
O
N
D
J
F
M
A
M
J
P.I. %
12
10
8
6
4
2
O
N
D
J
F
M
A
M
J

TABLE 7

Gonad and Pyloric caecum indices from littoral *A. rubens* collected from Kinkell Braes.

DATE	No. <u>A. Rubens</u> from which P.C.I. calculated	Mean P.C.I. %	No. A. Rubens from which G.I. Calculated	Mean G.I. %
30.10.1982	30	10.5	12	.54
1.12.1982	30	5.3	11	.47
16. 1.1983	30	6.4	15	1.1
18. 3.1983	30	3.34	29	2.61
10. 6.1983	30	11.9	29	3.72

As mentioned in Chapter 2, disparity in organ index levels is difficult to interpret when calculated from starfish of different size distributions.

3.4. Capture-recapture study of intertidal A.rubens.

As there are no reliable skeletal age indicators in asteroids (Smith, 1940; Hatanaka and Kosaka, 1959; Kvalvagnaes, 1972) of the kind found in echinoids (Moore, 1935), a number of attempts have been made to follow growth and displacement of starfish in the field by means of individual marking techniques. Whole A.forbesi have been immersed in the vital stains Neutral Red (Vernon, 1937) and Nile Blue Sulphate (Loosanoff, 1937). Vernon (1937) recorded that "traces of colour could still be observed ten months after staining".

For most capture-recapture studies, however, it is valuable to be able to determine the occasion on which a given animal was caught. Starfish arms can be numbered with respect to the madreporite, enabling individual staining of 31(using one stain) or 232(using two stains) five-armed starfish. In the present study individual marking using both Neutral Red and Nile Blue Sulphate was attempted for three months, but it was found that marks were not always easily discernible after this period in the field. Individual staining of large numbers of starfish is a lengthy procedure, and it may be that tissues were not immersed for long enough in stain solution.

Marking by scarification (Scheibling, 1980d) is not applicable to A.rubens on account of the nature of the integument and the small size of the madreporite. The use of tags sewn into the body similar to those used commercially for fish and crustaceans has not been widely successful in asteroids. Kvalvagnaes (1972) described how A.rubens were able to reject tags held by both steel wire and nylon thread: "Athwart the point of tag attachment the border of the arm dissolved, whereby an indentation was formed that gradually deepened until the nylon gut was reached and the tag released. The calcareous plates of the ambulacral groove were also partly dissolved at this point."

Kvalvagnaes (1972) and Paine (1976) observed a high proportion of four-armed starfish in the vicinity after tagging starfish thus. However, in both cases tags had been sewn into the proximal aboral arm surface. Since autotomy involves separation of the arm from the disc, it may be that affixing a tag close to the disc is placing it in tissue that has a predisposition to undergo the degeneration and regeneration necessary for autotomy and regrowth. A.rubens tagged in the aboral arm surface about half-way between disc and arm tip and kept in the laboratory aquarium showed tag persistence varying between three and 26 weeks (Chapter 4.2). Kvalvagnaes (1972) reported encouraging results achieved by writing numbers on the aboral surface of A.rubens using a marker pen containing a concentrated solution of Nile Blue Sulphate. He also showed A.rubens capable of freeing themselves from nylon harnesses.

In experiments following the movement of tagged intertidal Astrostole scabra (Hutton) in New Zealand Town (1980) found that the largest net change in location between consecutive searches was 13.5m in 35 days. Most A.scabra remained resident in the tide pools studied for <30 days. Some individuals reappeared in subsequent searches, and three were recovered 192 days after tagging.

Paine (1976) recorded net Pisaster ochraceus displacement of 3-3.5m.month^{-1}, and local subpopulations remained discrete . Galtsoff and Loosanoff (1939) demonstrated little net movement in Asterias forbesi.

Sublittorally, the tropical Linckia laevigata (L.) moves an average 2.6m.day^{-1} (Thompson and Thompson, 1982) but certain Antarctic asteroids may not undergo any displacement in a year (Dayton et al, 1974). Astropecten species show daily activity patterns (Ferlin-Lubini and Ribi, 1978), and A.johnstoni (Delle Chiaje) has been measured as moving 4.5m.day^{-1} (Pabst and Vincentini, 1978). This latter is as part of a migration this starfish performs annually during Winter into deeper water, returning in the Spring. Thus asteroids, particularly intertidal species, are not credited with extensive powers of locomotion. The Boghall A.rubens population appears to be a largely juvenile one, and a capture-recapture study was undertaken there in an attempt to measure starfish residence time in this habitat.

3.4.(ii). Materials and methods.

A.rubens were collected monthly from Boghall area B (Fig. 14). Two capture-recapture experiments were undertaken, using different methods of starfish marking. From April to June 1982 A.rubens were stained using the vital stains Nile Blue Sulphate and Neutral Red. Each starfish was picked up (using disposable gloves) and the arms dipped individually into concentrated stain solutions for 30-60 seconds. Individual staining of 232 five-armed starfish is possible using two stains, the arms being numbered with respect to the madreporite. This procedure was discontinued after four months as marks on control starfish in the laboratory could no longer be reliably read after this period of time.

From October 1982 to August 1983 A.rubens were marked by sewing through the epidermis on the aboral side of an arm nylon monofilament to which was attached a numbered plastic tag approximately 2x6mm. Tags were coloured on one side using a permanent marker pen. All tags released on a given occasion were of one colour (red, blue and black). A three-digit number was scored into the coloured side of each tag, and a hole made that would accept 2kg breaking strain nylon monofilament fishing line. The nylon was dipped into dilute NaOCl before use, and the sewing needle sterilised in a bunsen flame between each starfish. The air-cooled needle was inserted into the arm through the wall of a papula just dorsal to the adambulacral spines, emerging in the aboral surface. This operation was performed approximately midway between disc and arm-tip. A tight reef knot secured the nylon. Starfish were tagged in the laboratory and returned to the shore the next day.

3.4.(iii). Results.

Numbers of A.rubens recaptured on each sampling occasion (table 8) have been analysed by the Fisher-Ford method (Begon, 1979, see Appendix). The estimated survival rate of marked starfish was $.086.\mathrm{month}^{-1}$ (staining, April-June 1982), and $.09.\mathrm{month}^{-1}$ (tagging, October 1982- August 1983).

3.4.(iv). Discussion.

Previous attempts at marking starfish by sewing tags through them have resulted in a high proportion of tags being thrown (Kvalvagnaes, 1972; Paine, 1976). Laboratory-reared A.rubens tagged as above demonstrated tag persistence varying from three to 26 weeks. However, tags may not survive so well in the field. Nonetheless the same survival rate in the field was estimated by both staining and tagging in the same population.

TABLE 8

Capture-recapture study of littoral *A. rubens* from Boghall area B.

TABLE 8

Date	Sampling period (mins.)	Number collected	Of these, number tagged	Number released
STAINING				
25. 4.82	60	73	-	73
25. 5.82	60	94	1	93
24. 6.82	60	69	8	67
23. 7.82	60	98	6	-
TAGGING				
21.10.82	-	-	-	52
2.11.82	60	25	-	25
2.12.82	60	36	1	35
2. 1.83	60	35	3	35
2. 3.83	60	36	2	34
13. 5.83	60	59	2	58
26. 5.83	60	64	8	63
14. 6.83	40	84	6	81
12. 7.83	45	120	10	117
10. 8.83	45	102	13	-

A survival rate of 9% per month is very low and may indicate either a high mortality rate or a high rate of emigration from the study area. Most previous studies found that intertidal asteroids show little net movement (Paine, 1976). Town (1980), however, examining only two tide pools, showed Astrostole scabra were usually resident there for less than 30 days. In the present study no marked A.rubens were recovered more than one month after marking. There are three possible reasons for this: 1. Marked animals had a high mortality rate; 2. Tags had a very low persistence in the field; 3. The Boghall A.rubens population is a very labile one.

Sewing tags into starfish epidermis is reported to cause scarification and autotomy, and sometimes death (Kvalvagnaes, 1972). Death in stained starfish is rare (Kvalvagnaes, 1972) and only as a result of prolonged immersion of the whole animal in concentrated stain solution. Since both procedures in the present study have given the same estimated survival rate the first of these reasons can probably be rejected. Similarly, although tags can be easily shed (Kvalvagnaes, 1972), stain cannot be. It seems, therefore, that Boghall A.rubens have a short residence time on the shore. This is supported by the successive size-frequency histograms of the Boghall A population which indicate that A.rubens were emigrating throughout the months June to October (Chapter 3.2).

3.5. Summary.

Study of the population dynamics of intertidal A.rubens indicates that the population consists largely of juvenile individuals. Growth there is comparable with that observed by Guillou (1979), but lower than that of most sublittoral populations. It is suggested that there is a significant interchange of starfish between the littoral and the sublittoral, and marking experiments bear this out.

It may be that the shore communities cannot support A.rubens of R>60mm. and that starfish of this size migrate sublittorally. Town (1980) found that few Astrostole scabra specimens of R>140mm appeared intertidally, whereas in animals collected from depths of 20-146m R was>110mm. In A.scabra the onset of sexual maturity coincides with the adoption of an exclusively sublittoral habitat. This is not the case in A.rubens, but the reproductive effort of the littoral population studied was necessarily low on account of the absence of large individuals there.

Chapter 4.

LABORATORY FEEDING AND FORAGING EXPERIMENTS.

4.1 Introduction.

A full understanding of the ecology of any species cannot be gained by field study alone, but requires experimental manipulation in the laboratory also. In this Chapter several aspects of the feeding ecology of A.rubens are examined. Field and laboratory growth rates are compared, and also the presence of any group-moderated effects on individual feeding rate investigated.

Most work on prey selection in asteroids has been restricted to studies of diet choice. In this study the predator-prey interaction between Asterias rubens and Mytilus edulis is examined with regard to Optimal Foraging Theory. The relationship between predator and prey sizes was investigated in order to determine the criteria upon which prey selection is made.

4.2 Growth of Asterias rubens in the laboratory.

4.2. (i). Introduction.

The criterion by which size, and therefore growth, is measured in asteroids can be either increase in body radius (or maximum arm length "R"), or damp weight. Feder (1970) has pointed out that there has been little uniformity in methods used for determining arm length (Mead, 1900; Orton and Fraser, 1930, Bull, 1934; Galtsoff and Loosanoff, 1939; Smith, 1940; Vevers, 1949; Barnes and Powell, 1951), and attempts to convert values to some standard measurement generally diminished their accuracy. Furthermore, Feder (1970) found that successive arm length measurements in Pisaster ochraceus could vary within 30 mins by as much as 14.5%. In addition, arm length increments frequently did not mirror obvious growth of individuals. Bull (1934), however, found that records of weight became impractical as growth progressed, because while superficial moisture was easily removed in the smaller stages, this was difficult to do quantitatively as the animals grew larger. Feder (1970) also observed that P.ochraceus maintained in the laboratory and fed an abundance of mussels and kept continuously immersed adopted a more inflated appearance than field animals: for a given arm length these laboratory animals weighed more than comparable field individuals. These observations alone suggest that R may be the more reliable measure of body size of live starfish. Near St Andrews populations of A.rubens with markedly different size-frequency characteristics are found in close proximity. The size of intertidal A.rubens (Chapter 3.3) is more restricted than that of sublittoral populations (Chapter 2.4), and in the latter considerable variation was found between areas separated by only one or two nautical miles. From a comparison of growth rates in the laboratory of starfish originating from the littoral and sublittoral, one should be able to infer whether the presence of larger individuals sublittorally reflects greater age, a faster intrinsic rate of growth, or a higher quality habitat.

4.2. (ii). Methods.

Sixteen A.rubens from the rocky intertidal at Boghall (Fig. 1) and seven from the sublittoral sand of St Andrews Bay were reared in the laboratory between October 1982 and August 1983. Of the littoral individuals, seven were individually marked with plastic tags (see Chapter 3.5), the tags being periodically replaced as necessary (Table 9). The three groups of A.rubens were kept separately within 30 l fibreglass aquaria, each with a supply of fresh seawater, and with a superabundance of Mytilus edulis of all sizes. "R", the distance from the centre of the disc to the end of the longest arm was recorded monthly, when the tanks were also cleaned . The damp weight of the tagged animals was also recorded. M.edulis were replaced when depleted (approximately every 2-3 weeks). No attempt was made to regulate temperature, the profile of which can be seen in Fig. 18. "R" was measured as soon as possible after removal of the starfish from water in order to avoid shrinkage due to muscle contraction (Feder, 70). For those starfish also being weighed excess water was shaken off, and the starfish blotted with a paper towel in a standardised fashion for a further minute before weighing. Any remaining moisture was included with the starfish.

4.2. (iii). Results.

(a) Growth of littoral and sublittoral *A.rubens* in the laboratory.

Figure 20 presents the growth data for these experiments. In both cases a steady rate of growth was observed throughout the period. These data are adequately described by regression equations fitted by the least squares method. The equations are as follows:

Sublittoral *A.rubens*: $y=0.18x+35.8$ ($N=8$, $r^2=.96$, $p<.001$)

Littoral *A.rubens*: $y=0.15x+22.9$ ($N=9$, $r^2=.96$, $p<.001$)

There is no significant difference between the slopes of these two lines ($t=-1.18$, critical value $-2.37<T<2.37$): that is, the rate of growth-as expressed by R-is not significantly different for the two groups. The mean increase per month in R over the experimental period was 4.1mm (Littoral) and 4.7mm (Sublittoral). There was no indication in the present study of the thicker skeleton reported (Feder, 70) for laboratory-reared asteroids over those in the field.

(b) Growth of tagged *Asterias rubens* in the laboratory.

FIGURE 20

Laboratory growth-rates in A. rubens originating from sublittoral and littoral habitats. October 1982 - August 1983.

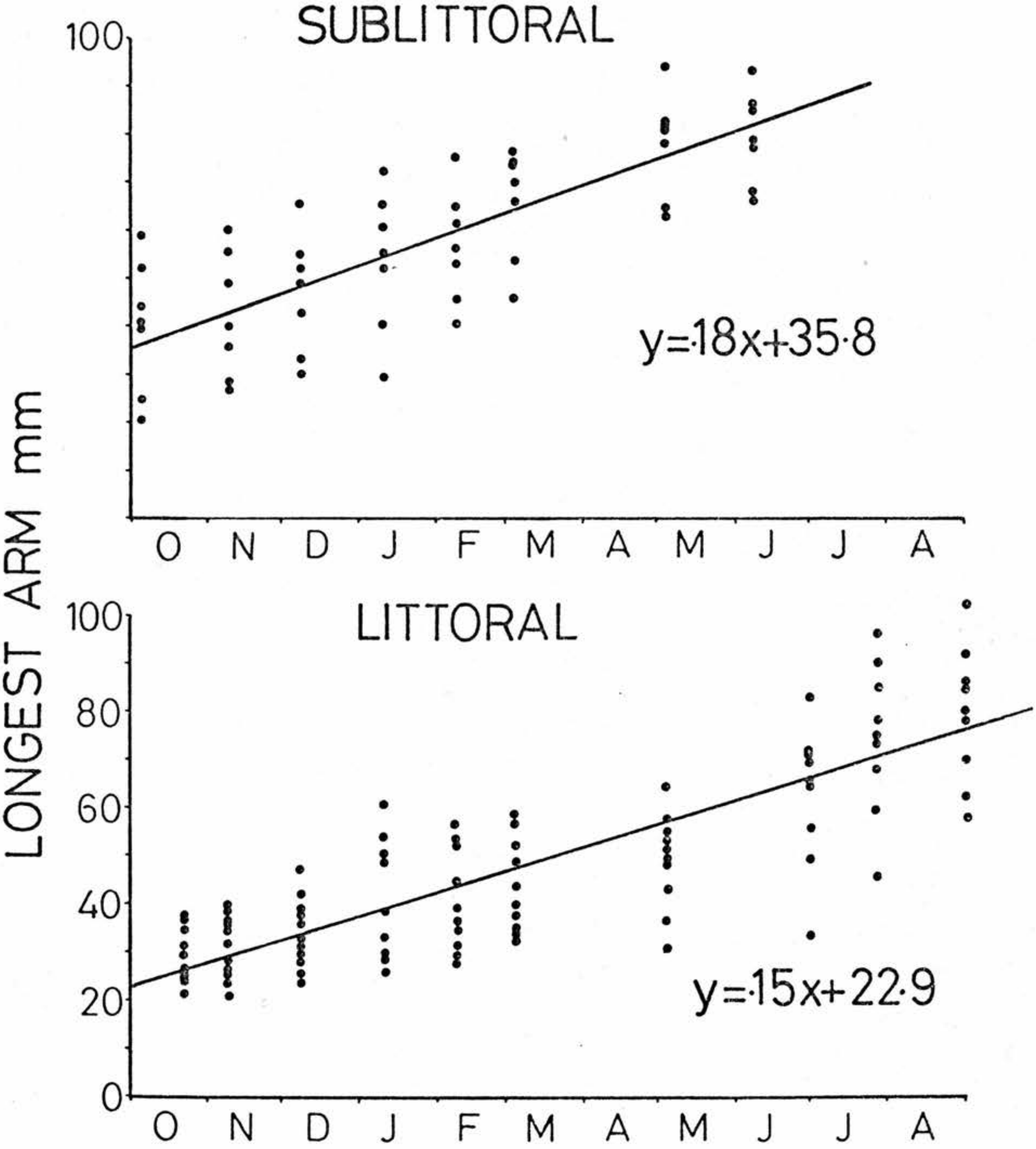

LONGEST ARM mm
SUBLITTORAL
100
y=·18x+35·8
O
N
D
J
F
M
A
M
J
J
A
LITTORAL
100
80
60
40
20
0
y=·15x+22·9
O
N
D
J
F
M
A
M
J
J
A

Figure 21 shows the growth of the seven marked A.rubens as expressed by both R and damp weight. Arm length increased in a linear manner which could be described by the least squares regression equation:

$$y=0.15x+22.9 \quad (N=9,\ r^2=.98,\ p<.001)$$

This is an average increase of 4.68mm.mo^{-1} .There is no significant difference between growth rates of tagged and untagged A.rubens ($t=-1.91$, critical value $-2.37<T<2.37$). Considerable variation in individual growth rate is, however, evident from the plots of increases in damp weight. Note that where weight increases indicate disparities within the group, these are not mirrored by the arm length data. For example, where arm length data suggest starfish number two did not grow in July and August 1983, it increased in weight by about 15% over this period. Tag longevity varied from between three to 26 weeks, and the dates on which tags had to be replaced are shown in Table 9. A.rubens numbers one and four died during one weekend in May when the water supply failed.

4.2. (iv). Discussion. Laboratory growth rates of A.rubens collected from the sublittoral and intertidal.

FIGURE 21

Growth of tagged A. rubens in the laboratory, as recorded by changes in both arm length and damp weight.

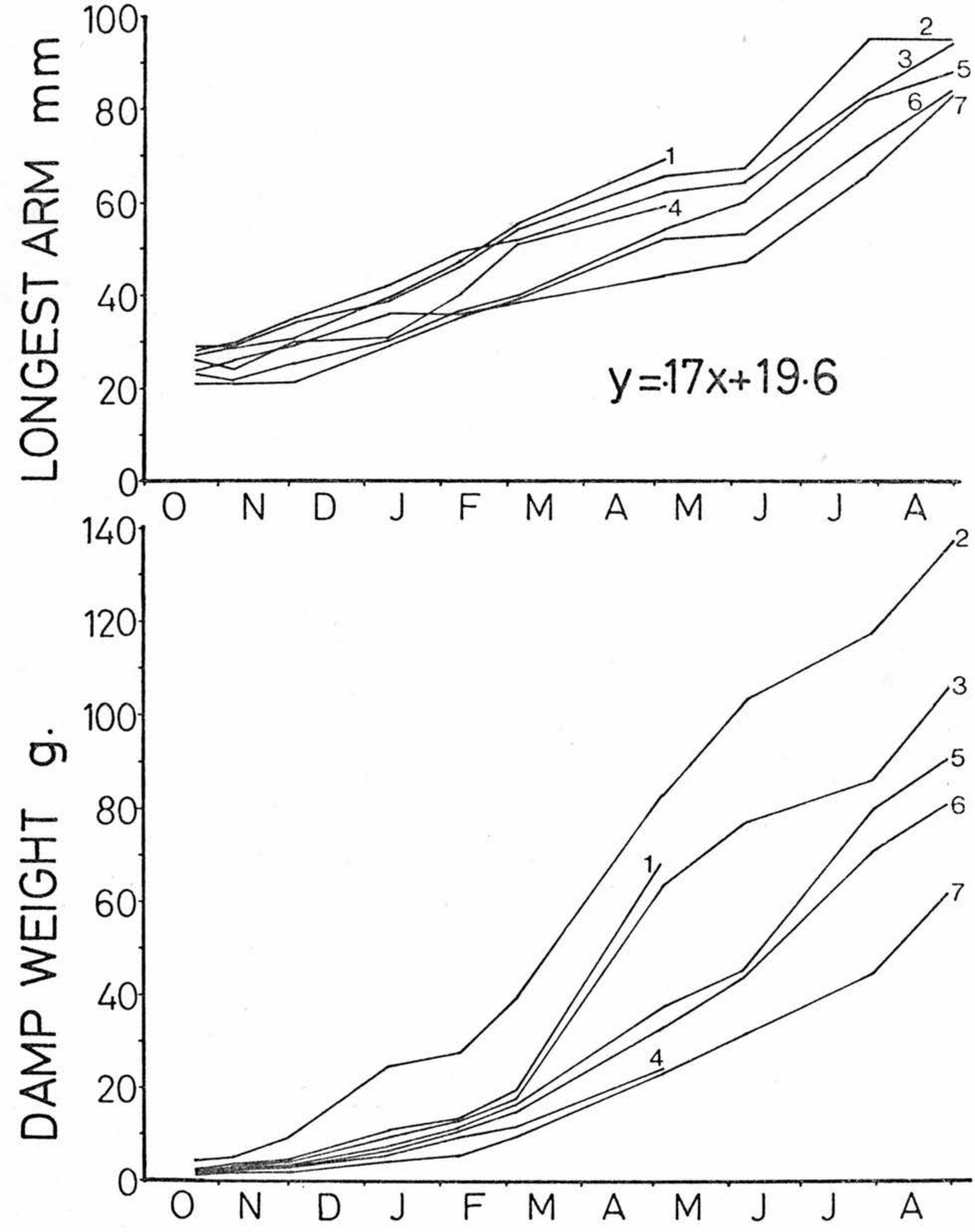

LONGEST ARM mm
100
80
60
40
20
0
1
2
3
4
5
6
7
y=·17x+19·6
O N D J F M A M J J A
DAMP WEIGHT g.
140
120
100
80
60
40
20
0
1
2
3
4
5
6
7
O N D J F M A M J J A

TABLE 9

Tag persistence in laboratory aquarium.

Tag No.	Tagged Initially	Date(s) Tag Replaced	Times Tag Replaced
001	21.10.82	17.1.83; (Died 5.5.83)	1
002	21.10.82	31.1.83; 30.7.83	2
003	21.10.82	12.4.83	1
004	21.10.82	(Died 5.5.83 with original tag)	0
005	21.10.82	9.12.82; 30.5.83	2
006	21.10.82	17.1.83; 7.3.83; 1.8.83	3
007	21.10.82	14.2.83; 7.3.83	2

The growth rate of all three groups of A.rubens appeared to remain constant throughout the year, with a mean increase of R of 4.5mm.month^{-1}. Field growth rates for A.rubens of the same size during the same period on the rocky shore averaged 1.5mm.month^{-1} (Chapter 2.3). Similarly Feder (1956) (in Feder and Christensen, 1966) in comparing growth of marked P.ochraceus in three field areas with that for well-fed laboratory specimens, found that in a period of 10 months (Mar-Jan) the mean increment of field individuals was only 20-30g, in contrast to more than 500g for laboratory animals.

Vevers (1949) recorded arm length increments of 12mm.month^{-1} in summer, but only 5mm.month^{-1} in winter, for A.rubens fed on M.edulis, Tellina crassa, and Chlamys opercularis (L.). No mention was made of the temperature at which Vevers' A.rubens were kept. However, the disparity between the maximum growth rates observed by Vevers (1949) and those found in the present study and by Bull (1934) is considerable. The presence of genetic sub-populations of A. rubens with phenotypic differences not detectable by the morphological taxonomist cannot be dismissed in the light of Binyon's (1961) and Mileykovskiy's (1969) findings of "physiological races" of this species with markedly different salinity tolerances and spawning temperatures respectively.

It is clear from the disparities in Fig. 21 that growth as measured by R and damp weight are not easily comparable. Damp weight may more accurately reflect growth increments in the laboratory since R is only reliable provided the arm length:arm width ratio remains constant. However, the tendency mentioned earlier for well-fed laboratory-reared starfish to develop an inflated appearance renders comparisons of the weight of laboratory and field animals difficult.

It is relevant that marking A.rubens by sewing plastic tags through the arms with nylon monofilament did not retard their growth, and nor was cannibalism or autotomy observed (Kvalvagnaes, 1972). Attempts at marking intertidal A.rubens in the same manner were characterised by a low proportion of recaptures (Chapter 2.4). Since a high number of starfish with open wounds or autotomized arms was not observed, it is not certain whether this reflects inadequate tag persistence in moving water or a mobile intertidal starfish population.

4.3. Feeding rate of A.rubens.

4.3. (i). Introduction.

In their review of the chemical perception of food by asteroids Sloan and Campbell (1982) found that "casual field and laboratory observations as well as controlled laboratory experiments, when combined, provide both positive (73%), negative (22%), and inconclusive (5%) evidence for asteroid olfaction. The negative results must therefore be regarded as significant". However, in Asterias species Y-maze experiments have conclusively shown attraction to whole prey items and to high and low molecular weight organic compounds (Castilla, 1972b; Zafiriou et al, 1972; Heeb, 1973; Castilla and Crisp, 1976). The evocation of more extreme responses such as humping and stomach eversion by prey homogenates, as demonstrated by Brauer et al. (1970) for Acanthaster planci and by Heeb (1973) for Asterias vulgaris suggest that in feeding aggregations the high concentrations of such compounds may lead to an overall increase in rate of feeding. The following experiment was designed to test this hypothesis in A.rubens by comparing foraging rates of starfish kept individually and as a group.

4.3. (ii). Methods

Twelve Asterias rubens of the same size were maintained on Mytilus edulis for two months, after being trawled from St Andrews Bay, in order to overcome any ingestive conditioning (Castilla, 1972a,b). The A.rubens were then divided into two groups of six. One group was placed in a 50l plastic aquarium, the other placed individually in 2.3l plastic tubs. Each container received a separate supply of fresh sea water: this precluded any group-mediated effect on the feeding behaviour of individual starfish. The sizes (R) of the starfish involved are shown in Table 10. To examine the presence of any group feeding response in A.rubens both starfish and mussel sizes were standardised. 150 M.edulis of anterior-posterior axis 30 mm (±1mm), were treated as follows. All epiphytes and epizoites were

TABLE 10

The number of 30mm *Mytilus edulis* consumed by six *A. rubens* with the starfish separate (top) and grouped.

Individual Asterias	R at Start Winter Expt. mm.	No. 30mm Mussels Eaten 12.1.83-12.2.83 (31 days) Mean Temp.=6.9°C	R at Start Summer Expt. mm.	No. 30mm Mussels Eaten from 1.7.83-1.8.83 (31 days) Mean Temp.=15.7°
1	67	17	72	37
2	59	27	71	63
3	67	34	85	69
4	69	17	81	63
5	63	10	79	41
6	72	15	72	57
	Mean=66.2mm	134	Mean=76.5mm	330
Grouped Asterias	86		94	
	72		87	
	69		82	
	69		81	
	62		73	
	60		64	
	Mean=69.7mm	151	Mean=80.2mm	366

scraped from the shells, the valves were forced apart and the water shaken from the mantle cavity. A Pasteur pipette connected to a compressed air supply and inserted between the valves ensured removal of all excess water. The mussels were then weighed intact. The mean mussel weight was 3.32 ±0.64g (s.d), n=150. For the experiments themselves only mussels of this length weighing ± 1 Standard Deviation of this mean weight, i.e. 2.68-3.96g, were used. Growth in M.edulis reflects both age and environmental conditions (Seed, 1969). The above procedure eliminated very young and very old mussels of this size lest strength of adductor muscle or some other factor affecting entry by A.rubens should be age- rather than size-dependent.

Individual A.rubens were presented with ten of these mussels, the group with 60. Experiments were examined daily and consumed mussels replaced. This feeding rate experiment was run for a 31 day period in winter (January 12-February 12, 1983; mean temp 6.9°C) and summer (July 1-August 1, 1983; mean temp 15.7°C).

4.3. (iii). Results

The numbers of M.edulis consumed by each A.rubens or group thereof are shown in Table 10. There is no significant difference in the feeding rate of starfish maintained individually and those held as a group either in winter (X^2=1.01)or summer (X^2=1.86). Both sets of starfish ate approximately 2.5 times as many mussels in summer as in winter, which is highly significant (Individuals X^2=82.8 p<.005.

Group $X^2=89.4$ $p<.005$)

4.3. (iv). Discussion.

Asteroid aggregations on bivalve beds are a common occurrence (see Sloan, 1980, for review). It is debatable whether such aggregations represent true social behaviour or whether they result from a common response to food presence or from marked gregarious settlement of larvae. The much-studied Acanthaster planci orientates more strongly to other conspecifics feeding on coral than to the live coral alone (Ormond and Campbell, 1974, in Sloan, 1980). The observation that A. rubens avoids the effluent of damaged bivalves (Castilla and Crisp, 1976) and yet is commonly found with two or more individuals tackling the same prey item (Hancock, 1974, Anger et al, 1977, Warner, 1979) suggests that the juices released by feeding conspecifics are a powerful attractant in this species also. In the present study no such combined feeding by two or more starfish on the same mussel was observed, although it may be that this only occurs with prey individuals that are sub-optimal on account of their large size (see Chapter 4.4). Mussels of 30mm are easily handled by A.rubens of the sizes present in these experiments (see Chapter 4.4). The tackling of a single bivalve by more than one A.rubens is more likely to be an attempt by the second or subsequent starfish to obtain a `cheap meal' (without having to invest so much effort in overcoming prey defences), than to be an intraspecific reaction enabling two starfish to feed where neither would have been capable on its own.

The A.rubens in the present study showed no accelerated feeding rate as a result of the presence of other feeding individuals, suggesting that although juices released by feeding conspecifics may act as an attractant, they do not stimulate foraging or feeding activity itself. In aggregations, however, the density of A.rubens can reach $97.m^{-2}$ (Brun, 1968). The elicitation of such responses as humping and stomach eversion (Heeb, 1973) is only observed when high concentrations of homogenate are presented in close proximity to the asteroid; and if such a response does cause an increased rate of feeding by starfish in an aggregation this may not be manifest under the experimental conditions pertaining here.

The observed accelerated rate of feeding in summer is in accordance with most temperate asteroid species in which "generally, as temperature increases feeding rate increases, until an opposite effect is evoked by extreme temperatures" (Sloan, 1980). Hancock (1958) reported that the feeding rate of Asterias rubens is maximal between 10 and 13°C, and A. amurensis (Lutken) also has an optimum feeding rate at a temperature below the maximum encountered in its natural habitat (Hatanaka and Kosaka, 1959).

4.4. Foraging behaviour of Asterias rubens.

4.4. (i). Introduction.

The relative sizes of predator and prey might be considered the fundamental determinant of predator-prey systems (see Schoener, 1971, for review). Asteroids are important predators with a potentially major role in the structuring of diverse marine habitats; for example, the temperate exposed rocky shores (Paine, 1969, 1974; Dayton, 1971), the Antarctic sublittoral (Dayton et al., 1974), and tropical coral reefs (Porter, 1972, 1974; Glynn, 1976). Indeed, they are frequently considered a pest on commercial bivalve beds (Galtsoff and Loosanoff, 1939; Smith, 1940 Dare, 1982). The foraging strategy of these predators, their rate of feeding and degree of prey selectivity, may therefore be important in understanding trophic structure within marine benthic communities.

Size relationships between asteroid predators and their prey are well documented for some rocky intertidal species. Leptasterias hexactis cannot, or does not, capture large prey (Menge, 1972) and the minimum prey size eaten by Pisaster ochraceus increases with body size (Menge and Menge, 1974). Both P. ochraceus and P. giganteus prefer larger mussels (Landenberger, 1968), and Paine (1976a) demonstrated a relationship between body size of P. ochraceus and the maximum size of Mytilus californianus consumed in the intertidal; above a certain critical size Mytilus achieves a refuge from Pisaster predation. For sublittoral Pisaster Paine (1976b) observed that the starfish may consume all Mytilus present, indicating that it is consumption time in the intertidal - and not mussel strength - that is the critical factor in providing a size refuge for littoral M.californianus. However Hancock's (1965) experiments with Danish Mytilus edulis demonstrated how effective a strong adductor muscle can be in reducing asteroid predation, and he suggested it may have evolved in these animals for this reason. Given sufficient time even the largest *Mytilus californianus* can be consumed by *Pisaster* on account of the presence of a gap between the valves, a "byssus door", allowing stomach insertion (Feder, 1970). The same is not, however, true for *Mytilus edulis* and Lavoie (1956) recorded that "only one among hundreds" of *A. forbesi* observed feeding was seen to gain access to *M. edulis* in this way.

There is no relationship between the size of *Meyenaster gelatinosus* (Meyen) and its prey the urchin *Loxechinus* in Chile because of an effective escape response in the latter (Dayton *et al.*, 1977). The escape response of the urchin *Strongylocentrotus* on flat rocky surfaces results in a maximum prey size limit for *Dermasterias imbricata* (Grube). On other substrata, however, this starfish traps the urchin in crevices and no relation between predator and prey sizes is observed (Rosenthal and Chess, 1972).

On soft substrata Birkeland (1974) found a significant trend for prey size to increase with the size of the asteroid *Hippasterias* feeding on the sea-pen *Ptilosarcus*. On the other hand *Luidia* prefers smaller ophiuroids when offered a choice (Fenchel, 1965; McLintock and Lawrence, 1981). This latter observation appears to be related to the efficiency of stomach-packing in this starfish. *Asteropecten irregularis* (Pennant) displays a distinct preference for smaller specimens of *Spisula subtruncata* (da Costa), to the extent that the stomach is frequently packed with prey of meiofaunal size (<2mm)

(Christensen, 1970).

For those asteroids that dig for bivalves in soft sediments an important factor determining whether a prey item is captured is depth of burrowing (Kim, 1969). Thus, for example, the presence of A. forbesi stimulates Mercenaria to burrow deeper (Doering, 1976). van Veldhuizen (1977) divided bivalves into three categories: 1."deep burrowers" in which larger bivalves burrow deeper, the largest being unattainable even to the largest starfish, 2."moderately deep burrowers" in which there is a relationship between size and depth of burrowing, but all can be captured by all but the smallest starfish, and 3."shallow burrowers" in which depth is not a function of prey size. Working with Pisaster brevispinus van Veldhuizen (1977) found a relationship between predator and prey sizes among the first two categories, but not the third.

The presence of a minimum prey size for asteroids has been noted both on hard (Paine, 1976) and soft substrata (van Veldhuizen, 1977). This is more likely to be a behavioural choice than due to handling inefficiences, as may be the case in the crab Carcinus maenas (Elner and Hughes, 1978), since the handling mechanism of asteroids involves groups of podia rather than limbs whose mechanical properties are determined largely by their size (Hughes, 1980).

A. rubens has been variously described as a specialist feeder (Gulliksen and Skjaeveland, 1973), and a generalist predator (Hancock, 1955; Annala, 1968). Evidence that A. rubens may select for maximum net energy intake per unit time is provided by Annala (1968), Anger et al. (1977) and Allen (1983). It is suggested to be an "r-selected" species (sensu MacArthur and Wilson, 1967) showing flexible growth that can respond very rapidly in the presence of abundant food. Aggregations of A. rubens have been reported since the 1840's (see Sloan 1980, for review) on such diverse prey items as oysters (Forbes, 1841) Mytilus (Sparck, 1932; Vinberg, 1967; Larsson, 1968; Mileykovskiy, 1968; Seed, 1969; Dare, 1982) Chlamys (Brun, 1968), Spisula (Warner, 1979), Crepidula (Hancock, 1955, 1958), and even Ciona (Gulliksen and Skjaeveland, 1973).

Invasions of intertidal Mytilus beds by A.rubens from the sublittoral are unpredictable in space and time, but raise interesting questions about the foraging behaviour of this starfish. Lewis (in Sloan, 1980) suggested that calm weather was an important factor in the build-up of these aggregations and Sloan (1980) concludes that they may "need a complex of environmental variables to be in the right sequence over a number of seasons" in order to occur. The shoreward migration is characterised by the complete removal of every Mytilus present (C.Todd pers.comm.), apparently regardless of size, and results in a well-defined predation line. Without studying the behaviour of A.rubens in the process of such an invasion it is not possible to know what proportion of mussels is actually consumed, and what is lost as a consequence of wave-crash on the weakened clumps.

In the light of these observations, and especially the indication that A.rubens will take M.edulis indiscriminately, it was decided to examine the foraging behaviour of Asterias rubens in the laboratory within the context of optimality theory. Optimal foraging theory predicts that natural selection favours an individual that gathers its food efficiently, thereby maximising its genetic contribution to the next generation (see MacArthur and Pianka, 1966; Emlen, 1966, 1968; Schoener, 1971; Estabrook and Dunham, 1976; Krebs , 1978). The parameter normally considered to be maximised is that of energy intake per unit time, although there are instances when requirements for specific nutrients are more important (Pulliam, 1975). This energy maximisation hypothesis (Emlen, 1966; Schoener, 1971) has received experimental support from both visual (see Werner and Hall, 1974; Pyke *et al*., 1977), and non-visual predators (Elner and Hughes, 1978; Hughes, 1980). In the starfish-mussel interaction each mussel has an associated cost in terms of time and energy required to handle it, and a benefit in terms of net caloric yield. Experimental determination of these two factors enables calculation of the value each prey item has to the foraging starfish. In the present study the diet of *A.rubens* foraging on *M.edulis* that differ in respect of size is compared with the energetically-determined "optimal" diet. *M.edulis* is reported as a preferred prey of *A.rubens* (Castilla and Crisp, 1970), and is one commonly encountered on the rocky shore. *A.rubens*, however, is a facultative scavenger capable of using many invertebrates for food (Sloan, 1980). Around St Andrews *A.rubens* is found in greatest numbers on sandy substrata in which the predominant macrofauna comprise *Echinocardium* and assorted bivalves (Chapter 2.3). By studying prey value and diet choice in the two bivalves *Mytilus edulis* and *Spisula subtruncata* some conclusions may be drawn regarding the relative suitability of these two habitats for *A.rubens*.

4.4. (ii). Materials and methods.

4.4. (ii). (a). Handling time experiments, Mytilus edulis.

Asterias rubens were trawled from St Andrews Bay and maintained feeding on M.edulis in the laboratory for at least five weeks before use. All mussels were collected locally from Kinkell Braes. Table 11 shows the sizes of 11 A.rubens (denoted A-K) for which handling times were measured. The experiments were run between February 2 1983 and June 6 1983; the seawater temperature varied between 5.5 and 11°C over this period (Fig. 18). Starfish were kept within individual 2.31 plastic containers, each with a separate water supply. Over the experimental period individual A.rubens were presented with mussels of a wide size range in order to establish the individual relationship between prey value and mussel size. Each starfish was starved for 24 h before being presented with a mussel; this was dropped adjacent to one arm or placed underneath it. In most cases A.rubens would immediately assume the characteristic humped-up position indicative of feeding. It is not possible to separate conquest time from eating time as it is for the crab Carcinus maenas (Elner and Hughes, 1978), so only a single record of total handling time (Th) is available. In the course of feeding the humped-up position becomes more relaxed, presumably once the adductor muscles have been overcome. Termination of the feeding bout is marked by discarding, and movement away from,

TABLE 11

Handling time experiments; the equations of power curves for each starfish.

	Asterias	$y=ax^b$ ($\ln y=\ln a+b\ln x$)				Longest Arm, "R" (mm)	Damp Wt (g)	Estimated Optimal Bivalve Size (mm)	Prey Value at this Optimum J.Min^{-1}
		a	b	r	n				
Mytilus	A	Fitted By Eye				116	168.2	59.1	23.5
	B	.057	4.13	.981	20	95	114	53.5	14.75
	C	.056	4.33	.984	19	86	101	47.0	8.2
	D	.071	4.01	.988	17	85	159.8	45.0	8.0
	E	.072	4.02	.986	15	75	84.3	42.0	7.6
	F	.088	4.08	.959	13	70	56.9	34.2	4.35
	G	.061	4.53	.973	17	73	70.9	50.0	7.9
	H	Fitted By Eye			16	59	36.0	27.2	5.1
	I	.08	4.30	.989	19	57	19.2	44.7	3.92
	J	.081	4.26	.962	21	45	12.3	38.0	4.5
	K	.094	4.38	.962	15	41	12.3	27.1	2.57
Spisula	1	Fitted By Eye			7	92	74.6	42.5	35.0
	2	Fitted By Eye			7	75	53.5	37.5	27.0
	3	Fitted By Eye			7	56	18.1	33.5	13.0
	4	Fitted By Eye			9	61	33.4	34.0	16.2

the empty mussel shell (Anger et al. 1977). In nearly all cases the mussel tissues are more or less completely removed except for a small amount of the posterior adductor muscle. If substantially more tissue than this remained at the end of feeding the result was disregarded. Handling time was defined as the interval between the positioning of the mussel beneath Asterias' mouth, and rejection of the empty shell. During this period the A.rubens were observed every 15 minutes where possible. If termination of the feeding bout was not actually observed it was estimated as the midpoint of the interval since the previous observation. If a starfish would not eat a mussel, the mussel was offered on succeeding days until accepted.

4.4. (ii). (b). Prey value, Mytilus edulis.

24 Mytilus edulis, covering the full range of sizes used in the handling time experiments, were collected from Kinkell Braes on April 13 1983. Ash-free dry weight (AFDW) was obtained by drying the soft parts to constant weight in a Chemlab Tissue Freeze Dryer and igniting the residue at 500 °C for 6 h. The mean calorific value of the flesh was calculated from ten of these using a Phillipson Microbomb Calorimeter calibrated with Benzoic acid standard ($26.435 KJ.g^{-1}$). From these a least-squares regression equation of prey energy content (E) on shell length was calculated. Prey value was, once again, defined as E/Th.

4.4. (ii). (c). Handling time experiments, Spisula subtruncata.

Four A.rubens (denoted 1-4), of sizes as shown in Table 12, were examined for handling time on the burrowing clam Spisula subtruncata. Four buckets 25cm deep were filled with sand to within 3cm of the top. Each Spisula was given 24h to burrow, during which time the A.rubens were removed to separate tanks, all handling being with disposable gloves. After this period the A.rubens were reintroduced, and observed at 15 minute intervals throughout the day. The method by which A.rubens burrows for bivalves has been described in detail elsewhere (Anger et al. 1977; Doering, 1981). Briefly, the starfish orientates itself with the oral disc over a buried clam. The podia of all five arms propel the sand beneath them centripetally, and the disc falls into the pit so constructed. Chemosensory abilities have been implicated in the ability of A.rubens to locate buried bivalves (Castilla and Crisp, 1976; Zafiriou, Whittle and Blumer, 1972). Once the clam is exposed oral tube-feet are attached to it and the starfish endeavours to pull it from the sand. The following times were noted: The start of digging, the commencement of feeding (assumption of a humped-up position), and the end of feeding. Th is defined as the period from the start of digging to the discarding of the empty shell. Digging times are recorded in Table 12, handling times in Fig. 22.

4.4. (ii). (d). Prey value, Spisula subtruncata.

TABLE 12

Times taken for *A. rubens* to disinter *Spisula subtruncata* and assume the feeding position.

	Spisula shell length, mm.	Digging time, mins.
1 R= 92mm 74.6g	17.0	7
	29.3	45
	34.2	19
	36.1	10
	50.2	24
2 R= 75mm 53.5g	23.4	10
	29.3	35
	35.7	46
	46.0	16
3 R= 56mm 18.1g	29.5	13
	32.0	12
	39.3	14
4 R= 61mm 33.4g	23.3	12
	28.0	21
	30.6	5
	36.8	15
	44.4	45

Six *Spisula* covering the full size range were collected from Tentsmuir beach on October 8 1983. These were dried to constant weight and energy value of the flesh was determined as for *Mytilus* (see above), and a least-squares regression equation of prey energy content on shell length calculated.

4.4. (ii). (e). Energy content.

The mean energy value of mussel flesh (corrected for endothermy, Paine, 1965) was determined as 21.3 $J.mg^{-1}$ AFDW (N=17). Mussel energy content (E_1) was related to mussel length according to the equation:

$\ln E_1$ (J) =3.017 ln length (mm) -2.28 (N=24, r^2=.98, $p<.001$)---(Equation 1)

The mean energy value of *Spisula* flesh was determined as 20.7 $J.mg^{-1}$ AFDW (N=6). *Spisula* energy content (E_2) was related to *Spisula* shell length according to the equation:

$\ln E_2$ (J) =3.244 ln length (mm) -2.27 (N=6, r^2=.98, $p<.001$) ---(Equation 2)

4.4. (iii). Results.

4.4. (iii). (a). Handling time experiments of A.rubens on M.edulis.

Th has been plotted against mussel length for the 11 A.rubens A-K in Figs. 23-26. Power curves have been fitted by least squares regression in all cases except for starfish A and H, where the observed increase of Th with Mytilus size was greater than that predicted by the model: in these two cases the curves have been fitted by eye (Table 11). In general Th increases rapidly with prey size until a size is reached that the starfish cannot handle. The longest Th recorded in which the mussel was completely consumed was 5115 minutes. (over 85 h) for A.rubens I. In the case of some very large Mytilus a starfish might reject the prey item several days later, opened but only partially consumed.

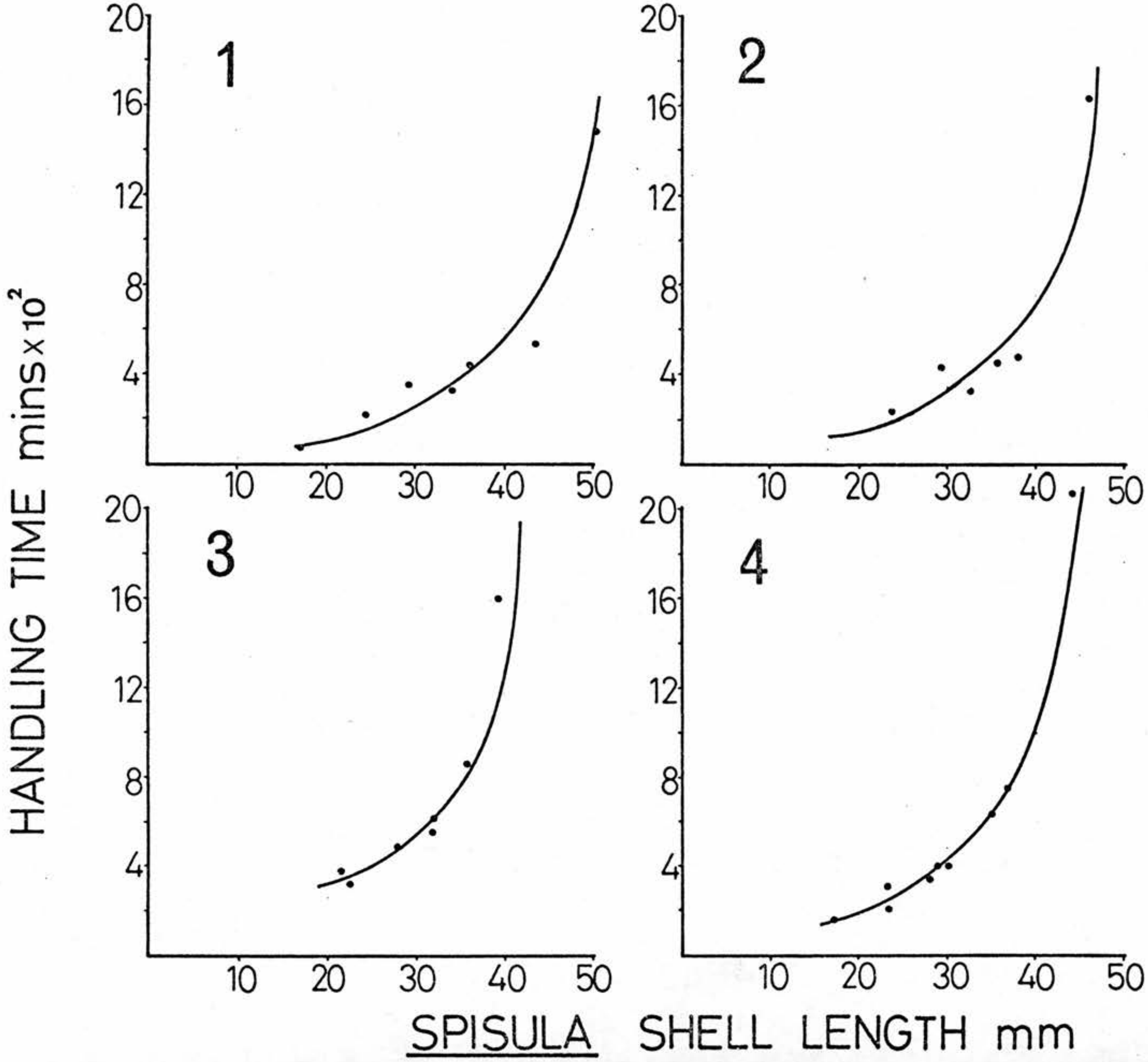
4.4. (iii). (b). Handling time of A rubens on Spisula subtruncata.

Th has been plotted against Spisula shell length for A.rubens 1-4 in Fig. 22. Curves have been fitted by eye in all cases since power curves did not match the marked increase in Th for the largest clam sizes.

4.4. (iii). (c). Prey value

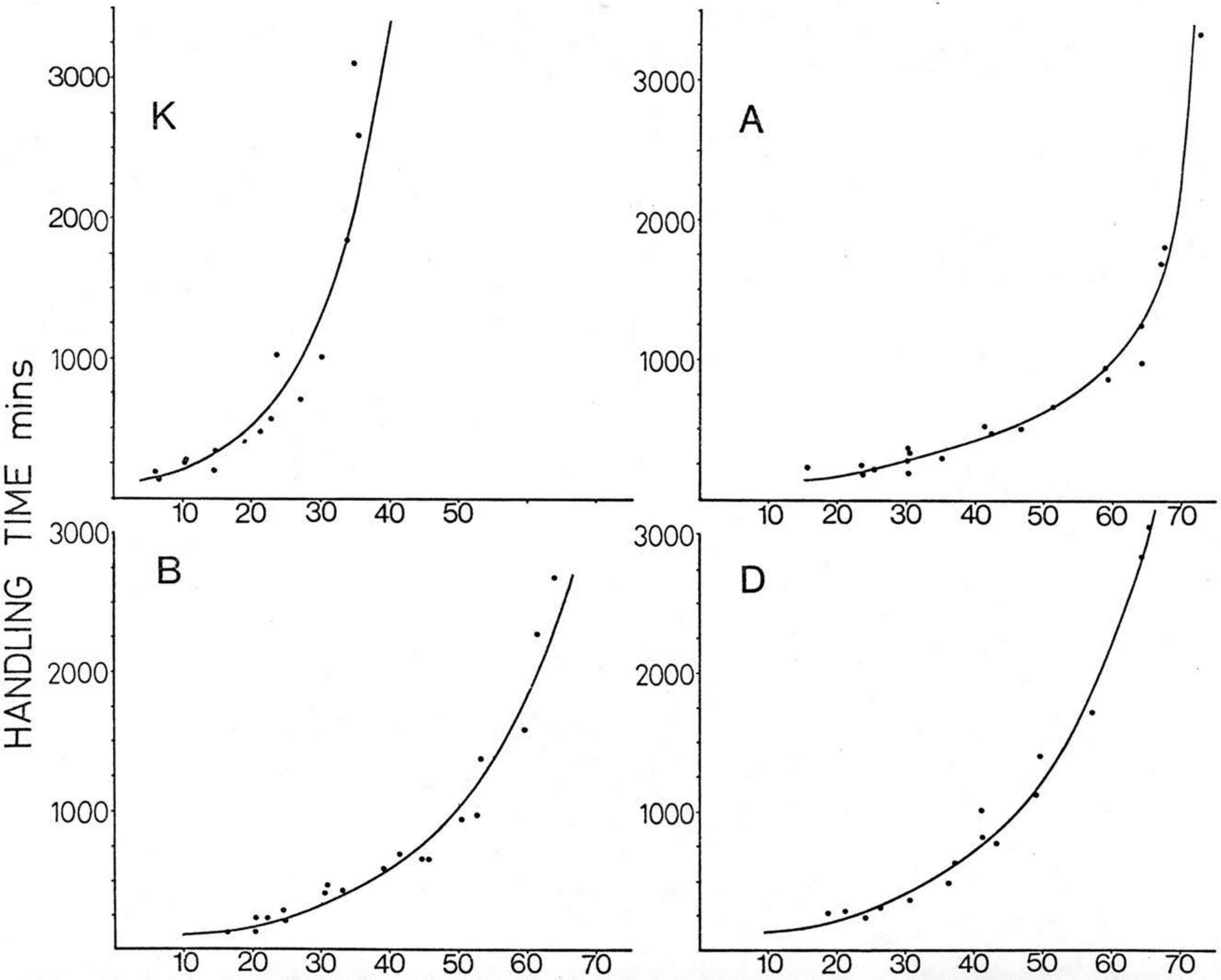
FIGURE 22

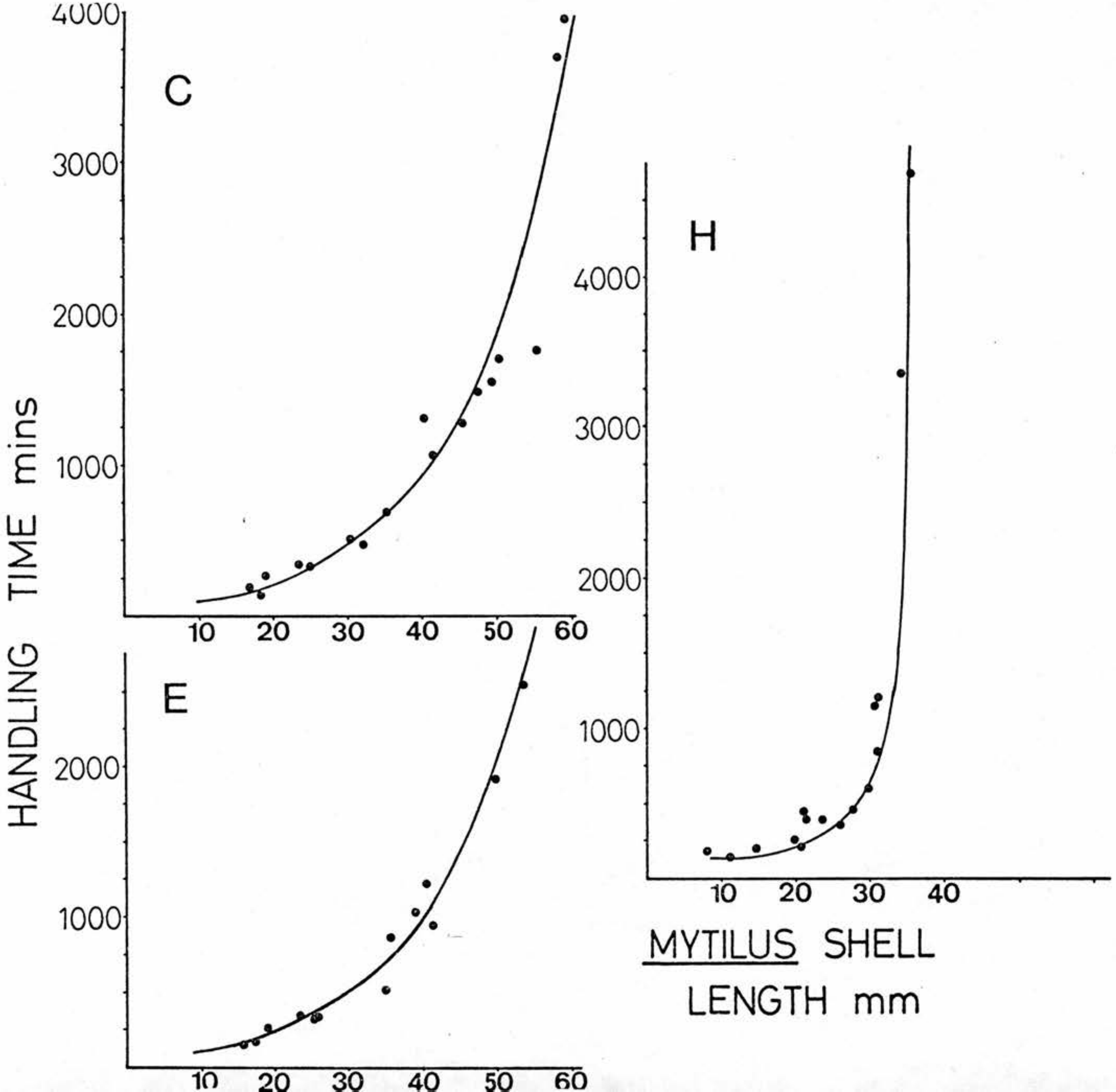
Curves of handling time (Th) of four A. rubens feeding on Spisula subtruncata. All curves have been fitted by eye.

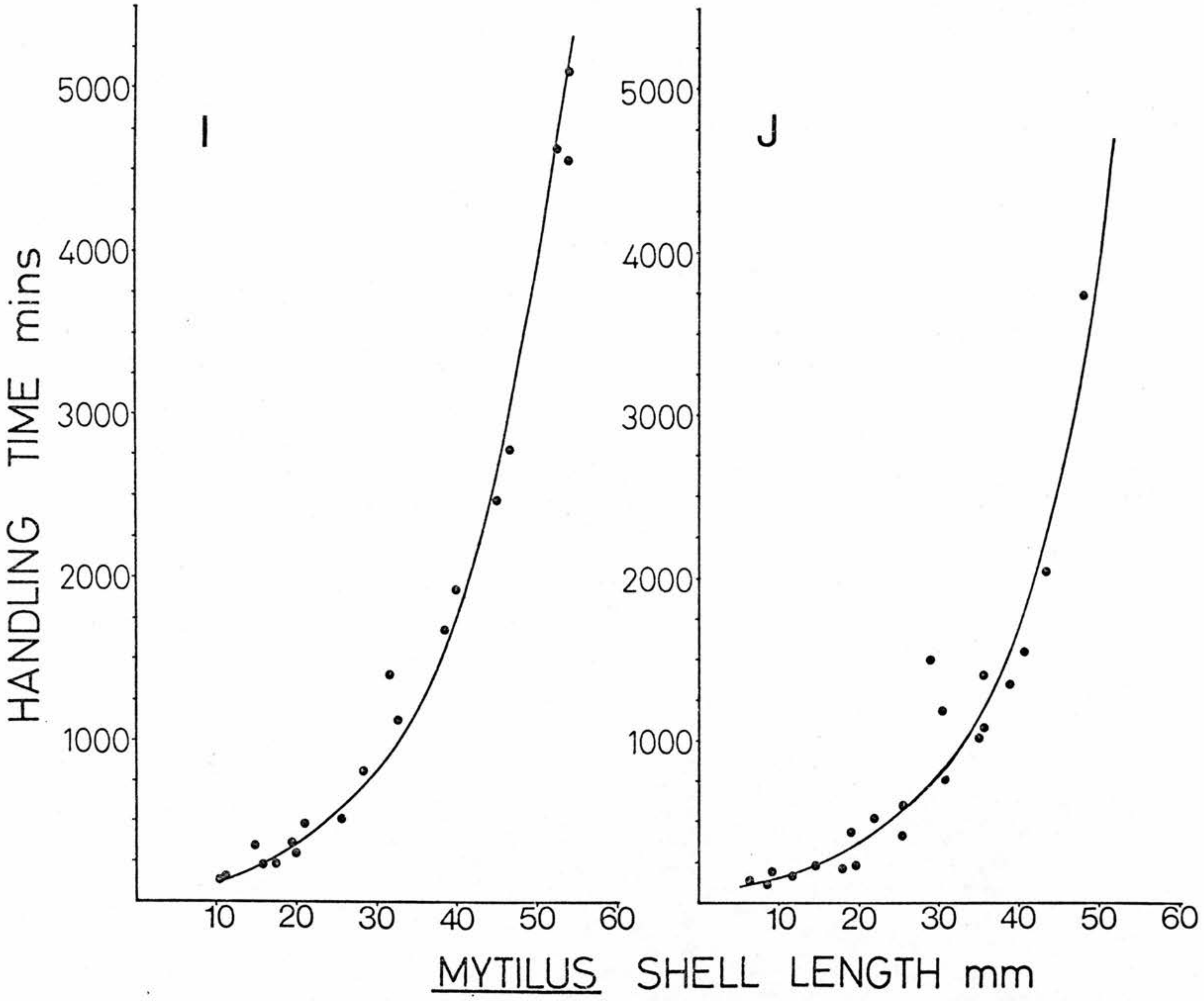

1
2
3
4
HANDLING TIME mins x 10²
20
16
12
8
4
10
20
30
40
50
SPISULA SHELL LENGTH mm

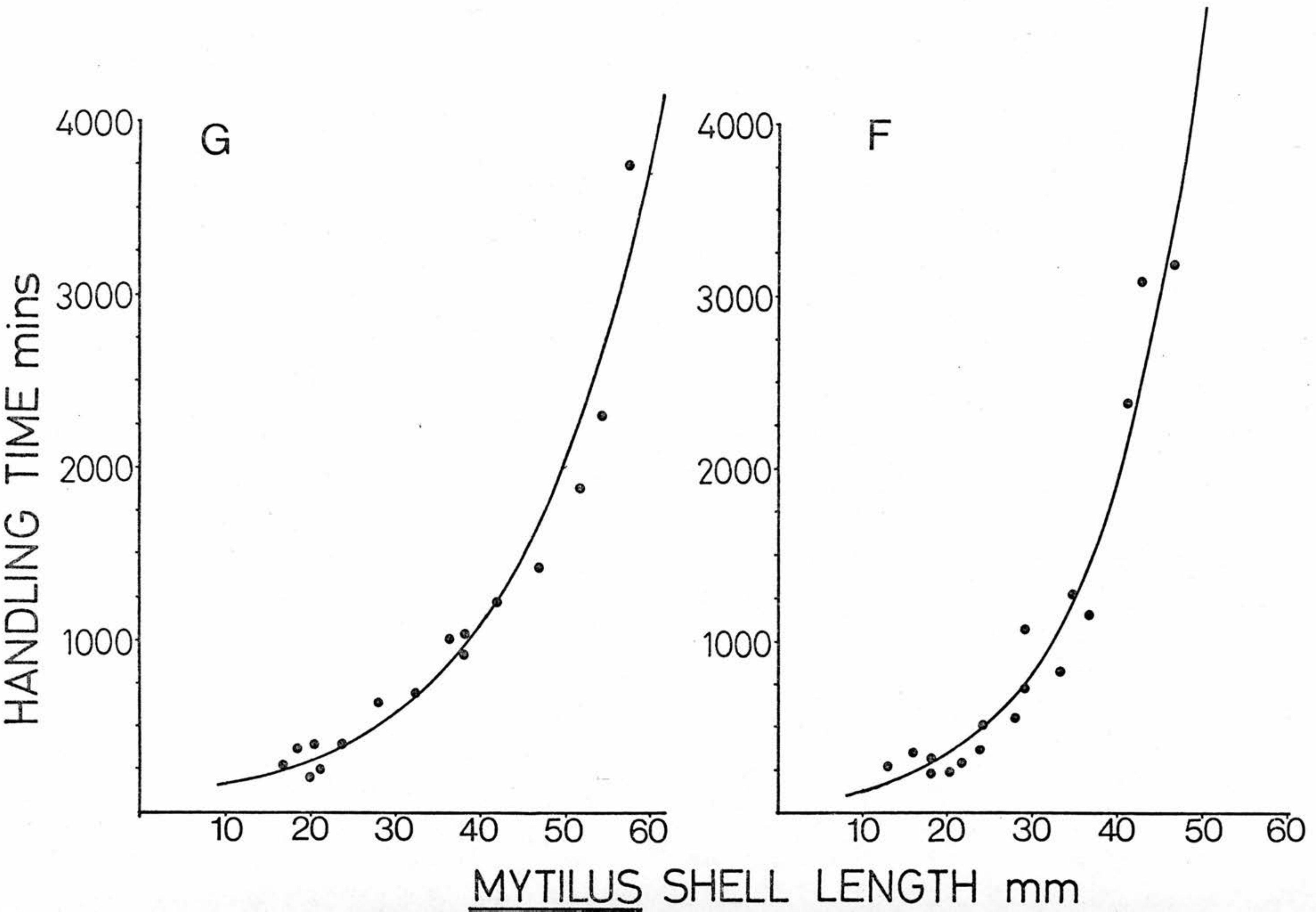
FIGURES 23-26

Curves of handling time (Th) of 11 A. rubens feeding on Mytilus edulis. Power curves were fitted by least-squares regression except for starfish A & H which were fitted by eye. Power curve equations can be found in table 11.


HANDLING TIME mins
K
A
B
D
3000
2000
1000
10
20
30
40
50
60
70


C
E
H
HANDLING TIME mins
4000
3000
2000
1000
10 20 30 40 50 60
MYTILUS SHELL LENGTH mm


I
J
HANDLING TIME mins
1000
2000
3000
4000
5000
10
20
30
40
50
60
MYTILUS SHELL LENGTH mm


HANDLING TIME mins
4000
3000
2000
1000
G
F
10
20
30
40
50
60
MYTILUS SHELL LENGTH mm

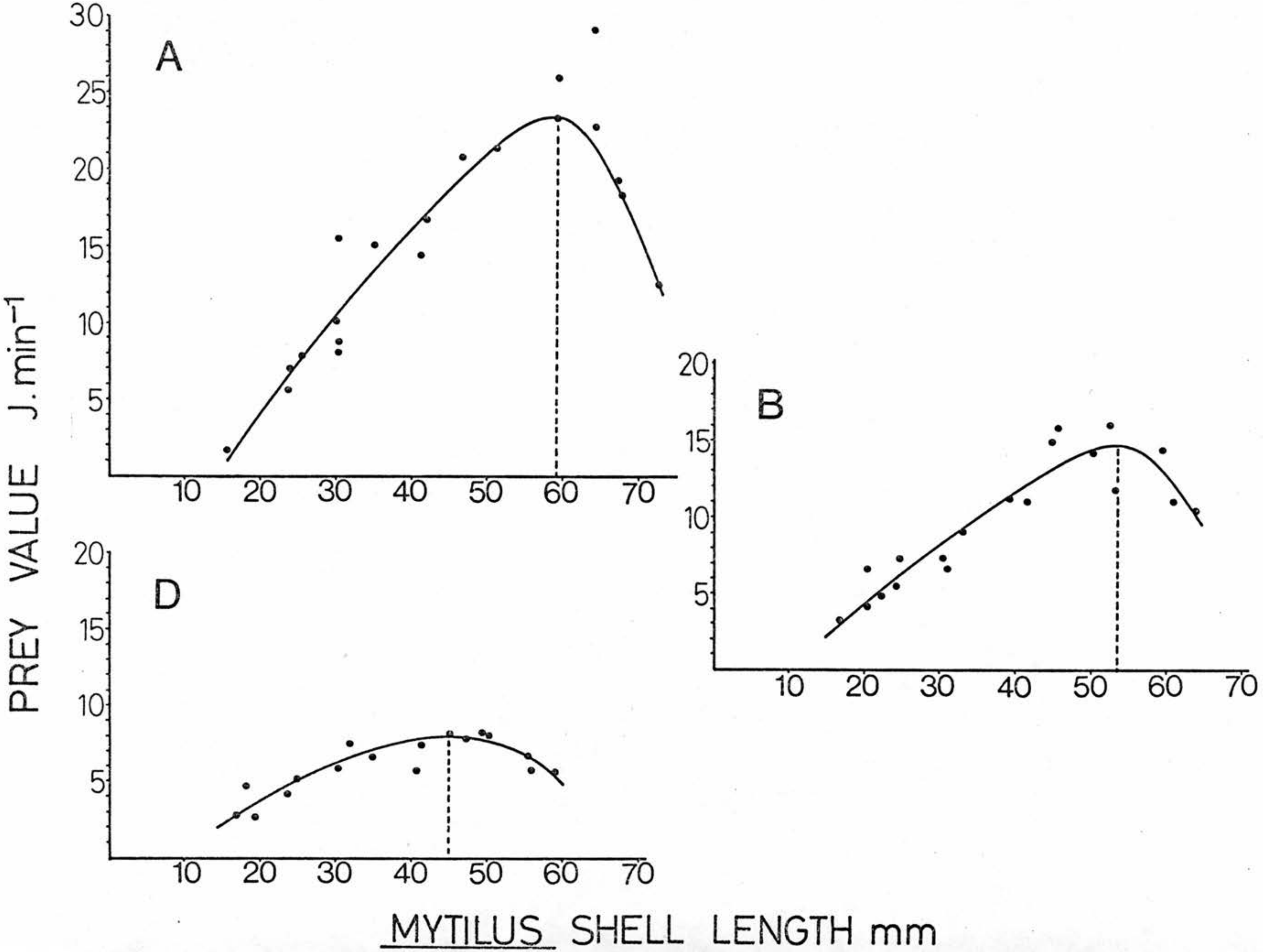
Prey value, derived from estimated net energy intake (from equations 1 & 2) and the observed total handling time, is plotted against *Mytilus* shell length in Figs. 27-29, and against *Spisula* shell length in Fig. 30. Curves have been fitted by eye in all cases. Prey value increased with prey size up to a maximum (*i.e.* "optimal" prey size) beyond which prey value then decreased. This presumably arises from the disproportionately long time required to gain entry and consume the flesh of the very largest bivalves. Although the basic form of the prey value curves is similar for a range of predator sizes, the slopes either side of the "optimal" are widely variable (see, for example, starfish A and D, Fig. 27). *Spisula* have a greater value to *A.rubens* than do *Mytilus* on account of the greater proportion of tissue comprised by a *Spisula* of given shell length (Fig. 31).

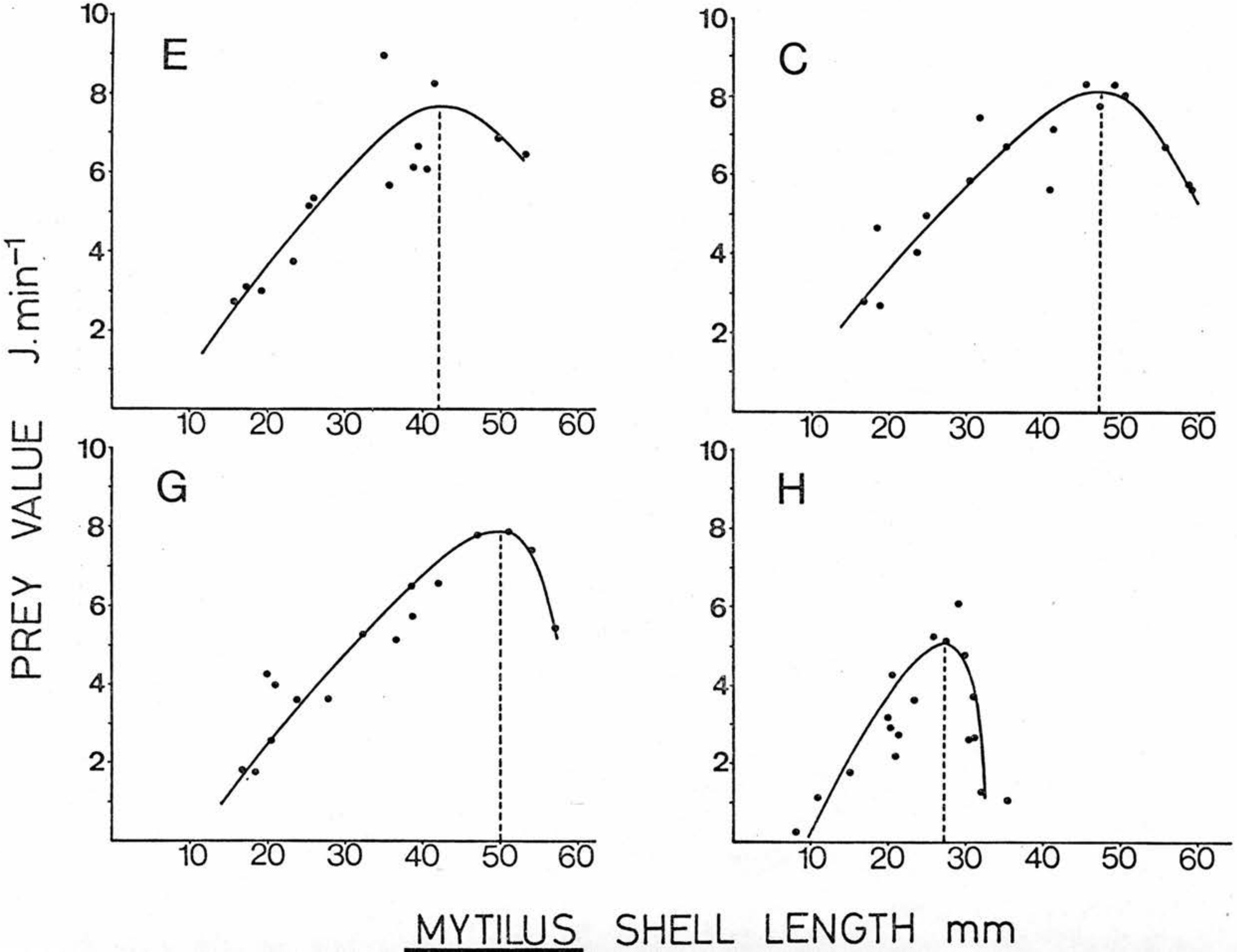
4.4. (iv). Discussion.

In all cases the prey value curves shown that for *A.rubens* feeding on both *S.subtruncata* and *M.edulis* there is a pronounced peak corresponding to a presumed "optimal" bivalve size. This "optimal" prey size increases with starfish size (Fig. 32). Above this "optimum" the benefit derived is outweighed by prolonged handling times. Once the effort has been expended overcoming a bivalve, optimality theory would predict complete consumption of the prey item. However, in certain circumstances (Table 13) *M.edulis* were

FIGURES 27-29

Prey value curves (E/Th) for 11 A. rubens feeding on M. edulus. Curves have been fitted by eye in all cases.


A
B
D
PREY VALUE J.min^{-1}
30
25
20
15
10
5
10
20
30
40
50
60
70
MYTILUS SHELL LENGTH mm


E
C
G
H
10
8
6
4
2
10
20
30
40
50
60
PREY VALUE J.min⁻¹
MYTILUS SHELL LENGTH mm

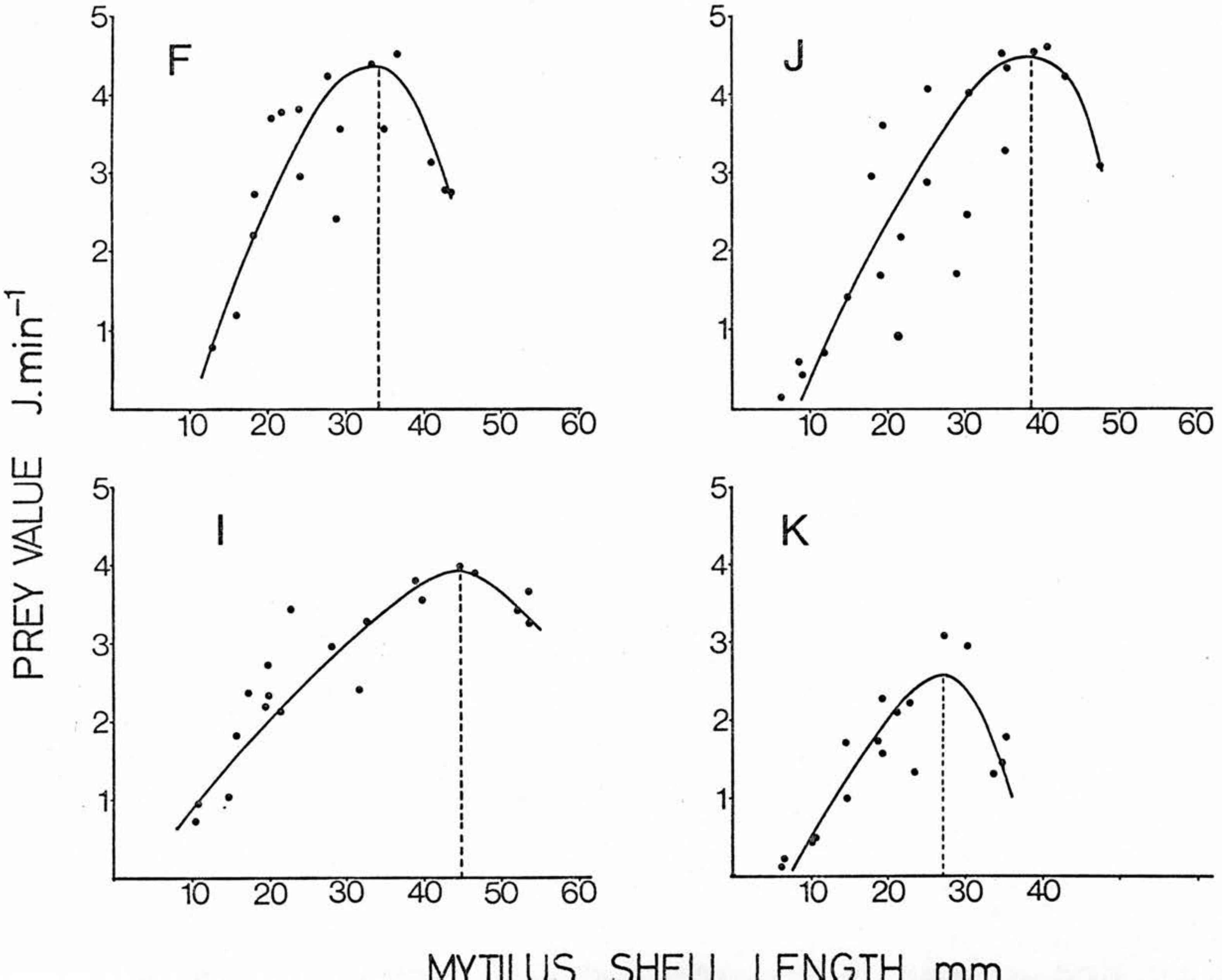

PREY VALUE J.min⁻¹
F
J
I
K
5
4
3
2
1
10
20
30
40
50
60
MYTILUS SHELL LENGTH mm

FIGURE 30

Prey value curves (E/Th) for four A. rubens feeding on Spisula subtruncata. Curves have been fitted by eye in all cases.

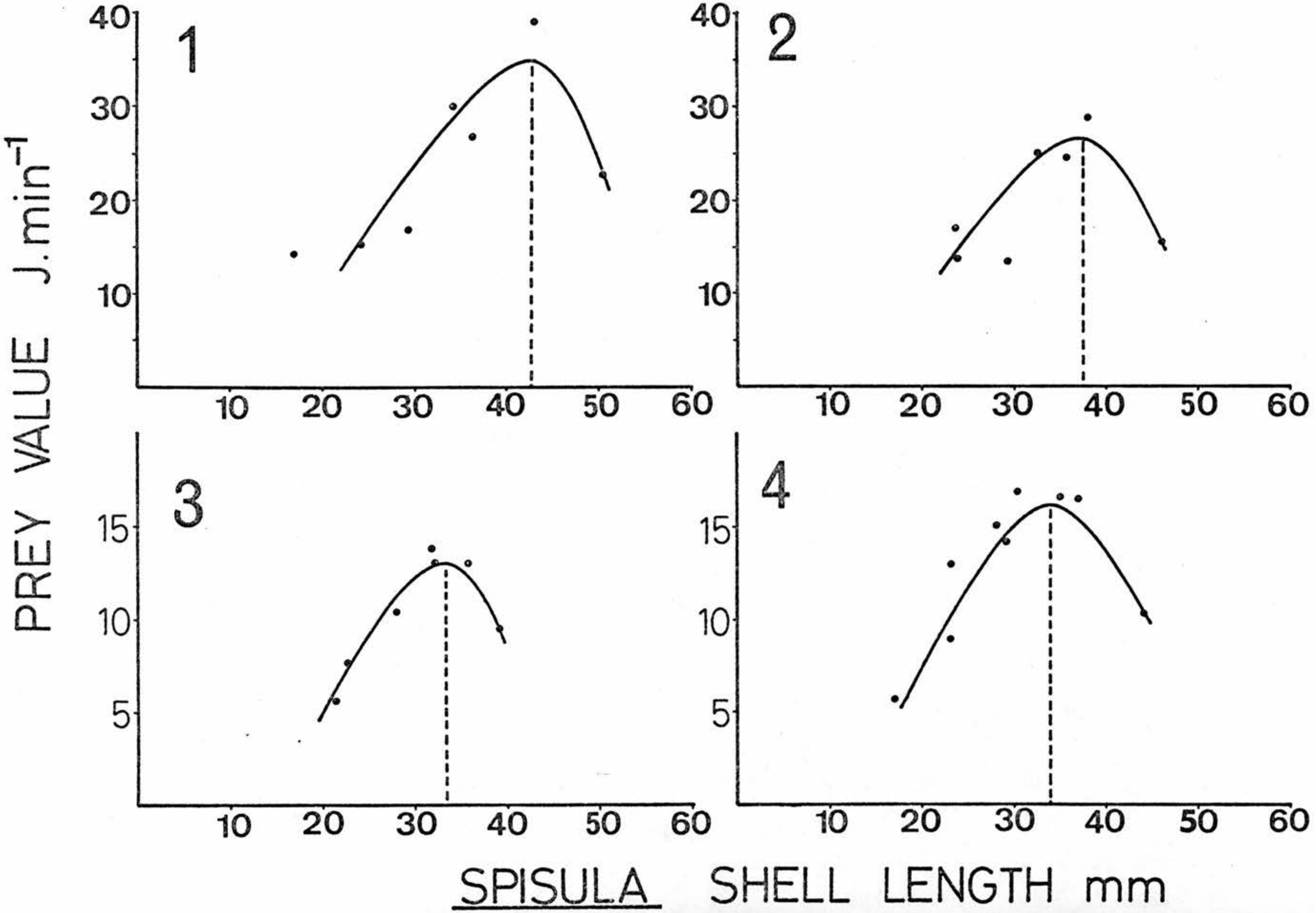

1
2
3
4
PREY VALUE J.min^{-1}
40
30
20
10
15
5
10
20
30
40
50
60
SPISULA SHELL LENGTH mm

FIGURE 31

The relationship between shell length and tissue content in *Mytilus edulis* and *Spisula subtruncata*.

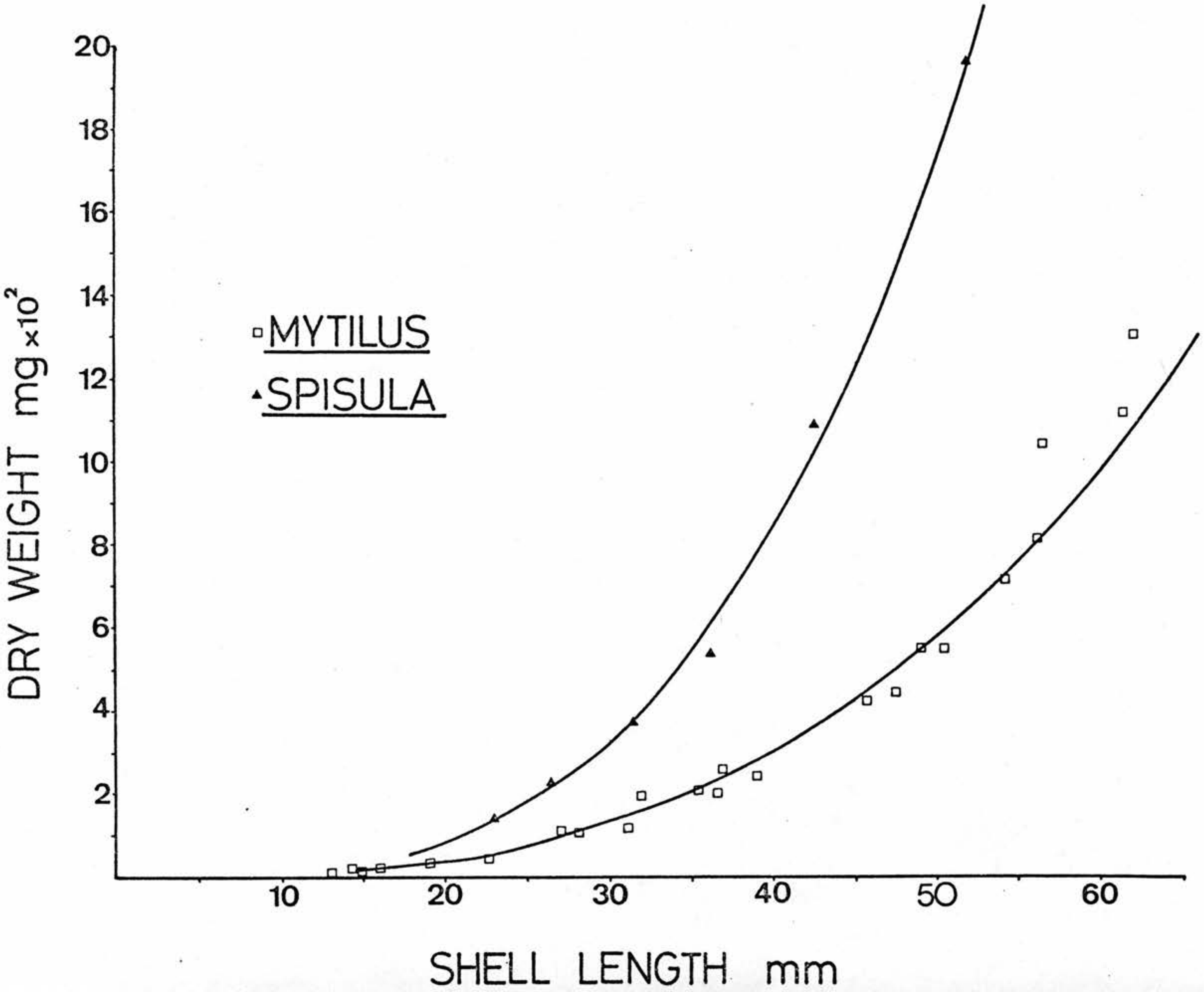

DRY WEIGHT mg ×10²
20
18
16
14
12
10
8
6
4
2
10
20
30
40
50
60
SHELL LENGTH mm
□ MYTILUS
▲ SPISULA

FIGURE 32

Estimated optimal prey sizes for *A. rubens* feeding on *M. edulis* and *S. subtruncata*.

M. edulis: $y = .376x + 15.1$

S. subtruncata: $y = .228x + 21.3$

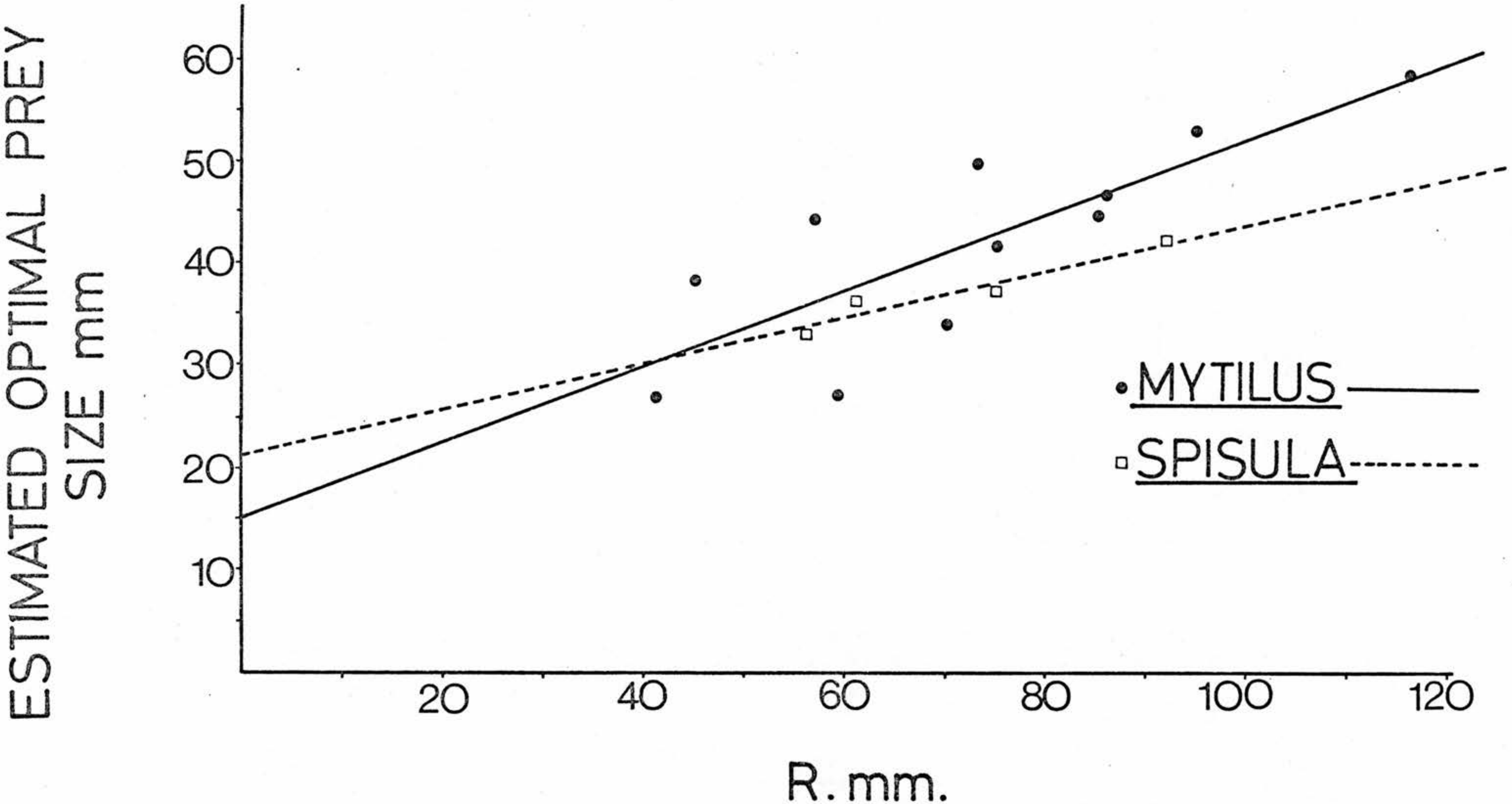

ESTIMATED OPTIMAL PREY SIZE mm
60
50
40
30
20
10
20
40
60
80
100
120
R. mm.
MYTILUS
SPISULA

TABLE 13

Six cases in which feeding on *Mytilus edulis* was terminated before the mussel was fully consumed.

Asterias R(mm)	Mytilus (mm)	Wt. (g)	Approx. Th before rejection (hrs.)	Final Mussel wt. (where recorded) (g)
41	24.2	1.47	109–119	
47	35.4	4.47	138–148	2.94
49	27.8	2.23	140–148	1.98
59	27.3	2.37	109–119	
70	35.7	5.50	48–60	
83	37.5	5.47	88	3.90

rejected unfinished. This rejection of mussels following investment of considerable time and effort was observed in Crossaster papposus (L.) by Hancock (1974), who suggested that "by the time entry by the Crossaster was achieved the flesh of the mussel had commenced to decompose and was no longer attractive". Crossaster probably gains access to Mytilus by means of some toxic secretion, not by force. Since A.rubens is a scavenger and will feed on carrion in the absence of preferred prey it is more likely that this behaviour in A.rubens results from satiation.

The times taken for A.rubens to dig Spisula from the sand and assume the feeding position seem to bear no relation to either starfish or clam sizes (Table 12). Allen (1983) noted that the depth to which Spisula burrows in 24 h is a function of size, and he recorded a rate of digging by A.rubens of 1-2 $cm.hr^{-1}$. Anger et al. (1977) estimated the digging time of A.rubens for Macoma balthica (L.) as the same order of magnitude as the feeding time. The short digging times in the present study suggest the Spisula were not fully buried, and total handling time may therefore be underestimated.

4.4. (v). Materials and methods, Foraging experiments.

Five Asterias rubens, of initial sizes as recorded in Table 14 were examined foraging on Mytilus edulis. The experiments were run using shallow glass aquaria 72 cm square, and 8 cm deep . A square of thin perspex sheet fitted closely inside the aquaria, resting about 1

TABLE 14

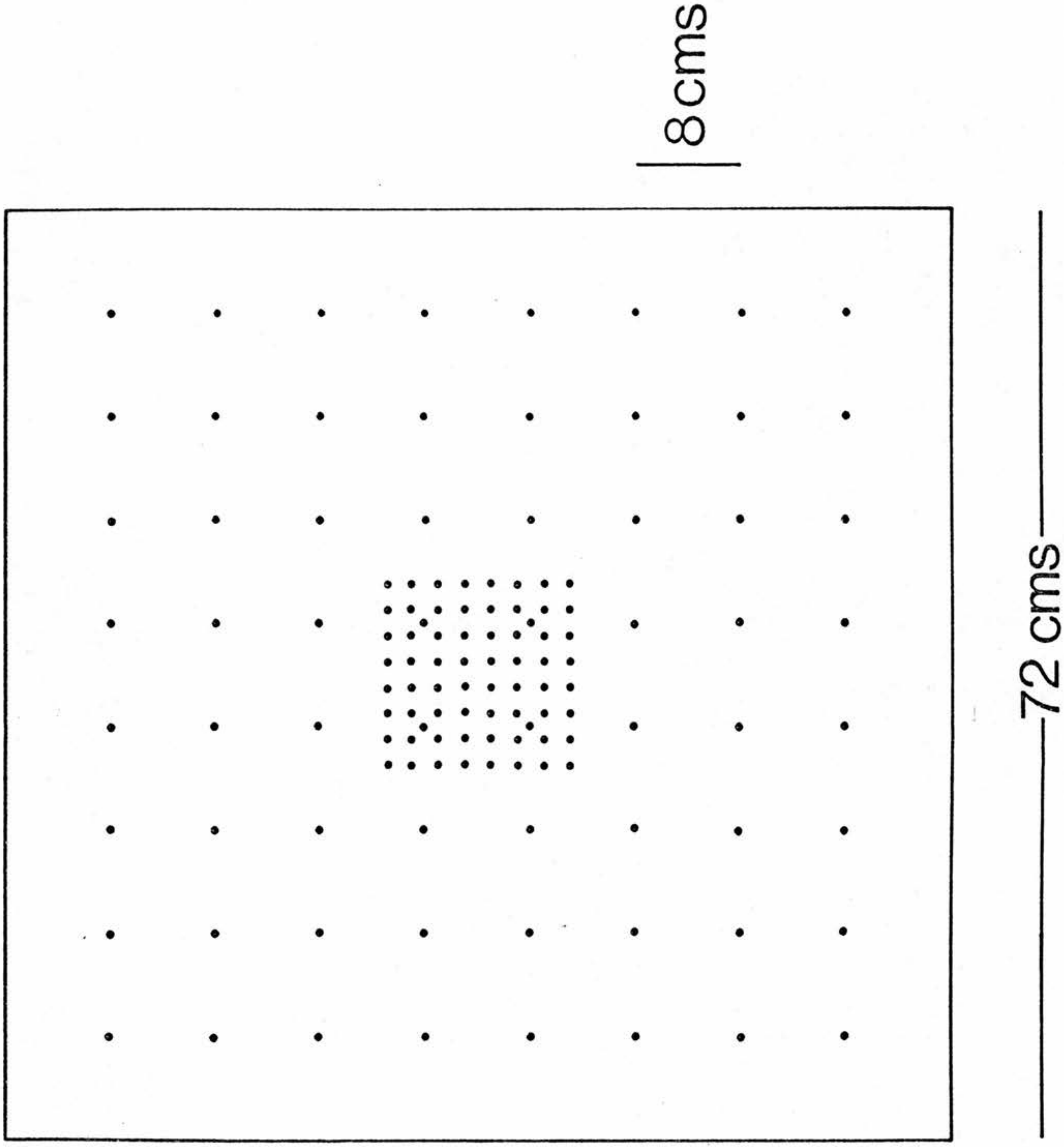
Size-specific foraging experiments of A. rubens on M. edulis. Starfish number three died at the end of the winter series of experiments, and was replaced with another of similar size.

	Start of Winter Experiments		Estimated Optimal Mussel Size (Fig 32) Asterias of this R	Mean Mussel Size Eaten		Mann-Whitney U Values	Level of Significance (Figs 34 to38)	Spawning Date (Where recorded)
				Dispersed 15.11.82– 6.1.83 (53 days)	Aggregated 31.1.83– 24.3.83 (53 days)			
	R (mm)	Damp Wt (g)	(mm)	(mm)	(mm)			
1	130	263	64.0	42.9	48.3	993.5	P .05	
2	123	188	61.3	26.8	43.2	670.0	P .001	
3	106	231*	55.0	54.7	55.7	401.5	N.S.	
4	89	118	48.6	32.5	50.6	248.5	P .001	
5	76	99	43.7	34.0	43.5	552.5	P .01	
	Start of Summer Experiments			Dispersed 1.6.83– 16.7.83 (46 days)	Aggregated 22.7.83– 5.9.83 (46 days)			
	R (mm)	Damp Wt (g)		(mm)	(mm)			
1	173	703	80.1	39.3	55.3	262.5	P .001	21.7.83
2	163	437	76.4	33.9	38.8	129.3	P .05	21.7.83
3	80	79	45.2	34.1	54.7	282	P .001	
4	130	398	64.0	42.4	49.3	494.5	P .05	
5	98	380	52.0	46.0	51.4	506	N.S.	13.7.83

* Died 6.6.83
New Asterias

FIGURE 33

Plan of aquaria used in laboratory foraging experiments. Each dot represents a hole in a perspex sheet laid over the aquarium floor, into which a mussel can be secured. The large (8cm) spacing was used in the "dispersed" condition; the small (2cm) spacing for the "aggregated" condition.


8cms
72 cms

cm clear of the floor thereof. Into this perspex sheet were drilled 64 holes in a square grid (Fig. 33), with an 8 cm spacing between each hole and between the edge of the grid and the sides of the tank. Earlier experiments on size-specific predation in asteroids have used prey items grouped into size classes (Kim, 1969; Hancock, 1974). In the present study discrete prey sizes were used to add resolution to prey size preferences. To the grid holes were randomly allocated a total of 42 mussels comprising six individuals of each size, notably: 5, 15, 25, 35, 45, 55, and 65mm (each ± 1mm). All mussels had been prepared as follows: after being scraped free of epiphytes and epizoites and dabbed surface dry with a paper towel the anterior end was abraded with fine sand paper. To the abraded area a 10cm cotton or monofilament nylon thread was glued using Araldite Rapid (TM). The mussel's threads were then secured into the grid holes by means of matchsticks. In spite of its name, to give Araldite Rapid time to harden fully required leaving the Mytilus out of water for longer than many of them, particularly the larger ones, were accustomed. Therefore 1-2 cm of slack thread was left between the matchstick and the mussel to allow for locomotion before embyssment; otherwise the larger mussels frequently detached themselves from the semi-hardened resin. Mussels that did free themselves and moved out of range of their matchsticks were replaced.

Each aquarium received a separate inflow of fresh sea water. A thin polythene sheet laid over the top of each tank and covering the water surface permitted the A.rubens to hang should they climb the tank walls. Mytilus that were consumed were replaced daily with others of the same size into the same holes.

In this the "dispersed" experimental condition the 8 cm spacing of prey items did not succeed in keeping the largest mussels entirely discrete. Juxtapositioning of adjacent Mytilus was tolerated provided neither was separated from its attachment.

For the subsequent, "aggregated", experimental condition a further 64 holes were drilled into the centre of the perspex sheet, each with a 2 cm spacing (see Fig. 33). Being aggregative the Mytilus, once secured as for the "dispersed" condition, formed a tight clump. Clearly, any separation of a mussel from its matchstick in this design did not necessitate replacement unless its movement lead it away from the clump. Consumed mussels were replaced daily as before.

In the "non replacement" condition 42 mussels were placed in the grid as for the "dispersed" condition, but once consumed mussels were not replaced.

The same five A.rubens were used throughout the course of these experiments, except for No. 3 which died in June 1983, of unknown causes. This animal was replaced by an individual of comparable size. In summary, the schedule of experiments was as follows:

1. Winter "dispersed" replacement expt. (15/11/1982-6/1/1983)

2. Winter "aggregated" replacement expt. (31/1/1983-24/3/1983)

3. Winter "dispersed" non-replacement expt. (1/4/1983-10/5/1983)

4. Summer "dispersed" replacement expt. (1/6/1983-16/7/1983)

5. Summer "aggregated" replacement expt. (22/7/1983-5/9/1983)

6. Summer "dispersed" non-replacement expt. (6/9/1983-21/10/1983)

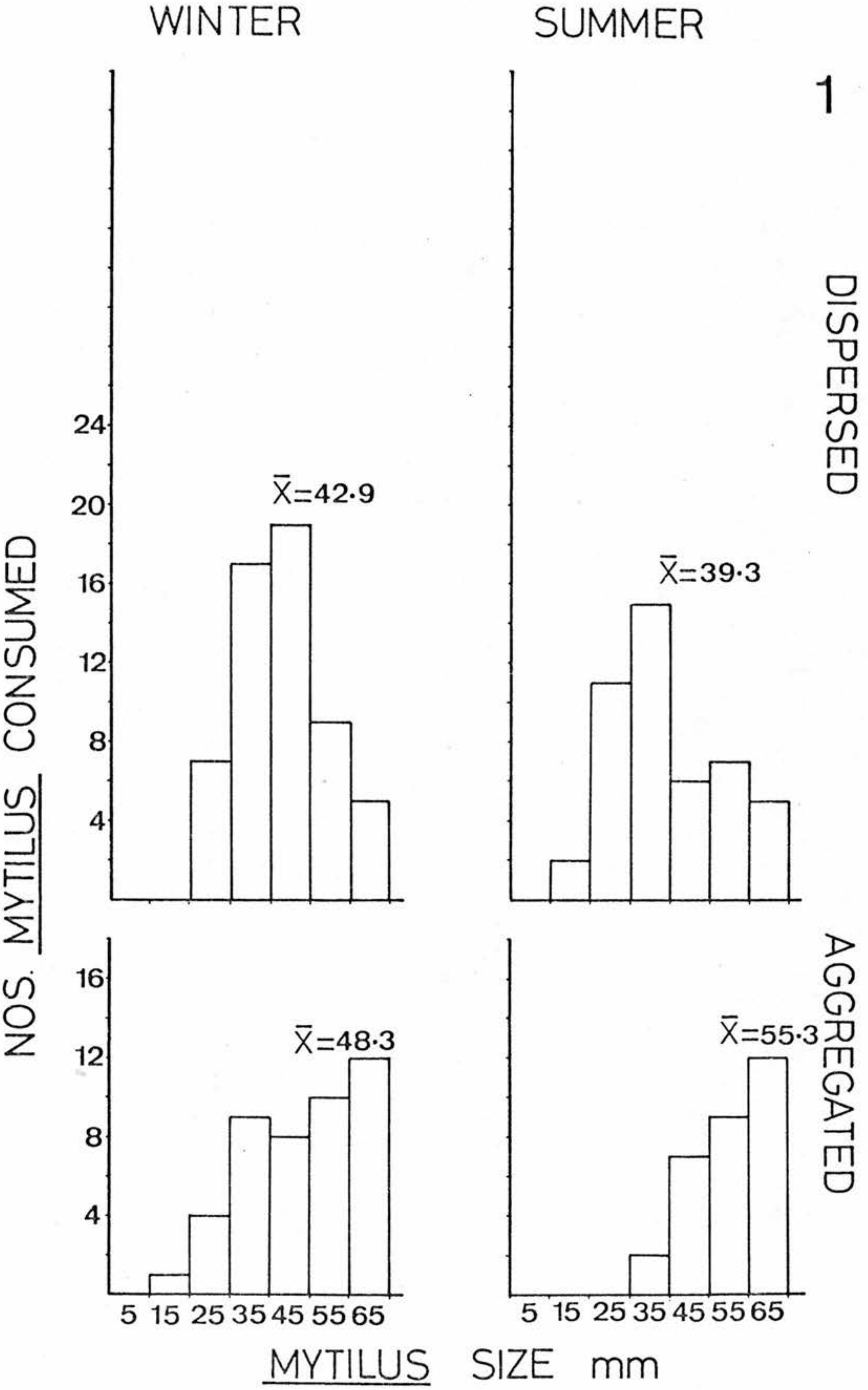
4.4. (vi). Results, foraging experiments.

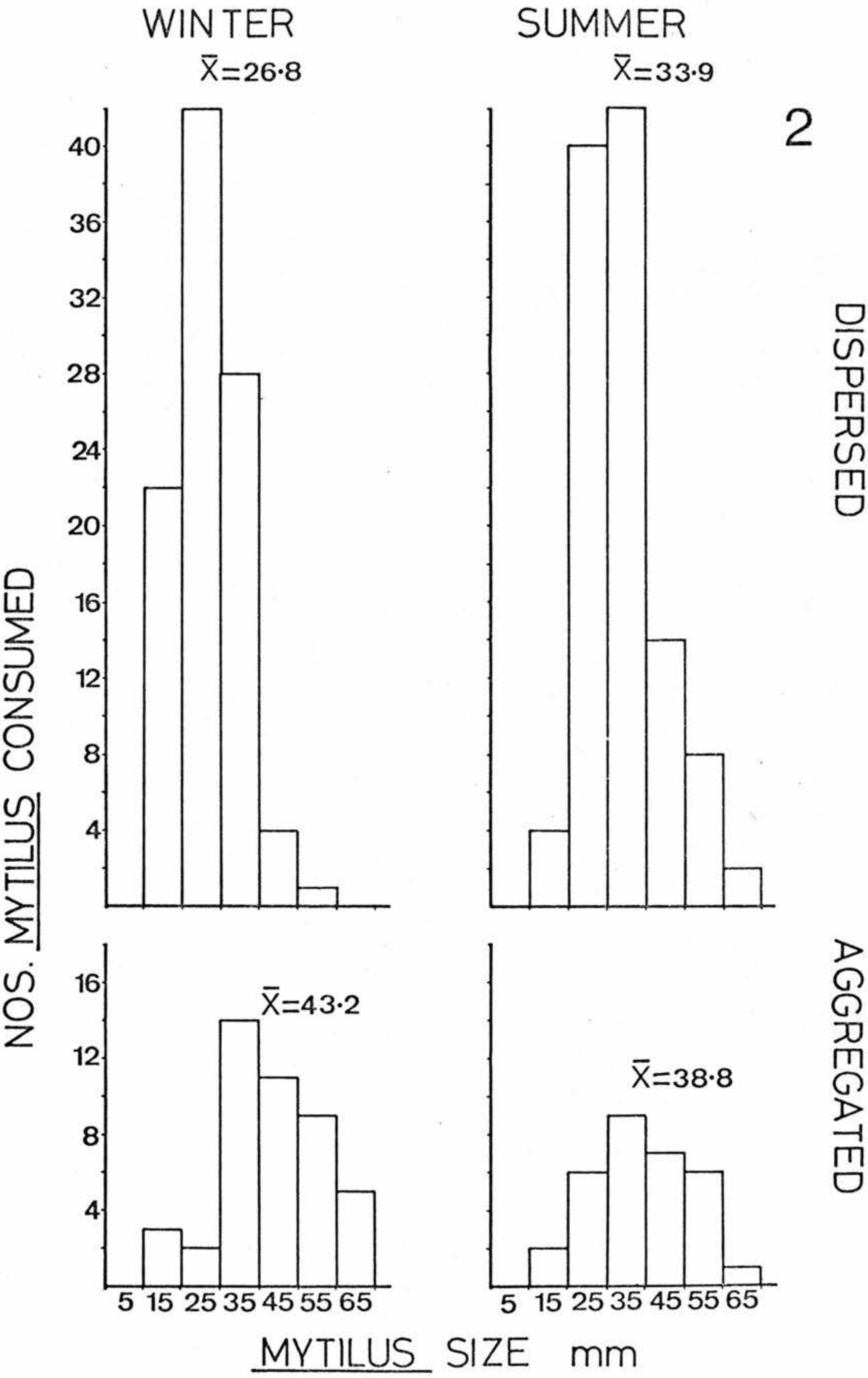
For each A.rubens the numbers of "dispersed" and "aggregated" Mytilus consumed in the treatments in summer and winter are shown in figs 34-38. Numbers eaten are comparable for the "aggregated" and "dispersed" treatments in either season, but not between seasons; this was achieved by running the experiments for longer in winter (53 days) than summer (46 days). A.rubens consumed more Mytilus when the prey items were "dispersed" than when "aggregated" . Frequently the sizes taken appear to be approximately normally distributed, showing that the full range of acceptable items was on offer, although the tails of the distribution may have been truncated (No.1, summer, "aggregated";No.3, summer, "dispersed"). In most cases a wide range of prey sizes were taken by individual starfish .

FIGURES 34-38

Numbers of *Mytilus edulis* consumed by each of five *A. rubens* during foraging experiments.

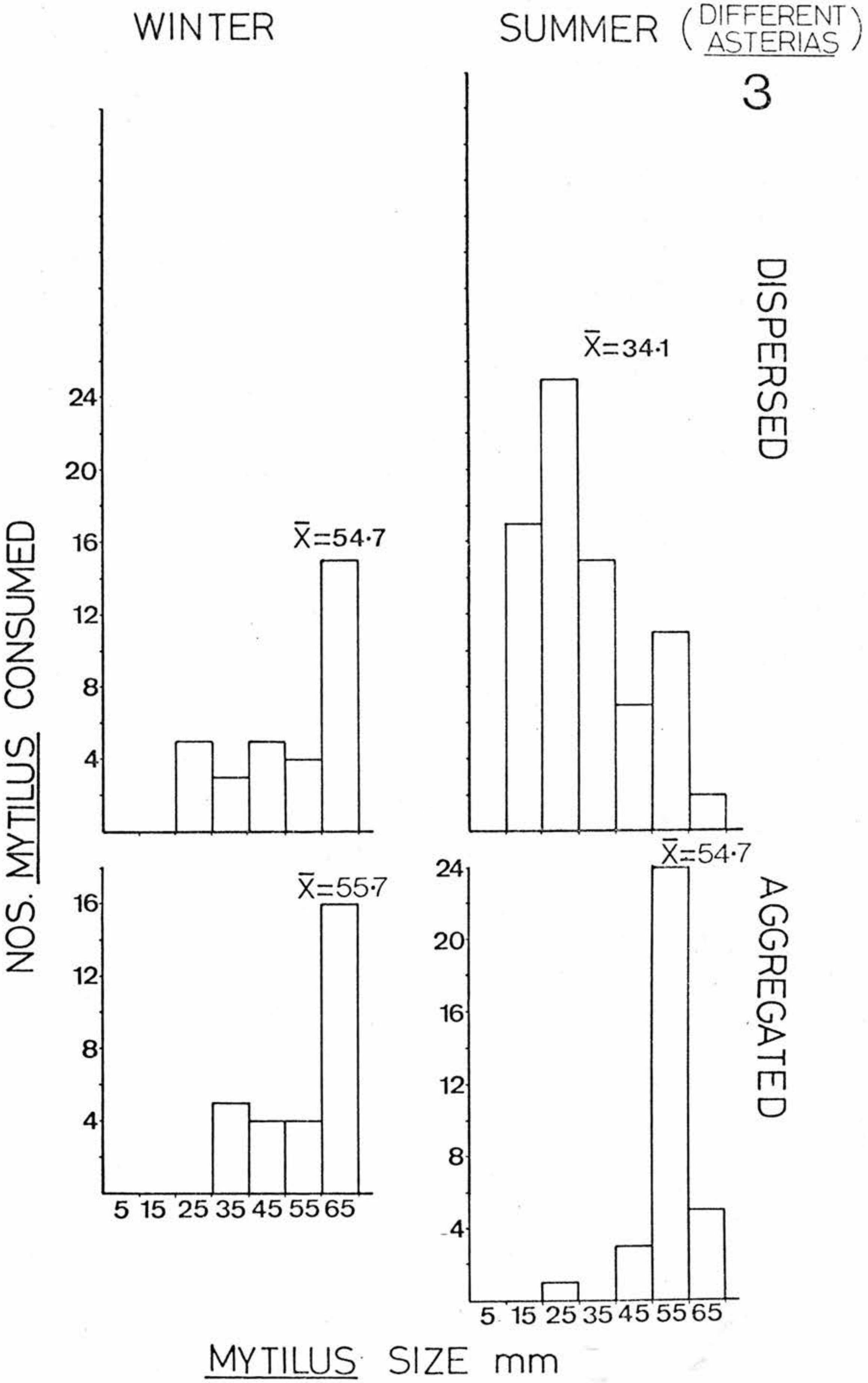
1


WINTER
SUMMER
DISPERSED
AGGREGATED
NOS. MYTILUS CONSUMED
24
20
16
12
8
4
X̄=42·9
X̄=39·3
16
12
8
4
X̄=48·3
X̄=55·3
5 15 25 35 45 55 65
5 15 25 35 45 55 65
MYTILUS SIZE mm



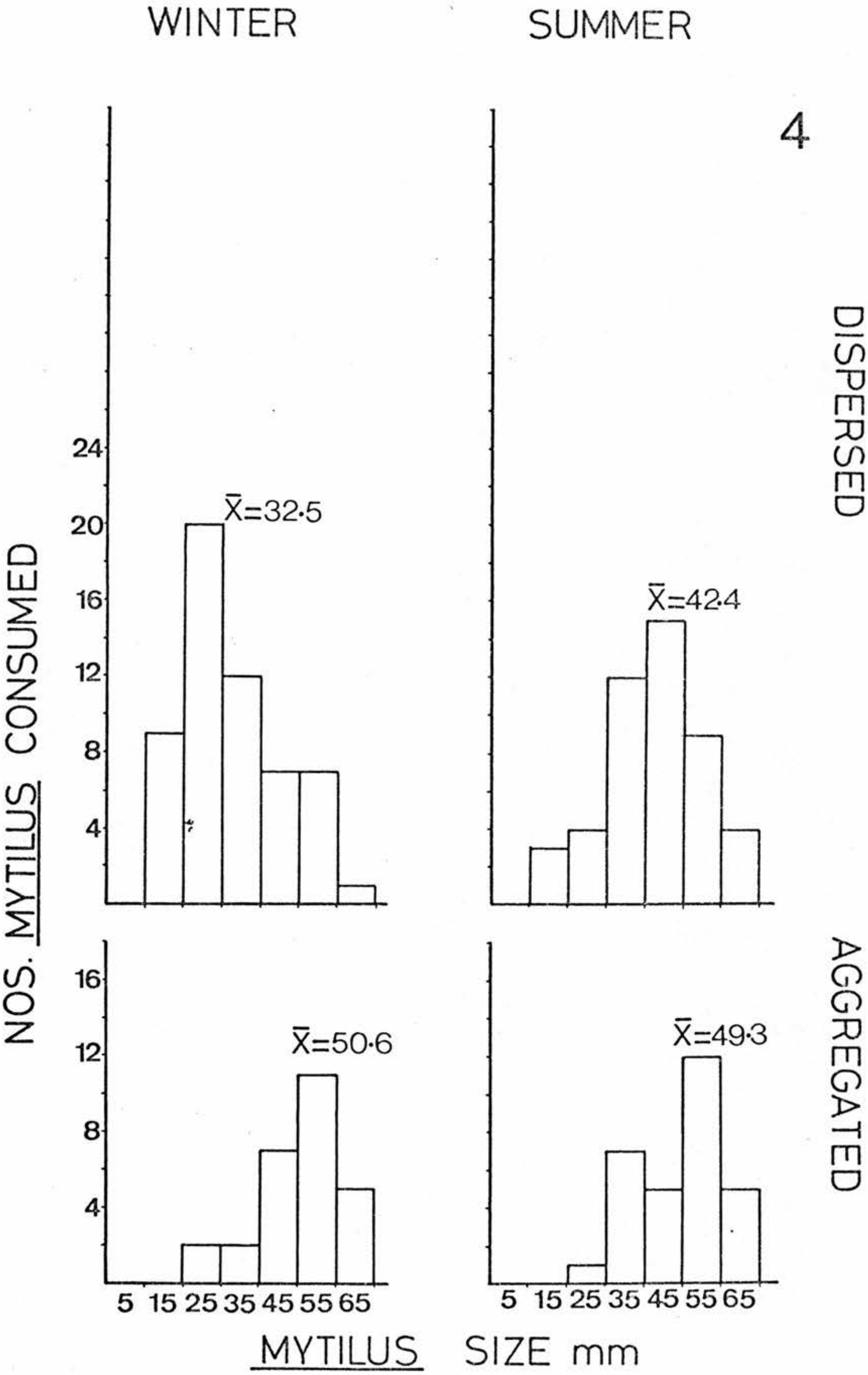
2

WINTER
SUMMER
$\bar{X}$=26·8
$\bar{X}$=33·9
$\bar{X}$=43·2
$\bar{X}$=38·8
DISPERSED
AGGREGATED
NOS. MYTILUS CONSUMED
40
36
32
28
24
20
16
12
8
4
16
12
8
4
5 15 25 35 45 55 65
5 15 25 35 45 55 65
MYTILUS SIZE mm

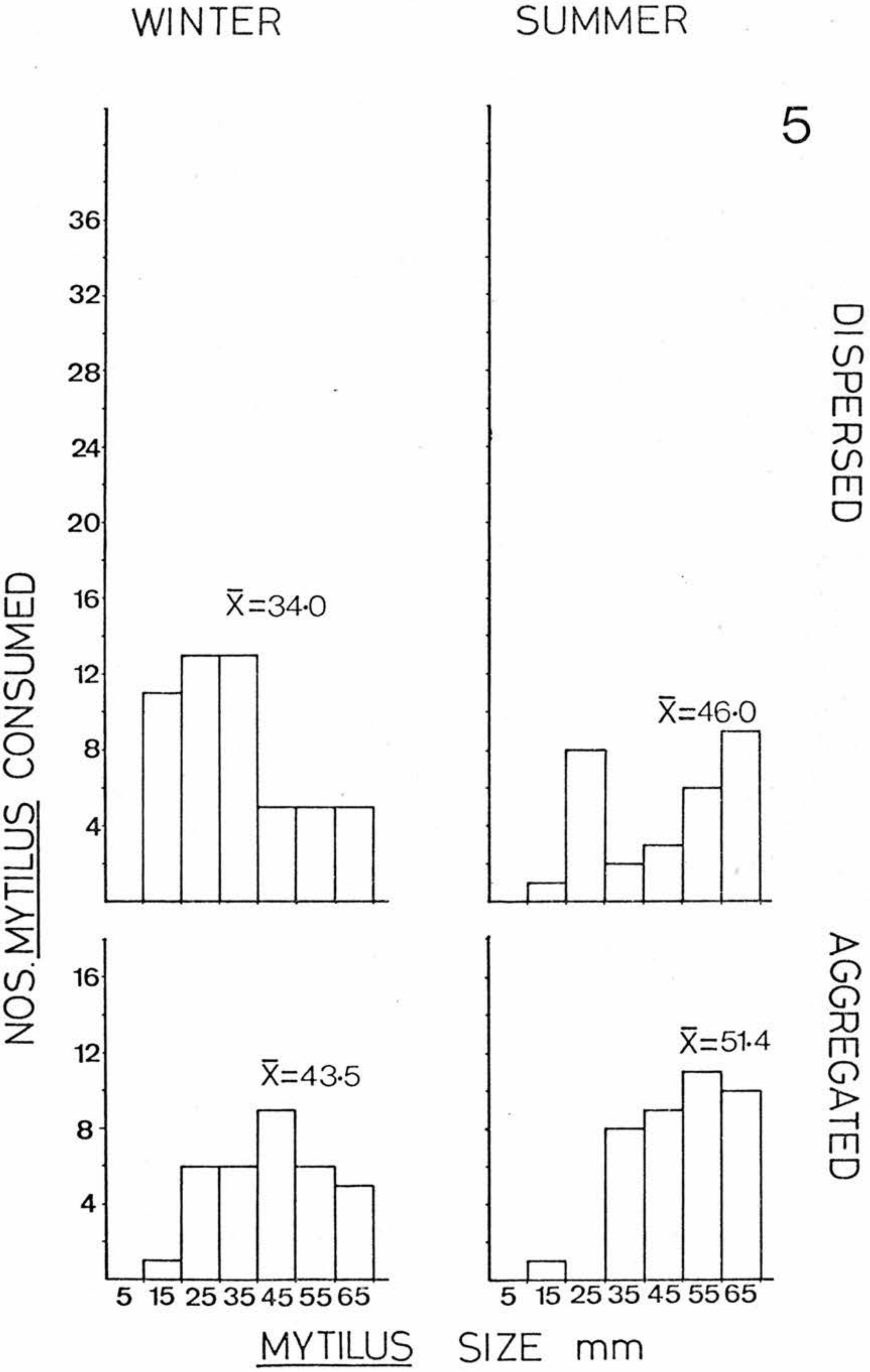

WINTER
SUMMER (DIFFERENT ASTERIAS)
DISPERSED
AGGREGATED
NOS. MYTILUS CONSUMED
X̄=54·7
X̄=34·1
X̄=55·7
X̄=54·7
24
20
16
12
8
4
5 15 25 35 45 55 65
MYTILUS SIZE mm

3

4


WINTER
SUMMER
DISPERSED
AGGREGATED
NOS. MYTILUS CONSUMED
24
20
16
12
8
4
X̄=32·5
X̄=42·4
16
12
8
4
X̄=50·6
X̄=49·3
5 15 25 35 45 55 65
5 15 25 35 45 55 65
MYTILUS SIZE mm

5


WINTER
SUMMER
DISPERSED
AGGREGATED
NOS. MYTILUS CONSUMED
36
32
28
24
20
16
12
8
4
X̄=34·0
X̄=46·0
16
12
8
4
X̄=43·5
X̄=51·4
5 15 25 35 45 55 65
5 15 25 35 45 55 65
MYTILUS SIZE mm

In all cases except two the A.rubens chose significantly larger prey items when they were "aggregated" than when "dispersed" (Mann-Whitney U- test, Table 14), levels of significance are shown facing the figures. A.rubens No.3 (winter) showed a particular preference for mussels in the 65mm category in both experimental conditions, and the feeding of No.5 (summer) was disturbed in July before it spawned.

For the "non-replacement" experiment numbers of Mytilus eaten per five days have been grouped together (Table 15) and the survivorship of six mussels in each size category is presented. A preference for particular size categories is discernible in many of the cases, the A.rubens taking successively less valuable (small and large) prey items as the preferred size classes were depleted. No 5mm Mytilus were consumed by any of the starfish in any of the foraging experiments. Whether mussels of this size would eventually be taken in the absence of other prey in the "non-replacement" experiments could not be established in the time available. A.rubens No.3 stopped feeding in April 1983 and subsequently died of unknown causes. Numbers 2 and 4 stopped feeding for a period during September, resulting in incomplete data sets for these two starfish in this experiment.

4.4. (vii). General discussion.

TABLE 15

Survivorship of a cohort of six *M. edulis* of each of seven sizes in the "non-replacement" condition.

	1							2							3							4							5						
'WINTER' Size (mm)	5	15	25	35	45	55	65	5	15	25	35	45	55	65	5	15	25	35	45	55	65	5	15	25	35	45	55	65	5	15	25	35	45	55	65
1.4.83	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6
5.4.83	6	6	3	4	6	4	6	6	5	5	5	6	6	6	6	6	6	5	5	6	5	6	6	6	5	6	6	5	6	6	5	6	6	6	5
10.4.83	6	6	3	3	6	2	4	6	4	3	2	4	6	6	6	6	5	5	5	3	3	6	6	6	5	6	3	5	6	5	2	4	3	6	5
15.4.83	6	5	2	2	4	2	2	6	1	3	2	4	5	4	6	6	4	4	3	3	2	6	5	6	4	5	2	4	6	5	1	2	3	4	5
20.4.83	6	4	2	1	4	1	1	6	1	2	1	2	5	3	Stopped Eating							6	5	6	4	4	2	3	6	5	1	2	3	3	3
25.4.83	6	4	1	-	3	-	-	6	1	1	1	-	5	3	Later Died							6	5	5	4	3	2	3	6	5	1	2	3	3	3
30.4.83	6	2	-	-	1	-	-	6	1	-	1	-	3	2	6.6.83							6	5	5	2	2	2	3	6	4	1	1	2	2	3
5.5.83	6	1	-	-	-	-	-	6	1	-	-	-	2	1								6	4	5	2	2	2	1	6	3	1	1	2	1	3
10.5.83	6	-	-	-	-	-	-	6	1	-	-	-	1	-								6	4	4	2	1	1	-	6	3	1	1	1	-	2
'SUMMER'																																			
6.9.83	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6
11.9.83	6	5	4	5	4	5	5	6	6	6	6	6	6	6	6	6	5	5	4	3	5	6	6	6	6	6	6	6	6	6	6	6	4	3	5
16.9.83	6	5	4	5	3	3	2	6	6	6	6	6	6	6	6	4	5	2	3	2	5	6	6	6	6	6	6	6	6	6	6	6	3	3	3
21.9.83	6	5	3	3	1	1	-	6	6	6	6	6	6	6	6	4	4	2	3	2	4	6	6	6	6	6	6	6	6	5	4	5	-	1	1
26.9.83	6	4	-	-	-	-	-	6	5	5	5	6	4	6	6	4	3	1	2	2	2	6	6	6	6	6	6	6	6	4	-	-	-	-	-
1.10.83	6	3	-	-	-	-	-	6	5	5	5	6	4	6	6	2	3	-	1	2	2	6	6	6	6	6	6	6	6	2	-	-	-	-	-
6.10.83	6	2	-	-	-	-	-	6	3	2	1	5	4	6	6	-	2	-	1	1	1	6	6	6	6	6	6	6	6	1	-	-	-	-	-
11.10.83	6	2	-	-	-	-	-	6	3	1	-	2	3	5	6	-	1	-	1	-	1	6	6	6	5	6	5	4	6	1	-	-	-	-	-
16.10.83	6	2	-	-	-	-	-	6	2	1	-	-	1	4	6	-	1	-	1	-	-	6	6	6	3	5	1	3	6	1	-	-	-	-	-
21.10.83	6	2	-	-	-	-	-	6	2	-	-	-	-	4	6	-	1	-	1	-	-	6	6	5	3	2	-	2	6	1	-	-	-	-	-

In experiments with Carcinus maenas foraging on M. edulis Elner and Hughes (1978) found that the predicted optimal size coincided with the observed preferred size. From this they concluded that Carcinus forages so as to maximise net energy intake. The estimated optimal mussel sizes for the five A.rubens in the present study are shown in Table 14 adjacent to the mean sizes consumed in the foraging experiments. In conditions of unrestricted prey availability A.rubens chose Mytilus somewhat smaller than the predicted optimal size. Paradoxically, a choice closer to the "optimum" was made when Mytilus were aggregated, in which condition the fewer total number of Mytilus consumed suggests foraging behaviour is constrained. The upward shift in mean mussel size taken in the aggregated condition was expected insofar as small Mytilus would become hidden within the interstices of the clump.

Various conclusions can be drawn from this disparity between the observed and predicted "optimal" prey sizes. The hypothesis that animals forage so as to maximise net energy intake, and that this confers a selective advantage, is the basis of optimal foraging theory (Hughes, 1980). However, foraging behaviours can deviate from those predicted as optimal on account of nutrient constraints (Pulliam, 1975), or the presence of predators or competitors.

If energy expended overcoming and handling a prey item increases disproportionately with prey size, the effect will be to lower the size of the predicted optimum. This may obtain in the starfish-mussel association in which the cross-sectional area of the adductor muscle will be proportional to the surface area of the shell, itself proportional to the square of the linear dimensions. Alternatively, it is a frequent observation that two or more A.rubens will attack the same bivalve. This seems to happen particularly at larger bivalve sizes (Anger et al., 1977; Hancock, 1974) in which the starfish that initiates feeding leaves exposed a section of shell gape through which a second starfish can gain access. The second or subsequent starfish thus obtains a meal at reduced cost, and to the detriment of the first starfish which has invested time and effort subduing the prey. Such interference between predators has been observed in Thais emarginata feeding on Balanus cariosus (Emlen, 1966; in Hughes, 1980). On soft sediments water movements are an important stochastic mortality factor (Sieling, 1960; and see Chapter 2.5). The humped-up position of a feeding starfish may project it through the boundary layer adjacent to the substratum, and the extended Th for a large bivalve may greatly increase the risk of dislodgement. Thus a large prey item may incur an additional risk element not apparent from these laboratory experiments, and not easily quantifiable in energetic terms. It seems that the accelerating rise in Th with large prey items is not offset by the caloric gain and in these circumstances A.rubens may act as a "time minimiser" rather than an "energy maximiser" (Schoener, 1971; Hughes and Seed, 1981)

Even in the "dispersed" foraging experiment the selection for a preferred Mytilus size category is far from well-defined and commonly all sizes from 15-65mm were included in the diet. The absence of a more rigorous size-selection mechanism in A.rubens may reflect a continual "sampling" of all prey types to obtain feedback on the quality of the environment. Alternatively, a finite recognition time is a characteristic feature of predators relying on chemosensory or tactile cues for prey identification and if this is extended, or there is a danger of prey misidentification, a predator may expand its diet to include suboptimal prey. Asterias species rely heavily on chemosensory cues for the location of prey (Castilla and Crisp,1970; Zafiriou et al.,1972), but these studies have shown that while this genus possesses the ability to locate prey with reasonable efficiency, behaviour in this respect is not infallible or clear-cut. It is therefore uncertain to what extent the wide range of mussels "sampled" in conditions of unlimited prey availability reflects an inability on behalf of the starfish to evaluate prey items that differ in respect of size, and to discriminate between them. It is reasonable to assume that bivalve surface area is the important determinant of prey size, since application of force to the valves by means of the tube feet gives the starfish access. Such a relationship between R and maximum prey size has been recorded by Needler (1941) for A.vulgaris, by Kim (1969) for A.amurensis, and by Hancock (1974) for A.rubens. In the field, however, A.rubens will normally encounter Mytilus in clumps, individual mussels being tightly packed against each other, and with only the posterior end exposed to the foraging starfish. The criteria by which prey are evaluated thus remain unclear.

In Morecambe Bay A.rubens removed all (>95%) of M.edulis they encountered in their summer swarm invasions of 1969 and 1972. (P.J.Dare, pers.comm.). Any mussel losses due to wave effects or to loosening of clumps were considered to have been negligible, and the predation line appeared to be due to a retreat stimulated by environmental changes and not due to any change in prey size/quality. The mussels in this area, however, were predominantly of 0+ and 1+ year classes (mean lengths 9mm and 25mm on July 1st 1969) (Dare, 1982), and as such were largely suboptimal for A.rubens of mean radius 6cm. At present it is not understood whether such invasions represent an extension of normal foraging behaviour as a response to food shortage or a distinct behavioural change. A full undertanding of foraging behaviour under these circumstances, and the degree to which the results shown here can be extrapolated to the field, awaits further study.

Chapter 5.

SUMMARY AND DISCUSSION.

St Andrews Bay *A.rubens* exist not as separate and discrete sub-populations but as a single dispersed population covering areas of different suitability. The sampling procedure devised - that of periodic samples taken from fixed locations - emphasises patchiness. It would be possible to interpret all results in terms of starfish recruitment solely amongst kelp holdfasts in the shallow rocky sublittoral, were it not for anomalous results from Trawl 1, a distance of two nautical miles from the shore. *A.rubens* were found in declining numbers with distance further north in the bay. The increase in mean size and the increase in minimum size from Trawls 2 to 4 is deduced as evidence of a gradual northward dispersal from shallow settlement grounds. Starfish reaching as far as Trawl 4 would encounter richer feeding grounds than those further south. However, the abundance of apparently juvenile *A.rubens* from Trawl 1, an area of poor food quality and quantity, implies that recruitment can occur on sandy substrata. Asteroids undergo a brief period during which the post-metamorph brachiolaria is attached to the substratum, and have been believed to require a hard substratum for this purpose. Alternatively, starfish arriving in the general area of Trawl 1 may cease growth or even shrink as a result of food shortage (*e.g.* Feder, 1970). A.rubens is capable of prolonged survival without food (Vevers, 1949), and may survive by actively uptaking dissolved nutrients from the seawater (Jangoux, 1976b, in Menge, 1982). The extent to which a starfish can resorb body tissues is unknown, and in the absence of any morphological method of age determination the possibility that these are stunted, older, starfish cannot be discounted. Although relatively small, pyloric caeca were present in A.rubens from Trawl 1; one might expect resorption of body tissues to occur only after food storage reserves had been depleted.

Paine (1976) found that particular rocky intertidal habitats tended to bear P.ochraceus up to certain asymptotic sizes. Once this size has been reached P.ochraceus has the option of adjusting growth to match energetic intake from local resources, or emigrating. He concluded that P.ochraceus normally undergo the former. Intertidal Astrostole scabra in Australia rarely have a radius larger than 140mm, and subtidal A.scabra are rarely smaller than 110mm. Most A.scabra emigrate permanently, and maturity coincides with the adoption of an exclusively subtidal habitat (Town, 1980). This would imply an ability on the part of the starfish to "decide" when the intertidal habitat is no longer sufficient, and to then emigrate. Indeed, since no A.rubens of R larger than 50-60mm were found intertidally at Boghall in the present study, something similar may be occurring here.

A.rubens are only found in the lower intertidal, and could only be found exposed in sufficient numbers at Spring Tides. The high rate of exchange between intertidal and subtidal starfish suggests we are simply glimpsing the edge of the sublittoral population, and that there is no discrete resident population of intertidal starfish.

The intertidal population around the southern edge of St Andrews Bay, such as it is, probably contributes little to the net reproductive pool of the whole St Andrews A.rubens population. Organ indices of littoral individuals are comparable with those from the food-limited starfish of Trawl 1. Nevertheless, growth at a mean rate of 1.5mm.month^{-1} was recorded from these starfish. The size-frequency histograms of sublittoral A.rubens showed no age-class progression, and a growth-rate is therefore not calculable.

In spite of a constant and characteristic size-frequency profile from each trawl, numbers of A.rubens per unit area fluctuated widely during the sampling period. Some of these fluctuations coincided with strong winds, and in October 1982 an easterly gale resulted in considerable size-specific mortality. The majority of A.rubens thrown onto the shore were the 0+ year class, found within dislodged Laminaria holdfasts. However, in spite of such abiotic mortality factors, the primary limiting factor for St Andrews A.rubens appears to be food shortage. Laboratory experiments showed that fully grown A.rubens would not consume M.edulis 5mm long. In the benthos from Trawl 2 the majority of bivalves were less than 5mm long, and only from Trawls 4 and 3 (North) were found bivalves of a suitable size for adult starfish.

Foraging experiments showed that when offered "dispersed" M.edulis of a range of sizes, A.rubens showed no clear-cut preference. A wide range of size classes was consumed, but these often approximated a normal distribution. The mean size, however, was significantly smaller than the size predicted as "optimal" by prey value calculations determined on purely energetic grounds. This contrasts with the results of Elner and Hughes (1978) who found that the crab Carcinus maenas preferentially consumed calorifically "optimal" prey. A.rubens consumed larger M.edulis when the mussels were allowed to aggregate, but a reduced feeding rate in these circumstances - which more nearly approximates to the conditions A.rubens encounters in the field - suggests that foraging behaviour is constrained. The mean size consumed when the mussels were aggregated is closer to that predicted as "optimal".

Disparity between observed and predicted prey choice may be explained by nutrient constraints (Pulliam, 1975). This will not pertain here, however, because different sizes of a single prey species were used, rather than 2 species of different biochemical composition. Alternatively, it is suggested that larger prey items may carry an associated risk element to the starfish not quantifiable in energetic terms. Warner (1979), for example, observed a bed of Spisula on which large numbers of A.rubens were feeding. More than half of the starfish were sharing bivalves, and the largest number observed feeding on 1 prey item was five. A starfish able to partake of anothers' meal is able to feed at a reduced cost. This bivalve-sharing occurs only at large prey sizes (Hancock, 1974; Anger et al, 1977). Again, a prolonged handling time spent in a humped-up position may increase risk of dislodgement by water currents if the starfish projects itself into the water column, or the effort required to overcome a bivalve may increase disproportionately with bivalve size.

In the absence of studies in Great Britain along the lines of those performed in the United States by Paine (1974, 1976a), Dayton, (1971), and Menge (1976, 1978, 1979), the impact of intertidal predatory asteroids on European shores remains unclear. There are similarities between the rocky shores of Europe and those of the Atlantic coast of the USA (Menge, 1982), where asteroids (Asterias vulgaris and A.forbesi) have a major impact on the community structure of protected to moderately exposed shores.

In the field M.edulis in a given area are usually of a comparatively uniform size, with the exception of very small individuals within the interstices of a clump. Mussel size is associated with immersion time, and is therefore a function of height on the shore (Seed, 1969). The most important prey limitation for A.rubens is that consumption be possible before the tide recedes. A rigid size-selection mechanism in A.rubens would therefore have no selective advantage, and the success of this species must be largely due to its behavioural flexibility.

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APPENDIX

The Fisher-ford Model

for full explanation see Begon (1979)

Date	Day	No. Captured	No. released	Time of Release of marks, j								
	i	n_i	r_i	1	2	3	4	6	8	9	10	11
21.10.82	1	-	52	-								
2.11.82	2	25	25	-								
2.12.82	3	36	35	-	1							
2. 1.83	4	35	35	-	-	3						
2. 3.83	6	36	34	-	-	-	2					
13. 5.83	8	59	58	-	-	-	-	2				
14. 6.83	9	84	81	-	-	-	-	-	1			
12. 7.83	10	120	117	-	-	-	-	-	-	9		
10. 8.83	11	102	-	-	-	-	-	-	-	3	10	

Day i	M_i	$M_{ij}(i-j)$
1	0	0
2	0	0
3	1	1
4	3	3
6	2	4
8	2	4
9	1	1
10	9	9
11	13	16
		38 $\sum_i \sum_j M_{ij}\ (i-j)$

Estimate $\phi=0.09$:

$M_1=0$

$M_2=0.09(0+52)=4.68$

$M_3=0.09(4.68+25)=2.67$

$M_4=0.09(2.67+35)=3.39$

$M_5=0.09(3.39+35)=3.45$

$M_6=0.09(3.45)=0.31$

$M_7=0.09(0.31+34)=3.09$

$M_8=0.09(3.09)=.28$

$M_9=0.09(0.28+58)=5.24$

$M_{10}=0.09(5.24+81)=7.76$

$M_{11}=0.09(7.76+117)=11.23$

$A_2=1$

$A_3=\frac{1\text{x}4.68}{4.68+25}+1=1.16$

$A_4=\frac{1.16\text{x}2.67}{2.67+35}+1=1.01$

$A_5=\frac{1.01\text{x}3.39}{3.39+35}+1=1.09$

$A_6=\frac{1.09\text{x}3.45}{3.45+0}+1=2.09$

$A_7=\frac{2.09\text{x}0.31}{0.31+34}+1=1.02$

$A_8=\frac{1.02\text{x}3.09}{3.09+0}+1=2.02$

$A_9=\frac{2.02\text{x}0.28}{0.28+58}+1=1.01$

$A_{10}=\frac{1.01\text{x}5.24}{5.24+81}+1=1.06$

$A_{11}=\frac{1.06\text{x}7.76}{7.76+117}+1=1.07$

Day i	M_i	A_i	$A_i m_i$
1	0	-	0
2	4.68	1	0
3	2.67	1.16	1.16
4	3.39	1.01	3.03
6	0.31	2.09	4.18
8	0.28	2.02	4.04
9	5.24	1.01	1.01
10	7.76	1.06	9.54
11	11.23	1.07	13.91
			36.87