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The ecology of Astropecten irregularis and its potential role as a benthic predator in a soft-sediment community.

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The Ecology of *Astropecten irregularis* and its Potential Role as a Benthic Predator in Structuring a Soft-sediment Community

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CHAPTER 6 **The Distribution and Occurrence of *Acholoë squamosa* a Commensal with *Astropecten irregularis***

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This thesis is dedicated in memory of my father

Paul Freeman 1931-1981

Summary

Astropecten irregularis is an important predator in the structure and organization of subtidal soft-sediment communities. Seasonal changes in the population dynamics of *A. irregularis* and its prey exhibit complex interactions with each other and the physical environment e.g. substrate, seawater temperature and tides. The dietary characteristics of *A. irregularis* has been examined at sites throughout the southern and western coastal waters of the British Isles. Although *A. irregularis* shows a strong seasonal preference for juvenile bivalves e.g. *Spisula subtruncata*, its diet broadly reflects the relative availability of prey and includes crustaceans, gastropods, polychaetes and echinoderms. During winter starfish migrate off-shore into deep water and during summer they form spawning assemblages. Changes in the arm length (growth) of *A. irregularis* is seasonal, where maximal growth occurs between mid-summer and mid-autumn. Cluster analysis and multi-dimensional scaling proved to be useful tools in the identification of seasonal patterns in the starfish diet. Laboratory experiments and x-ray radiographs were used to examine prey selection; interactions between prey density, prey survival within the starfish stomach (which varies with predator size) and prey profitability were identified. Capture and ingestion of different molluscan, crustacean and echinoderm prey have been described. Freshly caught starfish exhibited an endogenously controlled quadri-diurnal locomotory activity under continuous darkness, which coincided with expected slack water at high and low tides. In a laboratory flume starfish burrow into the sediment in response to strong water currents and form subsurface aggregations. The distribution and occurrence of the polynoid commensal *Acholoë squamosa* and its host *A. irregularis* is also reported.

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CHAPTER 1

General Introduction

Astropectinid starfish are conspicuous members of many subtidal benthic communities around the world (Christensen, 1970; Peres, 1982), feeding predominantly on small infaunal organisms such as molluscs and crustaceans (Christensen, 1970; Jangoux, 1982; Nojima, 1989; Lemmens *et al.*, 1995). Although previously a number of workers have investigated the general feeding biology of *Astropecten* (Hunt, 1925; Christensen, 1970; Burla *et al.*, 1972; Massé, 1975; Ribi and Jost, 1978; Franz and Worley, 1978; Nojima, 1989; Beddingfield and McClintock, 1993; Lemmens *et al.*, 1995; Freeman *et al.*, 1999) few studies have examined the role of *Astropecten* in structuring benthic assemblages at the community level (Christensen, 1970; Wurzian, 1983). Wurzian (1983) for example, studied the feeding rate of *A. aranciacus* which inhabits the shallow waters of the Adriatic Sea and concluded that this particular species had a much less significant role in the benthic community than had previously been expected. In the shallow coastal waters off the British Isles and Denmark, however, *A. irregularis* (Pennant, 1777) is considered to be an important predator of many infaunal species, particularly those associated with soft-sediment habitats where this starfish is known to have a significant effect on the population densities of the clam, *Spisula subtruncata* (Christensen, 1970; Freeman *et al.*, 1999).

The importance of asteroids as a controlling agent in the communities to which they belong has been well documented (Galtsoff and Loosanoff, 1939; Hancock, 1955;

Paine, 1966, 1976; Brun, 1968; Dare, 1982; Dayton, 1975; Menge, 1982; Paine *et al.*, 1985; Menge *et al.*, 1994; Navarrete and Menge, 1996). In some instances asteroids are known to cause extensive damage to commercially exploited shellfish beds worldwide. For example, *Asterias rubens*, is probably one of the most destructive predators of cultivated stocks of the mussel, *Mytilus edulis*, in northern Europe (Korringa, 1976; Dare, 1982) whilst other asteroids such as *Acanthaster planci*, have caused widespread destruction of many coral reef communities throughout the tropics (reviewed by Moran, 1986).

The key to the success of asteroids has generally been attributed to a range of characteristics that give these predators considerable versatility unlike that of many other benthic invertebrate predators (Menge, 1982). These characteristics include, indeterminate growth where starfish will continue to grow depending on the availability of food (Paine, 1976) a digestive system that is sufficiently generalized to allow a wide range of prey to be assimilated (Feder, 1959; Mauzey *et al.*, 1968; Lubchenco and Menge, 1978) extra and/or intra-oral digestion which enables these predators to handle both large or small prey items (Christensen, 1970; Dayton *et al.*, 1974) a sensory ability which is 'sophisticated' enough to enable prey, which may be buried in the sediment, to be located and in some asteroids e.g. *Pisaster giganteus*, an ability to 'learn' about its prey (Landerberger, 1966; Mauzey *et al.*, 1968; Dayton *et al.*, 1977) locomotory and attachment mechanisms such as, tube-feet and flexible arms, which permit rapid movement and firm attachment simultaneously, a variable number of arms which provide power and flexibility when adhering to either sediment or prey (Ferlin, 1973; Lawrence, 1987). Although our knowledge of such characteristics has been useful in understanding the role that asteroids play within the community, much of this information has hitherto been largely confined to those species which occur predominantly in intertidal habitats.

Paine (1966) clearly demonstrated the impact of *Pisaster ochraceus* on the structure and diversity of a mussel dominated community on the Pacific coast of North America by excluding starfish from certain areas of the rocky intertidal. In the absence of this important predator, its most preferred prey and the spatially dominant species, *Mytilus californianus*, showed a dramatic increase in abundance, whilst the overall diversity of other species within the community showed a significant decline. Paine (1969) later described *P. ochraceus* as a 'keystone species' a concept he used to define the relative importance of such predators within the community by the number of different attributes they possessed. These attributes included, a preference for competitively superior prey, *M. californianus*, a species which could potentially eliminate other organisms, a large body size relative to prey size, a functional response to increases in prey density, indeterminate growth and a relatively large foraging range (Paine, 1969, 1976; Menge, 1982). It has been suggested that *A. irregularis* may also be a 'keystone species' (Christensen, 1970) in soft-sediment subtidal communities. However, there has previously been relatively little evidence to support such a claim and more information is clearly required to determine the relative position of this asteroid within the community it occupies.

Few studies have investigated asteroids inhabiting subtidal regions (Hancock, 1958; Nauen, 1978; Sloan and Robinson, 1983) and even fewer have examined their significance within soft-sediment habitats (Christensen, 1970; Anger *et al.*, 1977). This may, in part, be attributed to the difficulties often associated with conducting direct observations or experimental manipulations on subtidal asteroids. For example, in many subtidal habitats scuba equipment or underwater cameras may be required to observe predator-prey interactions. In many cases, however, such observations may not always be feasible because of poor weather conditions, expensive equipment and/or costly manpower. More indirect methods such as beam trawls and benthic grabs, for example, have usually been employed in order to infer general predator-prey interacts or relationships. Since *A. irregularis* feeds by ingesting its prey intra-orally, this species is well suited for quantitative and qualitative investigations into asteroid feeding biology and consequently the role of this particular species within the community (Christensen, 1970). In this thesis the role of *A. irregularis* as a benthic predator is examined at a study site located within shallow water to the northeast of Red Wharf Bay. At this site soft-sediment habitats predominate and these are well known for their suitability as nursery grounds for many commercially exploited predators such as juvenile flatfish, *Pleuronectes platessa* and *Limanda limanda* (Basimi *et al.*, 1985; Carter *et al.*, 1991) and other non-commercial predator *A. rubens*, for example, which co-exists with *A. irregularis*, feeding on very similar prey items such as *S. subtruncata*, *Abra alba* and *Nucula turgida* (Allen, 1981).

The aim of this thesis has been to examine the general ecology and feeding habits of *A. irregularis* and to establish its importance as a benthic predator within a soft-sediment subtidal community. The thesis is divided into several chapters each one, except for chapters one and seven, containing its own introduction and discussion.

Chapter one provides general background information to the thesis, whilst **chapter seven** is a general discussion drawing together the most important aspects of each chapter and provides a focus for future research.

Chapter two examines the seasonal changes in the population dynamics, spatial distribution and reproductive biology of *A. irregularis* collected from the main study site in Red Wharf Bay. In addition, seasonal migration patterns of starfish based on both field and laboratory investigations are also presented. **Chapter three** investigates the seasonal changes in the diet and prey selection of *A. irregularis* with particular reference to the size of both predator and prey, and the abundance and biomass of prey. The chapter also discusses the role of *A. irregularis* in a the soft-sediment community in Red Wharf Bay and investigates the stomach contents of *A. irregularis* at various sites located within the southern and western waters of the British Isles. **Chapter four** examines prey preference by *A. irregularis* in laboratory aquaria, with particular reference to optimal foraging theory, and considers the mechanisms underlying prey selection based on predator and prey size, prey abundance and the retention time of prey within the starfish stomach. **Chapter five** identifies the different methods used by *A. irregularis* to capture its prey and investigates both exogenous and endogenous locomotory activity under varying water velocities within a laboratory flume. Changes in the daily illumination where constant conditions of light and dark are experimentally manipulated were also examined in the laboratory. The locomotory speed exhibited by different size classes of starfish and the changes in speed when prey items are encountered is also presented. **Chapter six** investigates the association between the commensal polynoid worm, *Acholoë squamosa* and its host *A. irregularis*. The distribution and abundance of *A. squamosa* around the southern and western coastal waters of the British Isles and the spatial distribution of this symbiont on its host are also examined.

CHAPTER 2

Spatial Distribution, Spawning and Population Structure of *Astropecten irregularis*

2.1 Introduction

In the coastal waters around the British Isles *Astropecten irregularis* inhabits a variety of different substrates ranging from coarse gravel to fine mud, although it is more commonly found in sand (Hunt, 1925; Holme, 1966; Christensen, 1970; Freeman *et al.*, 1998). All species of *Astropecten* are generally found either partially or completely buried within the sediment, but when foraging, they roam over the sediment surface where they are voracious predators of many infaunal invertebrates, particularly molluscs and crustaceans (Christensen, 1970; Ribi *et al.*, 1977; Ribi and Jost, 1978; Franz and Worley, 1982; Nojima, 1989; Lemmens *et al.*, 1995).

In benthic communities where *Astropecten* is common seasonal changes in the abundance of this predator can have a profound influence on the population structure and density of many infaunal invertebrates (Christensen, 1970; Morin *et al.*, 1985). For example, in Danish waters during the late summer months, newly settled juveniles of the clam *Spisula subtruncata,* a preferred prey species of *A. irregularis,* are almost totally eliminated as a result of starfish predation (Muus, 1966) whereas other molluscan prey, such as juvenile *Mya truncata* conveniently avoid periods of intense starfish predation by settling during the winter months when starfish are much less abundant and their feeding rates are substantially reduced (Christensen, 1970). Larger *M. truncata*, on the other hand, avoid starfish predation by occupying much greater depths within the sediment where they are largely inaccessible to foraging starfish (Christensen, 1970).

Few previous studies have examined the seasonal changes in the spatial distribution of *Astropecten* and these provide only limited confirmation that this genus is migratory (Burla *et al.*, 1972; Pabst and Vicentini, 1978; Nojima, 1983). Burla *et al* (1972) documented the off-shore migration of *Astropecten aranciacus*, a common asteroid in the shallower (<7m) inshore waters of the Mediterranean during the winter months. Nojima (1983) similarly reported winter migrations in another shallow water species, *A. latespinosus*, a common predator in Japanese waters.

Observations on the annual reproductive cycle and growth of *Astropecten* appear to be confined to just two studies, that by Nojima (1982) and Christensen (1970). Nojima noted that *A. latespinosus*, a common predator in the shallow coastal waters off Japan, spawn during the summer months whilst its rate of growth is generally greatest during the autumn months. Christensen, similarly observed spawning during the summer months in *A. irregularis* and that growth also followed a seasonal pattern. His observations, however, were based entirely on starfish kept under laboratory conditions and there appears to be no comparative studies of this particular species to field populations.

In this study the seasonal changes in the spatial distribution and abundance of *A. irregularis* in Red Wharf Bay, North Wales are examined, and the annual reproductive cycle and population structure of this important benthic predator are described.

2.2 Materials and methods

A bathymetric survey of the study area, approximately 3 x 5 km, was conducted using a 12 Koden Chromascope 200KHz echosounder linked to a RoxAnn system running Microplot for logging in Red Wharf Bay, Anglesey, North Wales (53° 20′ 50N 04° 06′ 00W) (Figure 2.1). Seawater depths ranged from 13m inshore and 28m offshore and the bottom substrate consisted of sandy sediments (Figure 2.2). Although a large population of *Astropecten irregularis* was discovered within the study area, an arbitrary boundary covering area approximately 1km^2 was established at the centre of the population. This area was further divided into sixteen plots (A1 to D4) each an area 0.65 of a square kilometer (0.25x0.25km). Monthly samples were collected between October 1995 and May 1998 during neap tides using a 2m or 3m beam trawl fitted with a 5mm^2 mesh. Although a single trawl was towed at a speed ranging between 1 and 1.5 knots for a period of 8min inside each of the sixteen sample plots by the University of Wales research vessels the Prince Madog or the Sandpebbler. However, single tows within each plots were not always possible and on occasion tows overlap plots or continued beyond the plot perimeter. The co-ordinates for each trawl, the number of starfish collected and seawater depth are presented in Appendix I. The distance over the ground covered by each trawl was determined by recording the ship's position with a Global Positioning System (GPS) when each trawl was shot and hauled; these co-ordinates were then used to relocate each plot on subsequent visits. In each catch the number of *A. irregularis* were recorded and the length between the mouth and the tip of the longest arm of each starfish measured to the nearest 0.1mm using vernier calipers. Most starfish were preserved in 5% formalin, although some were maintained in running seawater

Figure 2.1. The position of the study site (1km^2) in Red Wharf Bay, A-D and 1-4 divide the site into sixteen sample plots, which were trawled each month between October 1995 and March 1998; inset shows the location of the study site off the coast of North Wales.

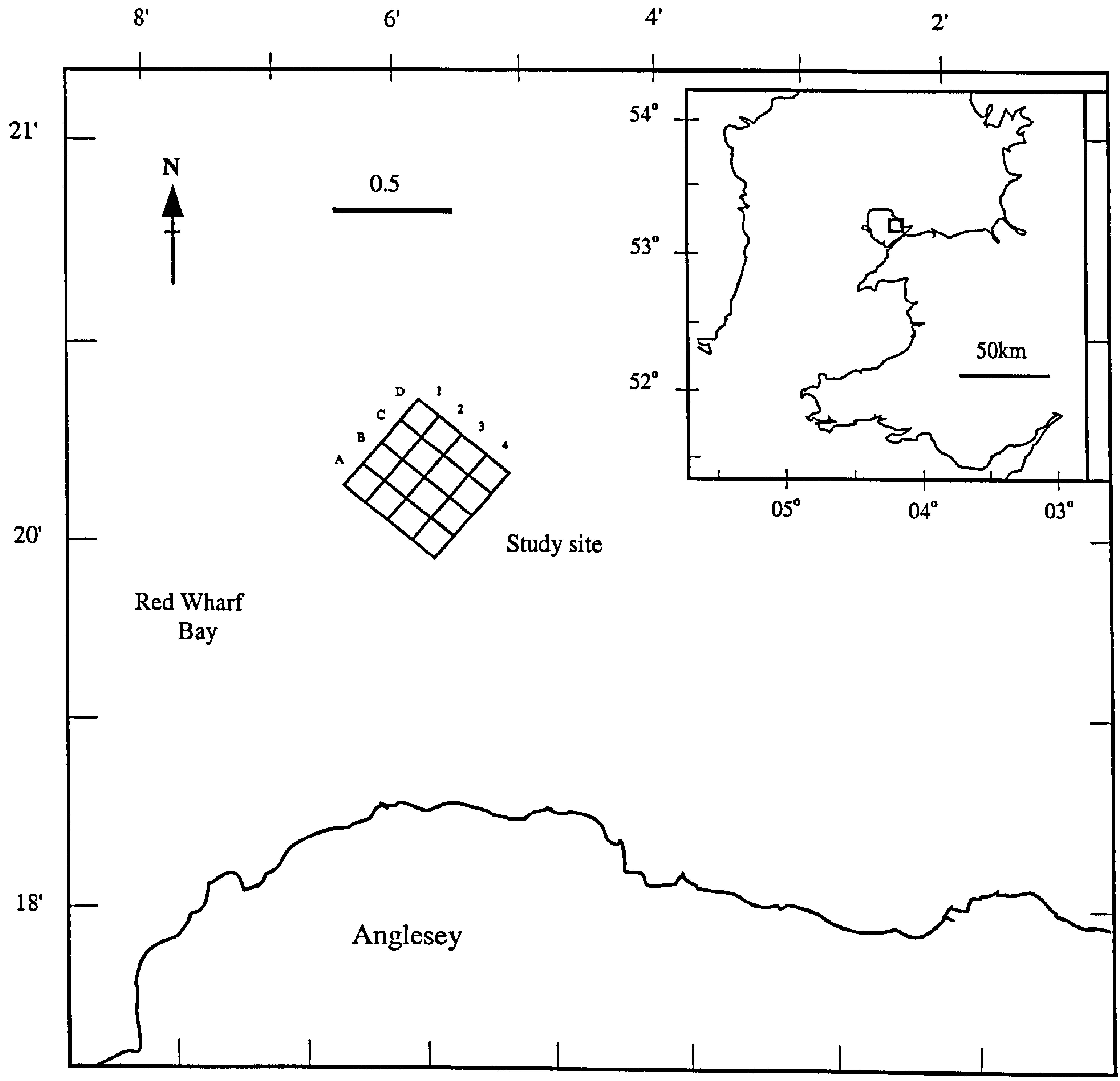
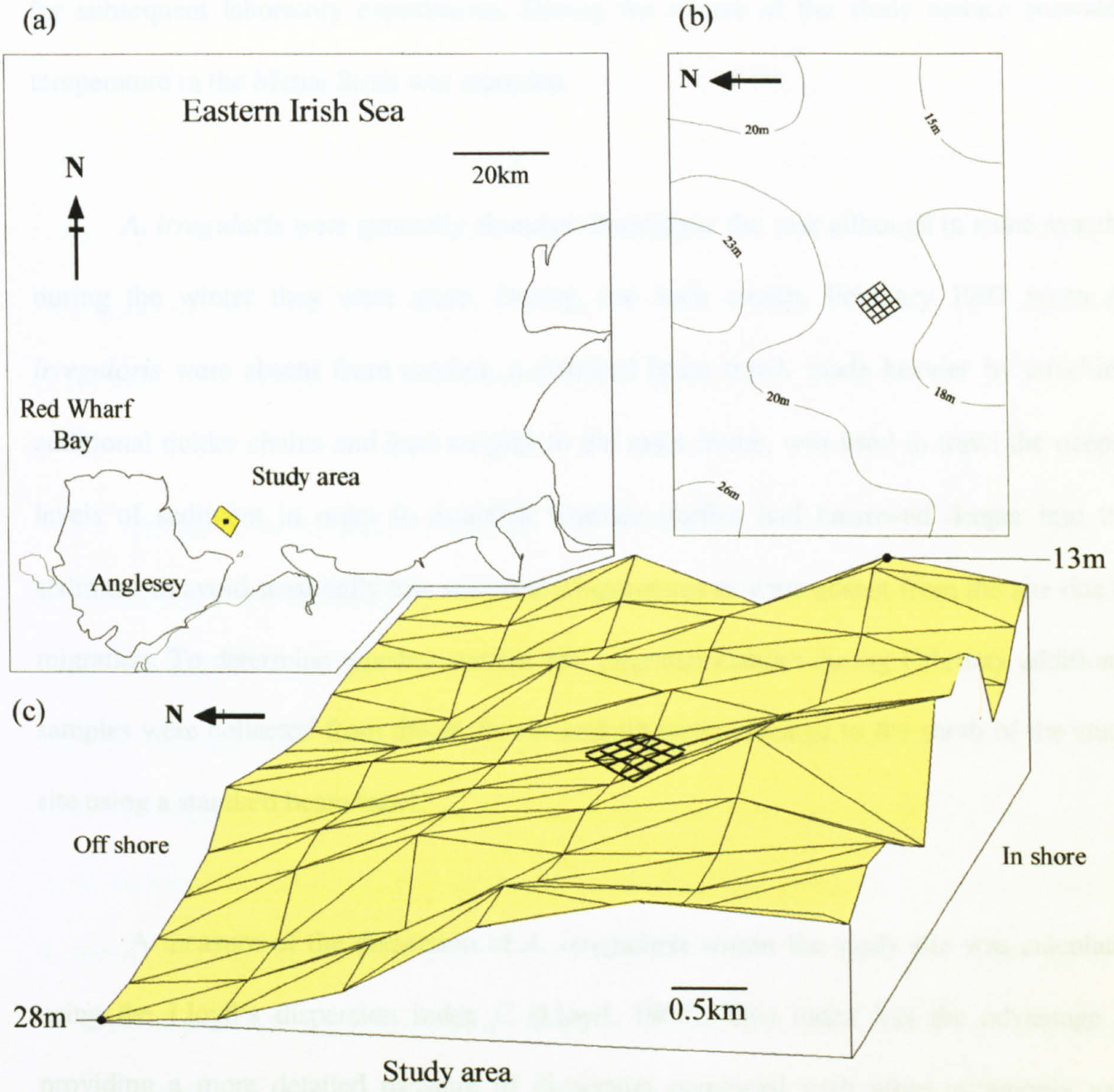

8'
6'
4'
2'
21'
20'
18'
N
0.5
A
B
C
D
1
2
3
4
Study site
Red Wharf Bay
Anglesey
54°
53°
52°
05°
04°
03°
50km

Figure 2.2. (a) Location of study area in Red Wharf Bay off the coast of Anglesey, North Wales. (b) A 2-dimensional contour map of the study area showing seawater depth, and (c) Bathymetric profile of the study area showing the deepest (28m) and the shallowest (13m) seawater depths, and the location of the sample plots (A1 to D4; central grid see Figure 1).


(a)
Eastern Irish Sea
N
20km
Red Wharf
Bay
Study area
Anglesey
(b)
N
20m
15m
23m
20m
18m
26m
13m
(c)
N
Off shore
In shore
28m
0.5km
Study area

for subsequent laboratory experiments. During the course of the study surface seawater temperature in the Menai Strait was recorded.

A. irregularis were generally abundant throughout the year although in some months during the winter they were scare. During one such month, February 1997 when *A. irregularis* were absent from catches, a standard beam trawl, made heavier by attaching additional tickler chains and lead weights to the main frame, was used to trawl the deeper levels of sediment in order to establish whether starfish had burrowed deeper into the sediment to avoid seasonally low seawater temperatures or were absent from the site due to migration. To determine whether starfish had migrated inshore during February additional samples were collected from the shallower inshore waters located to the south of the study site using a standard beam trawl.

A measure of the dispersion of *A. irregularis* within the study site was calculated using the Lloyd's dispersion index C (Lloyd, 1967). This index has the advantage of providing a more detailed measure of dispersion compared with other commonly used indices such as the dispersion coefficient k (see Elliott, 1977) and has previously been successfully used to investigate dispersion in other asteroid species (see Levin *et al.*, 1985). The Lloyd's index (C) is calculated as;

$$C = \frac{m}{\bar{x}}$$

where m is the mean crowding when data are negatively binomial and the value of m is calculated as;

$$m = \bar{x} + \frac{S^2}{\bar{x}} - 1$$

where $\bar{x}$ is the mean density of *A. irregularis* (ind.ha^{-1}) and S^2 is the sample variance. When C µ 1 the distribution is considered to be aggregated, otherwise it is considered to be uniform. For samples where n>30 a significance value was estimated using the *d*-criteria (Elliott, 1977). To quantify the seasonal changes in the spatial distribution of *A. irregularis* throughout the study site, between December 1995 and December 1997, the average number of starfish (ind.ha^{-1}) from each of the sixteen sample plots A1 to D4 were compared.

To determine the reproductive status of *A. irregularis*, a representative size range of between twenty and twenty-six formalin preserved starfish were selected from the monthly samples collected from Red Wharf Bay, between December 1995 and May 1998. These starfish were dissected under a low power binocular microscope, the gonad material from each individual removed and together with the starfish oven dried at 60°C for a period of three days and the dry weights estimated to the nearest 0.01mg using a top loading balance. A gonad somatic index was calculated as the proportion of the gonad dry weight (GDW) to the body dry weight (BDW) including the gonad weight. This method has previously been used by Nojima (1982) on his study of the reproductive cycle of *A. latespinosus* and is obtained as follows;

$$\text{Gonad somatic index} = \frac{\text{GDW}}{\text{BDW}} \times 1000$$

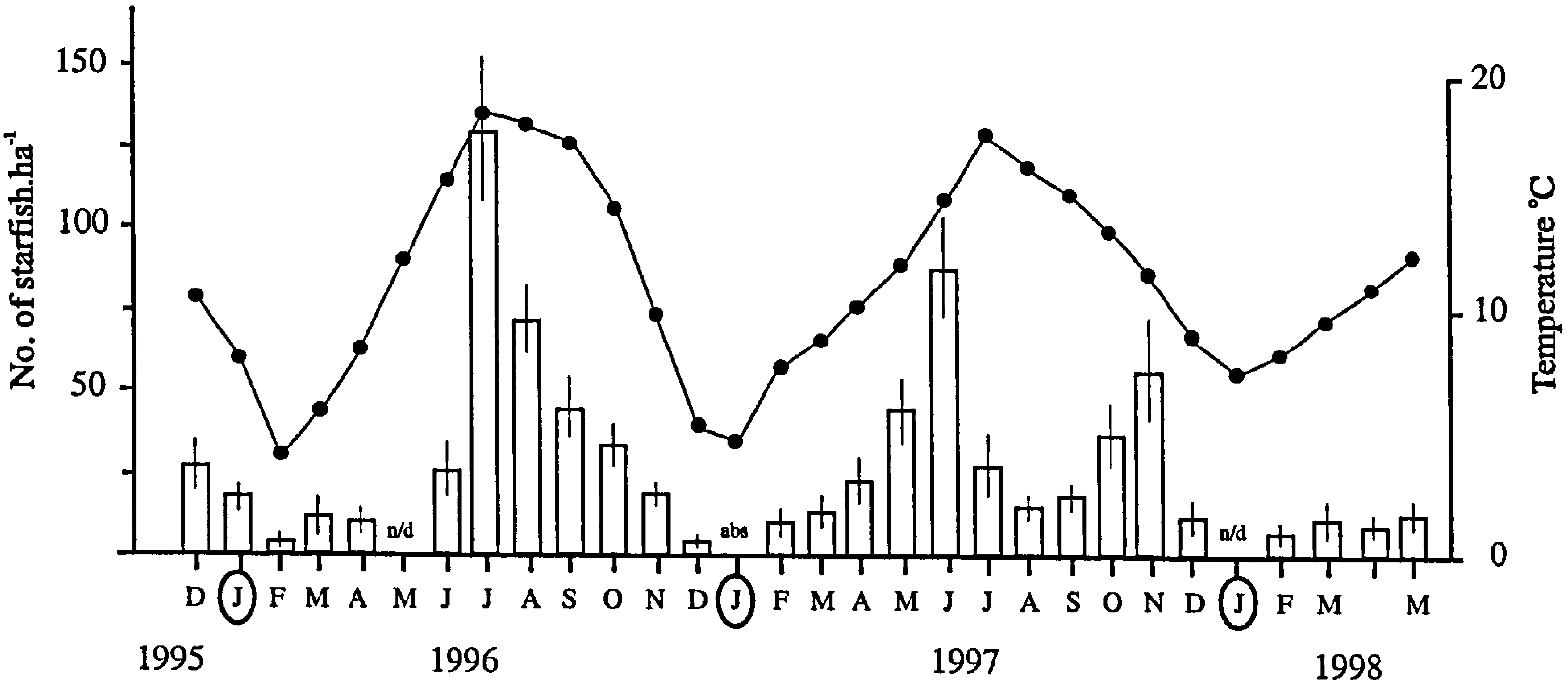
Growth of *A. irregularis* was estimated from the monthly size frequency data using the method of Bhattacharya (1967). This analysis fits normal distribution curves to the length frequency data to obtain estimates of the mean size classes for each sample set. However, this type of analysis usually fits several curves to the distribution data to resolve overlapping size classes, but in the Red Wharf Bay population there is only one main cohort of starfish and so the fitted normal distribution curve that best approximates this cohort was used.

The effect of seawater temperature on the burrowing depth and locomotory activity of *A. irregularis* was investigated in the laboratory. A total of eight starfish (arm length 30-48mm) were kept individually in aquaria (surface area 750cm^2) filled with sand to a depth of 10cm and supplied with running seawater maintained at a temperature of 18°C. Over a period of 54 days seawater temperature, which was thermostatically controlled, was reduced in increments of 2°C every six days until a minimum temperature of 2°C was reached. The position of each starfish and its depth in the sediment were recorded twice a day, in the morning and in the evening. Burrowing depth was estimated by gently probing the sediment with a specially adapted depth gauge (see Appendix II). Since starfish emerge from the same position once they have burrowed into the sediment following a period of foraging over the sediment surface, their movements could be detect between observations. The positions of each starfish were plotted onto a transparent plastic sheet which was marked appropriately with a series of grid squares (1cm^2).

2.3. Results

Astropecten irregularis showed marked seasonal trends in abundance, ranging from a mean of 130ind.ha^{-1} (0.013ind.m^2) in July 1996 declining to a mean of 6ind.ha^{-1} (0.0006ind.m^2) in December 1996; on one occasion in January 1997 starfish were completely absent from all beam trawl samples (Figure 2.3). Because *A. irregularis* is a

Figure. 2.3 The abundance (ind.ha^{-1}) of *Astropecten irregularis* (□± SE) and seawater temperature (-●-) in Red Wharf Bay between December 1995 and May 1998; n/d denotes no data; abs denotes starfish absent.


No. of starfish.ha^{-1}
150
100
50
Temperature °C
20
10
0
n/d
abs
n/d
D
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
M
1995
1996
1997
1998

burrowing starfish low population densities during the winter months may indicate that many individuals had burrowed deeper into the sediment in response to low seawater temperatures. However, the use of a heavy beam trawl, which allowed a much greater depth of sediment to be sampled, did not collect significantly (ANOVA F=0.14, $P>0.05$) more starfish than the standard lighter trawl (Table 2.1) suggesting that most starfish had probably migrated out of the study site during this period. In 1997 a second increase in starfish abundance occurred during October and November when around 50ind.ha^{-1} (0.005ind.m^{2}) were recorded at a time when starfish numbers were usually low <10ind.ha^{-1} (0.001ind.m^{2}) (see Figure 2.3).

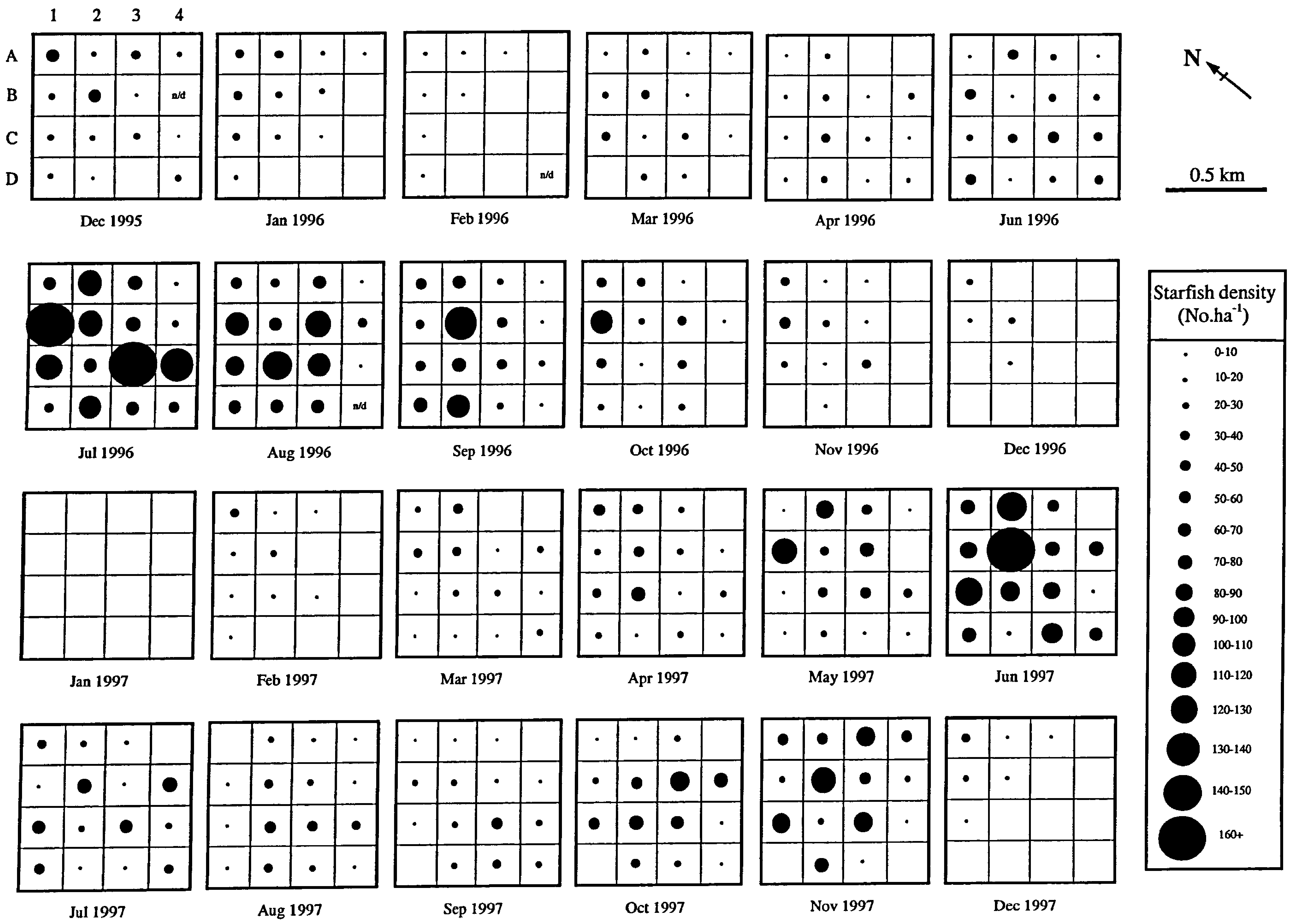
Table 2.1. Beam trawl characteristics and the number of *Astropecten irregularis* collected from Red Wharf Bay during February 1997.

	Weight[1]	Number of		
Trawl	(kg)	extra chains	trawls	Starfish[2]
Standard	35	0	16	17 (10)
Moderate	60	2	8	17 (12)
Heavy	85	4	8	18 (15)

[1] Values include chains and lead weights
[2] Values are mean (±SD)

Although the Lloyd's dispersion index (C) indicated that in Red Wharf Bay *A. irregularis* were highly aggregated in every month (Table 2.2), the value of C showed a general seasonal trend, with the exception of high values in December 1996 which had a very small sample range (2-11). Figure 2.4 shows the spatial distribution and abundance of *A. irregularis* within the study area which showed marked seasonal trends. In general, high starfish densities occurred during the summer months, whilst fewer starfish occurred

Figure 2.4. The spatial distribution of *Astropecten irregularis* within the main study site at Red Wharf Bay from December 1995 to December 1997; no samples were collected in May 1996; n/d denotes no data.


1
2
3
4
A
B
C
D
n/d
Dec 1995
Jan 1996
Feb 1996
Mar 1996
Apr 1996
Jun 1996
N
0.5 km
Jul 1996
Aug 1996
Sep 1996
Oct 1996
Nov 1996
Dec 1996
Jan 1997
Feb 1997
Mar 1997
Apr 1997
May 1997
Jun 1997
Jul 1997
Aug 1997
Sep 1997
Oct 1997
Nov 1997
Dec 1997
Starfish density
(No.ha-1)
0-10
10-20
20-30
30-40
40-50
50-60
60-70
70-80
80-90
90-100
100-110
110-120
120-130
130-140
140-150
160+

during the winter months. The overall pattern of distribution indicates that the starfish population appears to move northwards out of the study site at the beginning of winter and then return to the site towards the end of winter, again from the north. Although speculative, it is suggested that this northerly shift in their distribution is indicative of an offshore winter migration. This pattern of migration is also supported by samples collected from within the shallower more inshore waters, to the south of the study site, where *A. irregularis* were absent from beam trawl samples.

Table 2.2. Lloyd's dispersion index, the abundance of *Astropecten irregularis* (ind.ha^{-1}) and the number of trawls collected each month between December 1995 and December 1997 at the study site in Red Wharf Bay.

		Abundance of *A. irregularis*		
Month	Lloyd's index C	Mean (±SD)	Range	No. of trawls
1995				
December	17.6	29 (22)	5-83	15
1996				
January	31.8	23 (16)	3-43	18
February	45.8	8 (5)	2-16	29
March	29.4	16 (11)	3-35	22
April	20.4	13 (10)	2-33	28
May	-	-	-	-
June	25.4	31 (15)	5-50	17
July	81.2	130 (125)	15-405	36
August	63.6	69 (37)	7-122	17
September	51.9	48 (38)	5-134	19
October	45.5	34 (28)	8-109	23
November	54.2	19 (17)	3-55	16
December	80.1	6 (4)	2-11	16
1997				
January	-	-	-	16
February	35.9	13 (9)	4-31	16
March	24.3	17 (13)	2-40	24
April	36.1	27 (18)	5-75	16
May	52.1	45 (33)	6-109	17
June	62.9	85 (46)	9-194	17
July	52.9	32 (24)	3-70	16
August	42.9	18 (14)	2-41	23
September	41.1	21 (14)	4-58	20
October	38.3	37 (35)	5-75	18
November	53.9	54 (32)	7-108	19
December	46.8	13 (8)	2-21	19

During the summers of 1996 and 1997 and on one occasion in November 1997, high population densities of *A. irregularis* of between 120 and 160ind.ha^{-1} (0.012 and 0.016ind.m^{2}) were recorded within many of the sample plots throughout the study site (see Figure 2.4). The highest densities of starfish within any one plot were recorded in July 1996 (405ind.ha^{-1}; 0.040ind.m^{2}, plot C1) and in June 1997 (194ind.ha^{-1}; 0.019ind.m^{2,} plot C2). In general, following these periods when there were high starfish densities, there was a gradual decline in numbers during the onset of winter. The rate of this decline, however, varied between sample years; for example, following peak densities of *A. irregularis* in July 1996 (see Table 2.3) starfish numbers continued to remain relatively high >130ind.ha^{-1} (0.013ind.m^{2}) until October 1996, whereas in the following year numbers rapidly declined, from a maximum of >160ind.ha^{-1} in June 1997 to <32ind.ha^{-1} by mid-July and these numbers remained low through to October and November 1997, when there was an increase in numbers within the individual plots from >80ind.ha^{-1} (0.080ind.m^{2}) to >120ind.ha^{-1}.

Throughout the study period changes in the seasonal abundance and spatial distribution of *A. irregularis* appeared to follow a similar trend, although, in 1996 the maximum number of starfish occurred approximately one month later than that recorded in 1997; peak starfish densities in 1997 occurred in June, whereas in 1996 they occurred in July; during these months all samples were collected around the same period. This apparent time lag did not appear to coincide with any obvious differences in seawater temperature (see Figure 2.3).

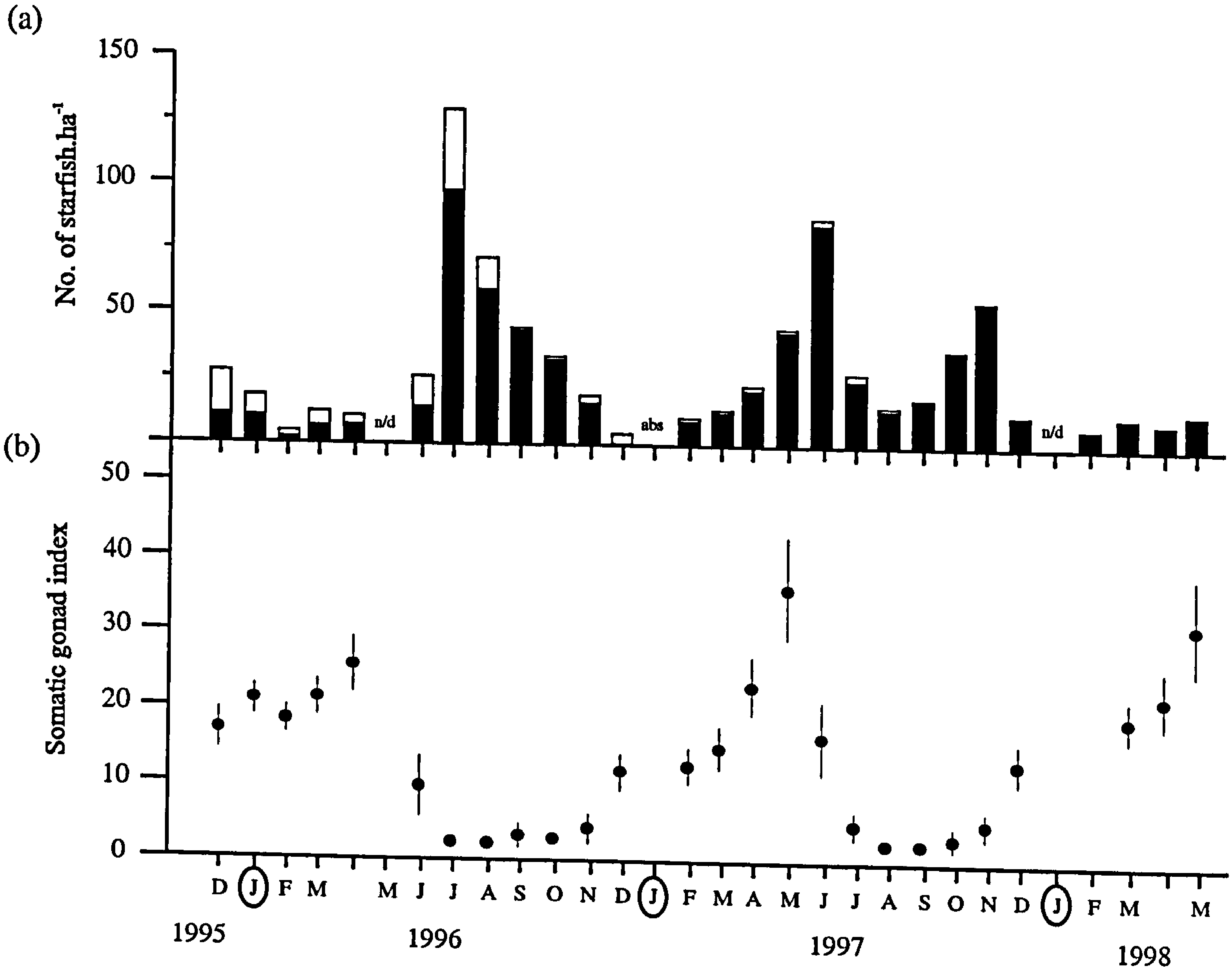
From dissections of a range of starfish sizes, those with arm length <24mm, had little evidence of gonad development, but those larger than 24mm contained ripe gonads (Table 2.3). Spawning in *A. irregularis* is shown by the rapid decline in the gonad somatic index from >25 to <4, in June in both 1996 and 1997 (Figure 2.5). This period coincided not only with an increase in seawater temperatures from ~8°C to >13°C and followed the appearance of proportionally higher densities of large sexually mature individuals within the population. Following spawning the gonad somatic index (<4) remained low until late autumn, thereafter, there was a gradual development in the gonads throughout the winter to early summer (see Figure 2.5). Following the main spawning period a few starfish were found with ripe gonads even as late as August.

Table 2.3. A comparison of the seasonal pattern of the gonad somatic index in large (arm length >24mm: range of mean values 27.7 to 34.6mm) and small (<24mm: range 21.0 to 23.6mm) *Astropecten irregularis* collected from Red Wharf Bay between December 1995 and October 1996.

		Gonad somatic index	
Month	n	Small[1] <24 mm	Large[1] >24mm
1995			
December	26	2.2 (1.9)	17.2 (8.2)
1996			
January	20	2.3 (1.4)	21.7 (4.4)
February	20	2.0 (0.9)	18.2 (5.7)
March	22	2.4 (1.2)	22.5 (7.2)
April	20	3.1 (2.5)	26.9 (10.4)
May	-	n/d	n/d
June	25	2.2 (2.0)	10.8 (4.9)
July	20	0.3 (0.2)	1.3 (0.2)
August	20	0.4 (0.2)	1.2 (0.2)
September	22	0.7 (0.3)	3.3 (2.2)
October	20	2.1 (0.5)	3.0 (1.0)

[1] Values are mean (±SD)

Figure 2.5. (a) The abundance (ind.ha^{-1}) of *Astropecten irregularis* and the percentage (■) of sexually mature starfish (arm length >24mm) and (b) Seasonal variation in the gonad somatic index of *A. irregularis* (>24mm) collected from Red Wharf Bay between December 1995 and May 1998; each value represents the mean ±SD.


(a)
150
100
50
No. of starfish.ha⁻¹
n/d
abs
n/d
(b)
50
40
30
20
10
0
Somatic gonad index
D
J
F
M
M
J
J
A
S
O
N
D
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
M
1995
1996
1997
1998

Changes in the size frequency distributions of *A. irregularis*, examined between October 1995 and May 1998, revealed marked seasonal differences in the growth of both mature (arm length >24mm) and immature starfish (<24mm) (Figure 2.6). In mature starfish increase in size was generally minimal in 1996 and 1997 between the months of April and July, whereas in smaller immature individuals growth was continuous during this period. In the largest cohort of *A. irregularis* the pattern of growth could generally be divided into two phases; 1) a period of almost zero growth where the modal arm length of starfish remained more or less constant at around 22mm, during October 1995 through to April 1996 and 2) a period, thereafter, where the modal arm length increased to approximately 34mm by November 1996. A similar pattern of growth occurred between November 1996 and August 1997 when the modal size class increased from 34mm to 42mm, although the overall growth rate was considerably reduced compared with the previous year. Recruitment of small starfish (modal size class 8 mm) to the population occurred between October and November 1996. By August the following year this cohort had grown to a modal size class of 22mm, but thereafter it was virtually indistinguishable from the main cohort of larger starfish within this population. No recruitment of small starfish was recorded in 1997. The arm length of starfish during the course of this investigation ranged from a minimum of 6mm to a maximum of 76mm. Figure 2.7 illustrates the seasonal growth pattern of *A. irregularis* between October 1995 and May 1998 based on the size frequency analysis using the method of Bhattacharya (1967).

In the laboratory *A. irregularis* (arm length 30-48mm) naturally burrow into the sediment and the depth of burrowing is related to seawater temperature (Figure 2.8a). At

Figure 2.6. Size frequency distributions of *Astropecten irregularis* collected between October 1995 and May 1998 from Red Wharf Bay; frequency data for December 1996 and May 1997 are not presented because the sample size was less than 12 individuals: curves fitted using mean values obtained by the method of Battacharya.

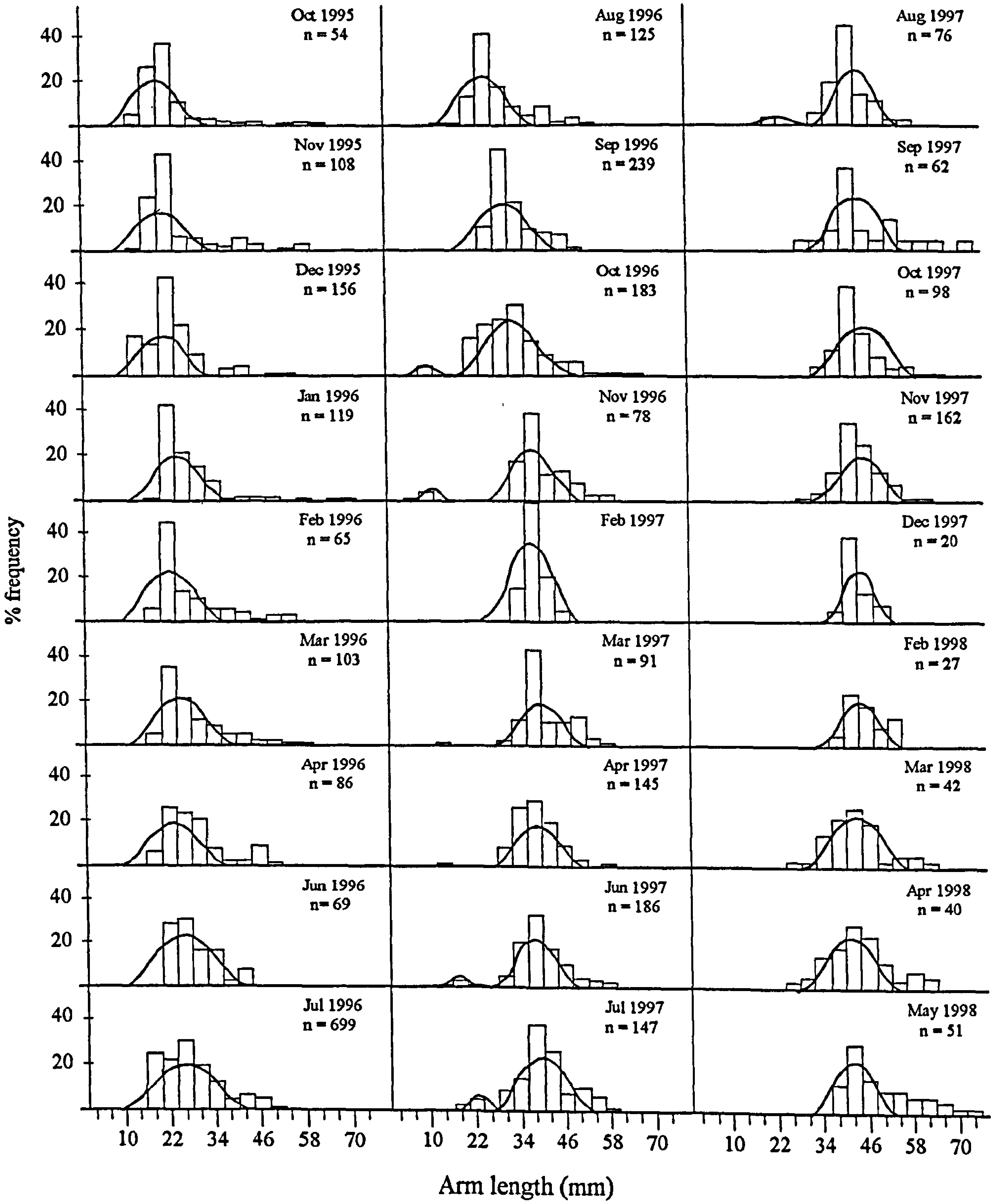

Oct 1995
n = 54
Nov 1995
n = 108
Dec 1995
n = 156
Jan 1996
n = 119
Feb 1996
n = 65
Mar 1996
n = 103
Apr 1996
n = 86
Jun 1996
n= 69
Jul 1996
n = 699
Aug 1996
n = 125
Sep 1996
n = 239
Oct 1996
n = 183
Nov 1996
n = 78
Feb 1997
Mar 1997
n = 91
Apr 1997
n = 145
Jun 1997
n = 186
Jul 1997
n = 147
Aug 1997
n = 76
Sep 1997
n = 62
Oct 1997
n = 98
Nov 1997
n = 162
Dec 1997
n = 20
Feb 1998
n = 27
Mar 1998
n = 42
Apr 1998
n = 40
May 1998
n = 51
40
20
% frequency
10
22
34
46
58
70
Arm length (mm)

Figure 2.7. Increases in the mean arm length of *Astropecten irregularis* collected between October 1995 and May 1998 from Red Wharf Bay; estimated from size frequency data using the method of Bhattacharya.

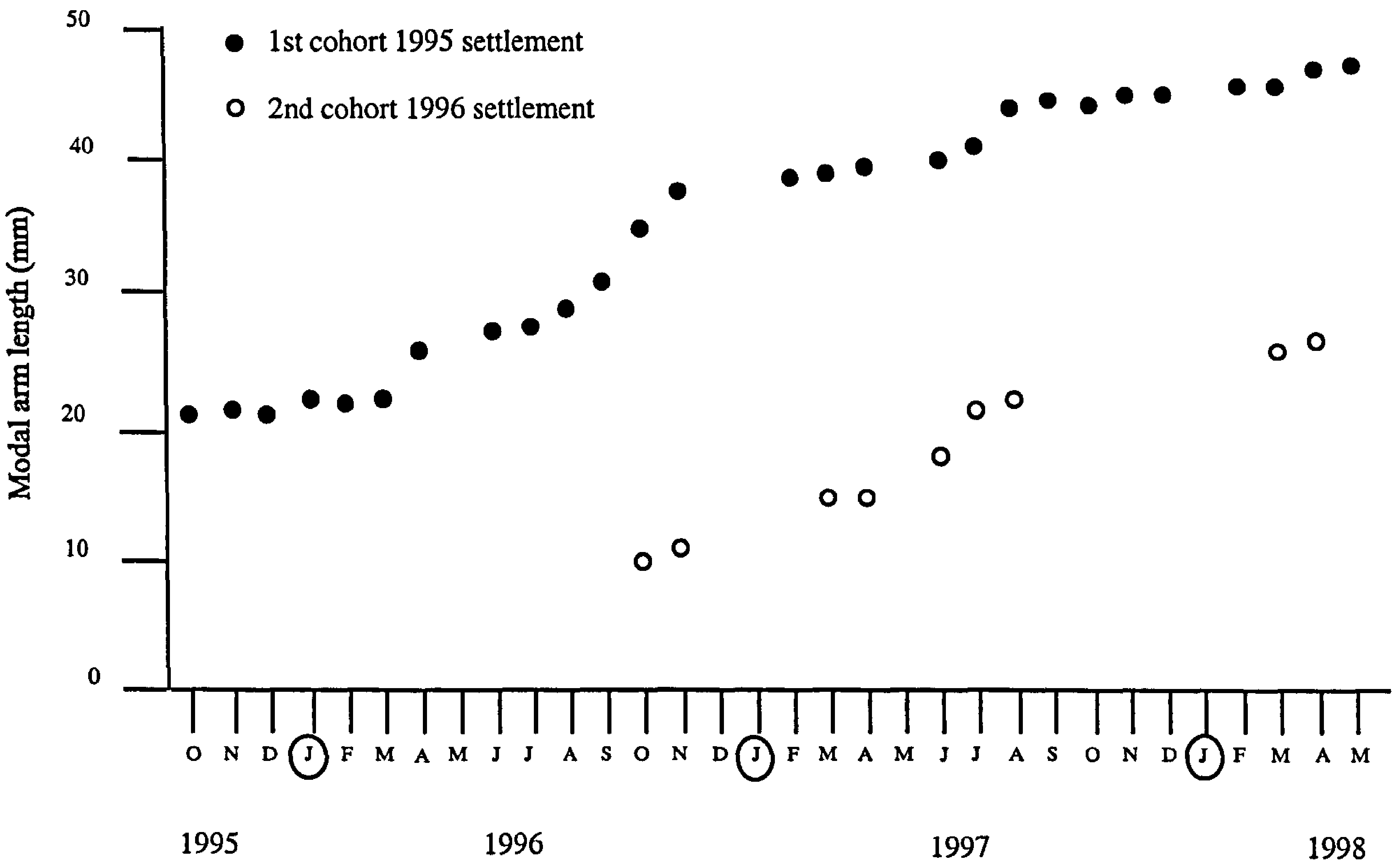
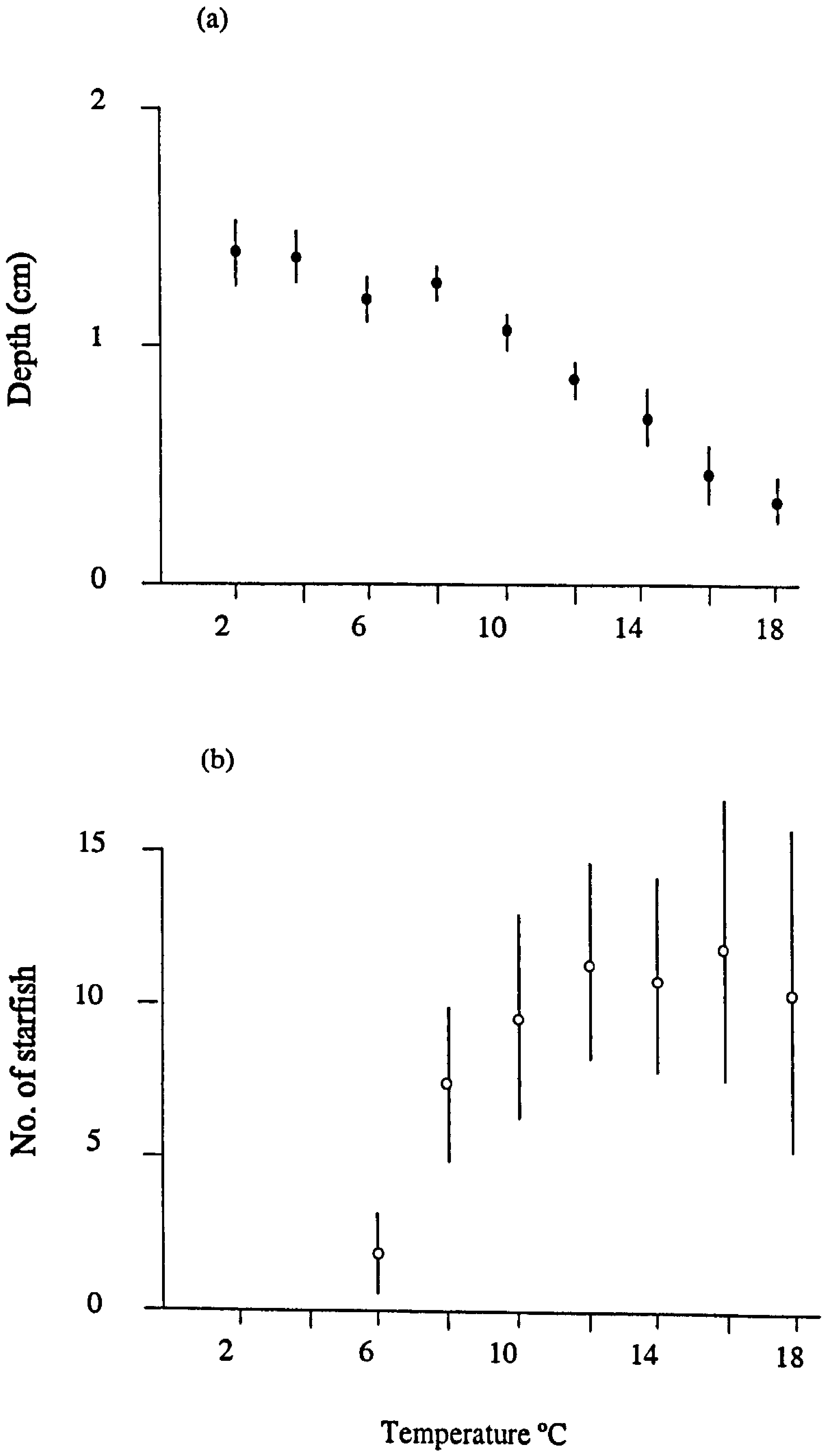

Modal arm length (mm)
50
40
30
20
10
0
● 1st cohort 1995 settlement
○ 2nd cohort 1996 settlement
O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M
1995
1996
1997
1998

Figure 2.8. The relationships between (a) the burrowing depth (-•-) of *Astropecten irregularis* and seawater temperature; (b) The number (–○–) of starfish that were either moving or had moved across the sediment surface during the course of the experiment, and seawater temperature; all values are means (±SD).


(a)
Depth (cm)
2
1
0
2
6
10
14
18
(b)
No. of starfish
15
10
5
0
2
6
10
14
18
Temperature °C

the coldest water temperatures (2°C) starfish burrowed to an average depth of 1.4cm. Overall the starfish only burrow to a shallow depth whatever the temperature, therefore it is unlikely given the depth penetration of the beam trawl (>5cm) that starfish would not have been dredged during the winter. Moreover, observations of the starfish burrowing in the laboratory indicate that the depth to which individuals may burrow may be limited by an apparent requirement to maintain permanent contact with the sediment surface, either by means of an arm tip or an elevated part of the upper central body, presumably to sense the conditions prevailing in the overlying water.

The number of starfish that had either moved or were moving over the sediment surface declined sharply once the seawater temperatures fell below 8°C and all activity ceased at temperatures <4°C (Figure 2.8b). Since the locomotory activity of *A. irregularis* is inhibited by low seawater temperatures (<6°C) this would suggest that starfish would not be able to migrate into deeper waters once temperatures fall below 6°C. The cessation of locomotory activity may explain why some starfish were still caught within the study site during the winter (February 1996) when seawater temperatures were at their lowest (4°C) and were completely absent when seawater temperature was 8°C in January 1997.

2.4. Discussion

In Red Wharf Bay *Astropecten irregularis* exhibited a seasonal pattern of abundance with the highest densities occurring during the summer and the lowest densities or even a complete absence of starfish during winter. Christensen (1970) similarly noted that *A. irregularis* was apparently scarce at his study site in Danish waters during the coldest months of the year and speculated that these starfish 'hibernated' by burrowing deeper in the sediment to avoid the lowest seawater temperatures. The use of a heavier beam trawl during winter failed to reveal significant numbers of starfish which may have burrowed deeper within the study site. Since *A. irregularis* were absent in samples collected from the shallower inshore waters, located to the south of the site, it is suggested that starfish migrate off shore during winter rather than burrowing deeper into the substratum or moving further inshore.

In the laboratory *A. irregularis* demonstrated a tendency to burrow deeper into the sediment as seawater temperatures fell below 8°C. However, if this experiment reflects the depths to which starfish normally burrow in the field, then in Red Wharf Bay *A. irregularis* would not have avoided being dredged during winter. Moreover, starfish always appeared to maintain contact with the sediment surface, either by an arm tip or an elevated part of the upper central body, presumably to maintain contact with and sense the conditions prevailing in the overlying water. Perhaps this need to maintain contact with the overlying water may limit the depth to which starfish burrow. Christensen (1970) noted that under laboratory conditions *A. irregularis* was unable to resurface once it had been placed beneath 4cm of sediment.

Winter migrations into deeper water have previously been documented for other echinoderms including the sand dollar, *Dendraster excentricus*, Morin *et al* (1985). Few previous studies, however, have reported such behaviour in *Astropecten* and most of the information that is available is largely confined to species inhabiting shallower (<10m) inshore waters. In the Mediterranean, for instance, *A. jonstoni* retreats into deeper waters during winter in order to avoid heavy wave surges, even though in these deeper water sites starfish are subjected to predation by *A. aranciacus*, which feeds almost exclusively on *A. jonstoni* (Pabst and Vicentini, 1978). Nojima (1983) noted that during winter *A. latespinosus* migrated into deeper water in order to avoid strong wave surges which could easily dislodge starfish from within the sediment, causing individuals to roll on the surface for some considerable distance. In Red Wharf Bay, strong onshore wave surges increase in frequency during winter (Rees *et al.*, 1977) and it seems likely, therefore, that *A. irregularis* similarly retreats to greater water depths in order to obtain shelter from these conditions.

During the summer months, high population densities of *A. irregularis* in Red Wharf Bay coincided with an increase in the number of sexually mature individuals within the population. Since species of *Astropecten* like other asteroid echinoderms release their gametes into the sea, fertilization will be facilitated when mature starfish congregate at high population densities. Nojima (1982) similarly reported dense spawning assemblages in *A. latespinosus* during the summer months in Japanese waters. Aggregations during spawning in other asteroids *Leptasterias polaris* and *Acanthaster planci*, are known to occur following the release of pheromone-like chemicals into the water column in order to attract other sexually mature individuals. Close proximity of spawning individuals will clearly ensure dense gamete concentrations and, therefore, increase the chance of fertilization (Beach *et al.*, 1975; Hamel and Mercier, 1994).

In Red Wharf Bay during the late autumn of 1997, however, *A. irregularis* were also highly abundant. This apparent second increase in the abundance of starfish coincided with a successful settlement of the bivalve *Fabulina fabula*, *Thracia villosiuscula* and the crustacean *Diastylis rugosa*, species which when available are readily consumed by *A. irregularis* (see Chapter 3). It seems likely, therefore, that this autumnal increase in abundance represents a feeding, rather than a spawning assemblage, a phenomenon well documented for other asteroids (Anger *et al.*, 1977). The Lloyd's dispersion index revealed that *A. irregularis* is highly aggregated throughout the study site in Red Wharf Bay. Similar aggregation patterns are commonly found in other asteroid species. For example, in the eastern Irish Sea, *Asterias rubens* are frequently encountered in dense aggregations within the subtidal zone (Dare, 1982). In this present study the Lloyds dispersion index (C) may not have been the most appropriate index to use as a measure of the spatial distribution of *A. irregularis.* The number of starfish collected within each trawl ranged from 0 to 63, suggesting that this pattern of frequency would be more appropriately described using the mode, which is a more robust statistic than the mean. There are many alternative measures of dispersion and for a review of these measures see Smith *et al*, 1977. Despite this the C index indicated that the Red Wharf Bay population was aggregated throughout the year, changes in the actual values in this index suggest that starfish are nevertheless more highly aggregated during the summer months. In addition to the overall seasonal variation in the abundance of *A. irregularis*, the spatial distribution within the sample area also showed marked seasonal changes with densities ranging from 0 to >160ind.ha^{-1} (0.016ind.m^{2}) in individual sample plots.

During winter there was a gradual disappearance of *A. irregularis* from the southern corner of the study site and a continued presence of starfish within the northern most corner, which strongly suggested that starfish migrated offshore in a northerly direction. The bathymetric profile of the study area showed that seawater depths greatly increase to 28m at the more northerly offshore location and presumably starfish move into these areas during winter to obtain shelter from strong onshore wave surges. The approximate distance from the centre of the study site in Red Wharf Bay to these deeper offshore regions is 2km. Based on the average cruising speed of *A. irregularis* and the total number of hours starfish move over the sediment surface each day in the laboratory (see Chapter 5) a medium-sized starfish traveling continuously in a straight line could, theoretically, complete this distance in ~26 days (~175m.d^{-1}). Field observations, however, show that on average the daily distance crawled by other species of *Astropecten* are considerably shorter. *A. aranciacus* (arm length between 120 and 140mm) for example, covered a maximum of ~23m.d^{-1} (Burla *et al.*, 1972) whereas *A. jonstoni* (50mm) covered only ~5m.d^{-1} (Pabst and Vicentini, 1978). If these distances generally reflect those covered by all species of *Astropecten*, then it seems unlikely that *A. irregularis* could reach areas where seawater depths are noticeably deeper. Several studies have noted that *Asterias forbesi* and *A. rubens* are able to roll like a ball over the substratum during strong tidal currents in order to cover greater distance than those otherwise obtained by crawling (Loosanoff, 1958; Anger *et al.*, 1977). In chapter 5 laboratory observations of *A. irregularis* maintained in a flume under different water velocities have demonstrated that starfish can cart-wheel over the sediment surface up to a distance of 4m without any apparent harm. This would tend to suggest that in the natural environment if *A. irregularis* were to be washed out of the sediment by strong wave surges or tidal currents they would be sufficiently robust to withstand being moved around by these turbulent conditions. Perhaps *A. irregularis* uses an alternative mechanism, like rolling on the sediment surface during periods of strong tidal currents, to cover large distances during migration.

In 1996, the overall abundance of *A. irregularis* throughout the sample plots A1 to D1 remained relatively high compared with 1997. In 1996, however, the gradual decline in the number of starfish to values of less than 20ind.ha^{-1} following peak summer densities (which were associated with spawning assemblages) took approximately five months, whereas, in 1997 this seasonal decline occurred over a period of only two months. Why starfish densities during the summer of 1996 remained noticeably higher and for longer than in 1997 is still unclear, although their occurrence on the sea bed may at least in part be due to the availability of food. During the summer of 1996 there was a heavy settlement of juvenile *Lagis koreni*, a prey species which when present at high densities is readily consumed by *A. irregularis* (see Chapter 3). Alternatively, fewer starfish had returned to the study area following the 1997 winter migration into deeper water. Whilst this might reflect the winter mortality of starfish, larger starfish are generally associated with greater water depths (Freeman *et al.*, 1998).

Relatively few studies have reported on the period of spawning in species of *Astropecten* (Christensen, 1970; Nojima, 1983). *A. irregularis* has been observed to spawn in the laboratory between May and June (Christensen, 1970). Findings from this investigation indicate that *A. irregularis* spawn in Red Wharf Bay during the early summer (May-June) following a rise in seawater temperatures above 12°C. After spawning there is a period when little or no growth in the gonads which remain relatively quiescent until late-summer early-autumn. Thereafter, gonad weight gradually increase throughout the winter and spring months reaching its maximum value by early summer. Nojima (1982) similarly noted that the reproductive development in *A. latespinosus* occurred during the winter and spring months, with a ten-fold increase in the gonad somatic index by the end of this period. The onset of gonad development in *A. irregularis* in Red Wharf Bay coincides with the autumnal settlement of a cohort of *Spisula subtruncata*, which formed an important component of the starfish diet (see Chapter 3). It seems, therefore, that the onset of reproductive development in *A. irregularis* coincides with a period when the preferred and most numerically abundant prey species is available.

Although it has previously been suggested that several environmental factors may be important in initiating the annual reproduction in echinoderms (Boolootian, 1966; Giese and Pearse, 1974; Barnes, 1975) seawater temperature and the availability of food appear to be among the most important (Gonor, 1973a, 1973b; Dehn, 1980a). Rising seawater temperatures, which in Red Wharf Bay coincided with periods when the gonad index of *A. irregularis* was maximal may serve as a cue for spawning.

Laboratory observation on growth has been extensively documented in asteroids (Hancock, 1958; Rasmussen, 1965; Christensen, 1970; Feder, 1970; Nauen, 1978; Barker, 1979; Guillou, 1980) fewer studies, however, have actually established growth in field populations (Crump and Emson, 1978; Nojima, 1982). Laboratory estimates on asteroid growth generally show a greater increase in the size of individuals than that normally expected within field individuals. Christensen (1970) for example, noted that under laboratory conditions, where food is highly abundant, *A. irregularis* can gain an 18-fold weight increase over one year, nearly twice that in starfish collected over the same period from the field. Growth in the Red Wharf Bay population of *A. irregularis* showed a distinct seasonal pattern, in which a period of maximum growth occurred between mid-summer and mid-autumn. A similar pattern has also been described for other temperate asteroids (Christensen, 1970; Nauen, 1978; Barker, 1979). In tropical species such as *Acanthaster planci* and *Linckia laevigata*, (Yamaguchi, 1974) however, there appears to be no such seasonal growth, suggesting that seasonal patterns are a characteristic of only temperate asteroids.

Seasonal variations in the linear growth rate as measured by the arm length of *A. irregularis* varied according to the size and reproductive state of starfish. Larger sexually mature individuals (arm length >24mm) exhibited minimal linear growth during the period of gonad development (November to April) whereas linear growth in smaller starfish mainly immature individuals (<24mm) continued throughout this period. Nojima (1982) also found sexually mature *A. latespinosus* (arm length >25mm) exhibited no obvious increase in size during the period of reproductive development, when energy reserves which might otherwise be used for somatic growth were diverted towards reproduction.

During the main period of growth the modal arm size of the main cohort within the Red Wharf Bay of *A. irregularis* increased from around 22mm in June 1996 to 38mm in November 1996 (see Figure 2.6). In 1997, however, the growth of this same cohort was much slower, so that by November the modal arm size had increased to 42mm. A reduced growth rate as starfish increase in size (age) has also been reported in other asteroids e.g. *Asterina gibbosa* (Crump and Emson, 1978). In October 1996 a small cohort of *A. irregularis* (modal arm size 6mm) entered the Red Wharf Bay population and subsequently grew to reach a modal arm size of 22mm in August 1997, but by September 1997 this cohort could no longer be differentiated clearly from the main population. Since no further recruitment of juveniles to the main starfish population occurred during 1997 and 1998, it is suggested that recruitment in Red Wharf Bay in only intermittent. Christensen (1970) noted that poor recruitment of *A. irregularis* in Øresund over a period of ten years was possibly due to the low levels of suitable available prey, which evidently was a characteristic of that particular location. Moreover, the overall size of *A. irregularis* in the Øresund population appeared to remain considerably smaller in body size than other nearby populations where food was abundant, again generally reflecting the poor growth conditions.

One main characteristic of early growth in asteroids is a rapid development in body size following settlement (Nojima, 1982). Such rapid growth ensures that juvenile starfish reach a size where the risk from predation is greatly reduced (*per. comms.* R. H. Emson). Based on a backwards extrapolation of the rate of the new cohort of *A. irregularis* in the Red Wharf Bay within the first few months (see Figure 2.6), it is estimated that the main population was approximately one year old at the time sampling started in October 1995. Thus, it is estimated that in 1998 the age of the modal size class of *A. irregularis* (arm length 42mm) within the Red Wharf Bay population was ~3.5years. Christensen (1970) noted that under laboratory conditions *A. irregularis* lived up to ~10 years, whereas Nojima (1982) reported that under field conditions *A. latespinosus* survived up to a maximum of 4 years. Generally, no precise method to determine the age of asteroids has been described, although recently growth bands were detected on the ossicle plates of the brittle star, *Ophionotus victoriae*, (Daham and Brey, 1998) which have been successfully used to determine its age, such a method, however, is not possible with asteroids (*per.com.* R. H. Emson).

Christensen (1970) noted that under laboratory conditions the foraging activity of *A. irregularis* was greatly reduced or even stopped altogether at seawater temperatures as low as 4°C. In the present study laboratory experiments support these findings, where the locomotory activity of *A. irregularis* is greatly reduced when seawater temperatures fall below 8°C and ceases altogether below 4°C. Occasionally, in Red Wharf Bay, such low seawater temperatures were recorded during the winter months. Since low seawater temperatures inhibits locomotory activity then once temperatures fall below 4°C starfish would presumably be unable to migrate into deeper water, thus exposing any remaining individuals to an increased risk of being washed ashore during strong onshore wave surges in winter. Rees *et al.*, (1977) has reported large numbers of *A. irregularis* were washed on to the beach at Red Wharf Bay following strong winter storms. The marked reduction in the abundance of starfish during periods of low seawater temperature suggests, therefore, that temperature may be an important factor in regulating starfish density within the study area in Red Wharf Bay.

CHAPTER 3

Seasonal Changes in the Diet and Prey Selection by *Astropecten irregularis*

3.1. Introduction

Few previous studies have investigated the dietary characteristics of *Astropecten irregularis* or have examined the role of this starfish in structuring soft-sediment communities. Hunt (1925) examined the stomach contents of *A. irregularis* from the English Channel and found that although a wide variety of different benthic fauna including crustaceans, echinoderms, polychaetes, foraminiferans and various carrion had been consumed, the most commonly occurring prey items were molluscs. Christensen (1970) similarly found that in Danish waters *A. irregularis* was a highly selective predator feeding mainly on juvenile bivalve molluscs such as *Spisula subtruncata.* Moreover, since *A. irregularis* fed almost exclusively on *S. subtruncata,* which was usually the most numerically abundant prey species within the benthos, Christensen suggested that this important predator shared a similar predator-prey interaction to that previously documented between the intertidal starfish, *Pisaster ochraceus*, and mussels *Mytilus trossulus.* Christensen concluded, therefore, that *A. irregularis* could possibly be regarded as a keystone species as defined by Paine (1969).

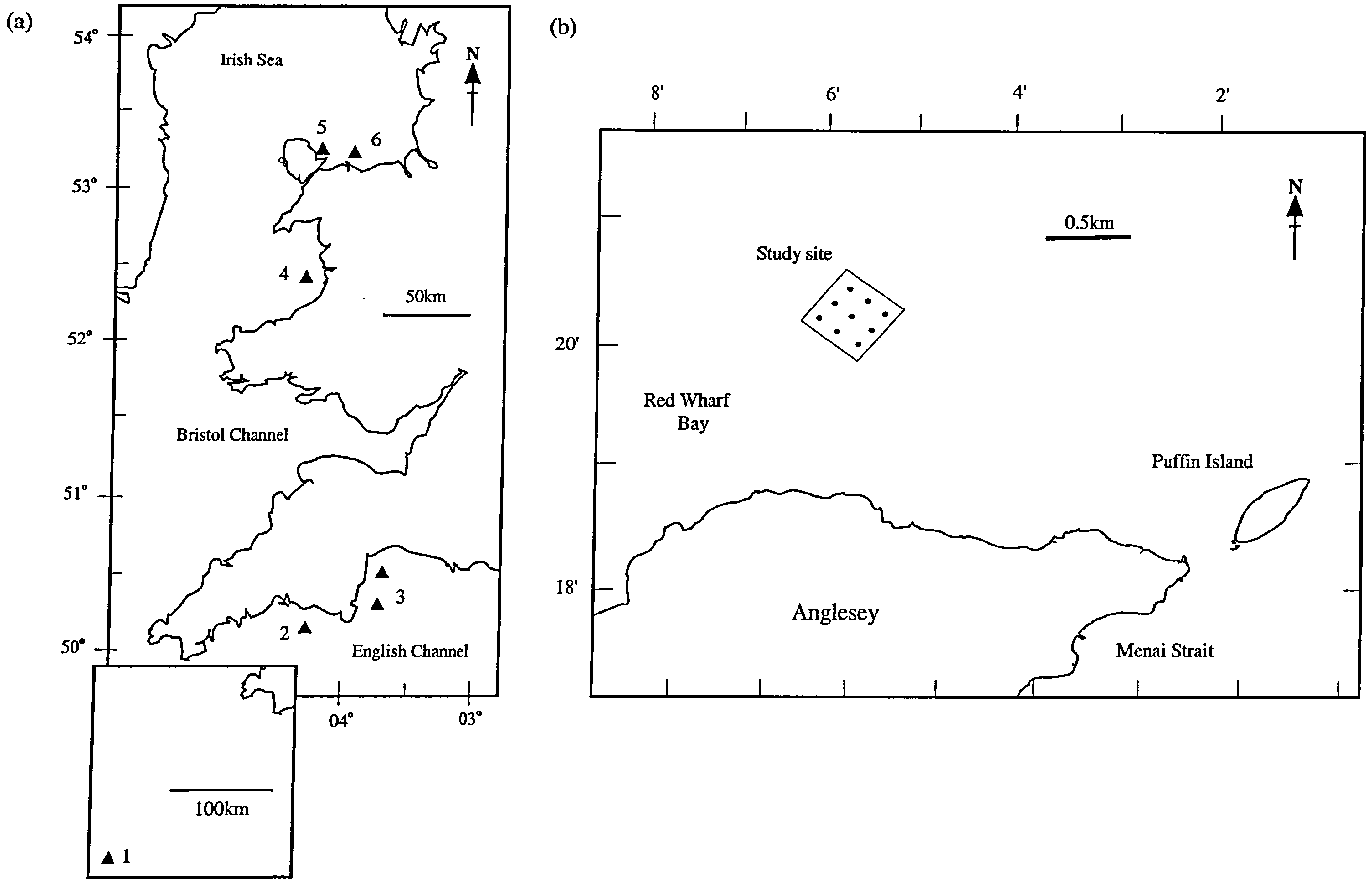
Many other species of *Astropecten* are known to share similar feeding characteristics to *A. irregularis.* Nojima (1989) for example, noted that *A. latespinosus* was a highly selective predator which during the summer months fed mainly on small venerid bivalves, such as *Vermolpa micra*, however, during winter when this bivalve was less abundant the starfish became less-selective and fed on a wider range of prey as well as detrital material from within the sediment. Hyman (1955) noted that *A. articulatus* lacked the capacity for extra-oral digestion and therefore prey species were limited to those which could be ingested whole. Beddingfield and McClintock (1993) on the other hand, showed that when *A. aranciacus* was fed a range of different size classes of prey, it consistently selected the smallest items available. Similar size-selective predation has been reported in several other species of *Astropecten* where the prey consumed were smaller than the mean size of those available within the surrounding benthos (Doi, 1976)

In this study the stomach contents of *A. irregularis* collected from various locations off the southern and western coasts of the British Isles are examined and the seasonal changes in the abundance, biomass and size of prey, and prey selection by *A. irregularis* at a study site in Red Wharf Bay, North Wales are documented.

3.2. Materials and methods

In order to compare the composition of prey within the diet of *Astropecten irregularis* from different geographical locations, samples of starfish were collected from six sites off the southern and western coasts of the British Isles (Figure 3.1a). In July 1995 and during late October - early November 1996 samples of *A. irregularis* were collected from all the southern sites (1-3) using a French dredge or a beam trawl, fitted with a

Figure 3.1. (a) The location of study sites (▲) off the southern and western coasts of the British Isles. Site 1 is ca. 200km south-west of the Scilly Isles; and (b) The location of the main study site (□) in Red Wharf Bay (site 5) North Wales and the general location of nine benthic sampling stations (●).


(a)
54°
53°
52°
51°
50°
04°
03°
Irish Sea
Bristol Channel
English Channel
N
50km
100km
1
2
3
4
5
6
(b)
8'
6'
4'
2'
20'
18'
N
0.5km
Study site
Red Wharf
Bay
Puffin Island
Anglesey
Menai Strait

$5mm^2$ mesh. At all the western sites (4-6) samples of *A. irregularis* were collected using a 2m or 3m beam trawl also fitted with a $5mm^2$ mesh. Collections from sites 4 and 6, however, were made only in March 1997. At the main study site (5) in Red Wharf Bay, North Wales (53°20'50N 04°06'00W) monthly samples of *A. irregularis* were collected between October 1995 and May 1998. The University of Wales Research Vessels the Prince Madog and Sandpebbler were used to tow a single beam trawl at a speed of 1.5 knots for a period of 8mins. The ship's Global Positioning System (GPS) provided the necessary co-ordinates to enable each sample station to be relocated on subsequent visits (see Materials and methods in Chapter 2). Samples of *A. irregularis* were collected only during neap tides and individual starfish were measured to the nearest 0.1mm between the mouth and the tip of the longest arm; they were then subsequently preserved in 5% formalin.

In Cardigan Bay (site 4) Red Wharf Bay (site 5) and Colwyn Bay (site 6) benthic grab samples were collected using a Day grab ($0.1m^2$) at the same time the *A. irregularis* samples were obtained. In Red Wharf Bay a more detailed survey of the benthos was obtained from samples collected on average every two months from nine stations located within the main study site (see Figure 3.1b) between November 1995 and November 1997. On board ship all grab samples were sieved in order to separate coarse shell material and bottom substrate from the benthic fauna, before preservation in 5% formalin. In the laboratory the stomach contents of *A. irregularis*, together with the benthic fauna, were identified, counted and measured to the nearest 0.1mm along their longest axes. Biomass estimates of seven different prey species were obtained from specimens collected locally from a sand bank, removed from benthic grab samples and the stomach contents of starfish, these included four bivalves, *Spisula subtruncata*, *Nucula nitidosa*, *Chamelea gallina* and *Cerastoderma edule*, one gastropod, *Polinices polianus*, one cumacean, *Diastylis rugosa* and one polychaete, *Lagis koreni*. Although a range of different prey size classes (2-15mm) were used to determine biomass estimates, it was not always possible to find a complete range of prey sizes. To obtain a full range of estimates for all prey size classes, the regression of prey dry flesh weight and shell or body length was used to predict weight. Prey were oven dried at 60°C for a period of three days and the dry weights measured to the nearest 0.01mg using a top-loading balance. Biomass estimates of two echinoderm species *Ophiura ophiura* and *Echinocardium cordatum* were obtained from the literature (see Holme, 1953).

Seasonal variations in the diversity of all prey species within the stomachs of *A. irregularis* were expressed using the Shannon index of diversity (H') (see Magurran, 1988). The index is calculated as follows;

$$H' = -\sum_{i=1}^{n} pi \quad \log_2 \quad pi$$

where i = prey species; pi = the proportion of i in the sample, n = total number of species in sample. Although many different prey species were found within the stomachs of *A. irregularis* throughout the study period only a selected number of prey species represent the main seasonal dietary trends in the stomach contents of starfish and are presented in the results section (3.3). The abundance (%) of prey species found in the stomachs of *A. irregularis*, benthic grab samples and a complete list of all species from other study sites off the southern and western waters of the British Isles, including carrion have been tabulated in appendix III, IV and V respectively.

Stomach contents of *A. irregularis* collected between October 1995 and December 1997 from Red Wharf Bay were subjected to multivariate analysis, using the PRIMER analytical package (see Clarke and Warwick, 1994). A cluster analysis using the Bray-Curtis index of similarity and the group-average method of linkage on root-root transformed data was performed on the faunal species present within all monthly samples. Similarities between monthly samples were then identified into seasonal groups and the 2-dimentional relationship between these different groups were investigated using multi-dimensional scaling (MDS). The seasonal relationship between each group, seawater temperature, the abundance and biomass of each prey taxa/species were explored, superimposing these parameters on the appropriate sample co-ordinates provided by the MDS ordination.

'Indicator species' for each group were identified using a similarity of percentages (SIMPER) procedure. This procedure examines the contribution that each species makes to the average similarity within a group as identified by the cluster analysis. Species which are more evenly distributed between similar samples and are more abundant within a group, will contribute to a greater extent to the overall group similarity. For instance, when the abundance of a particular species is consistent throughout the data set, the standard deviation of its contribution is low and the ratio of average contribution/average SD of contribution ($\mathrm{Ave}_{con}/\mathrm{SD}_{con}$) will be high, thereby typifying that group; this contribution is otherwise known as the ‘ratio value’.

To determine the feeding preferences of *A. irregularis*, all fauna found within the stomachs and within benthic grab samples were compared using the Chesson’s (1978) feeding preference index (α). This index has the advantage of being unaffected by the relative abundance of prey species (see Lechowicz, 1982) and is obtained by the equation:

$$\alpha = \frac{In\left[\left(p_i - r_i\right)/p_i\right]}{\sum In\left[\left(p_i - r_i\right)/p_i\right]}$$

where i = prey type; p_i = number of prey in the environment of type i; r_i = number of prey type i in the stomach. When α is > $1/n_i$, and where n_i = the number of different prey types, the feeding preference is significant. The feeding preferences of *A. irregularis* from samples collected during March 1997 from Cardigan Bay (site 4) and Red Wharf Bay (site 5) where seawater depth (15-20m) and substrate composition (sand) are similar, were then compared.

To examine the relationship between starfish and prey size, the maximum prey length of all individual species found in the stomachs of starfish from five size categories, arm length 10-20mm (very small) 20-30mm (small) 30-40mm (medium) 40-50mm (large) and 50-60mm (very large) were recorded. The maximum number of prey found within the stomach contents of starfish from these five size categories was also recorded.

3.3. Results

The main physical characteristics of the six sample sites and the abundance of the major prey taxa found within the stomachs of *Astropecten irregularis* showed marked inter-site variability (summarized in Table 3.1). In general, bivalve prey showed the least amount of variability and accounted for >60% of all prey taxa found in the diet at all sites. Echinoderms (~10-17%) and gastropods (~13-25%) were recorded generally more abundant at the southern sites (1-3) where the sediment was somewhat coarser and seawater depths (30-180m) greater than at the more westerly sites. Crustaceans (~4-14%) and polychaetes (~0-5%) on the other hand, were more abundant at the westerly sites (4-6) where the substrate was mainly sand and seawater depths were much shallower (15-20m).

An examination of the major prey species occurring within the stomachs of *A. irregularis* at sites 1-6 also exhibited a high degree of inter-site variability (Table 3.2). *Parvicardium spp.*, for example, was the most abundant bivalve prey in the diet of starfish collected from the three southern sites, occurring in ~43-70% of all stomachs examined at each site, but was completely absent from those starfish examined in western sites. *Spisula subtruncata* and the crustacean *Diastylis rugosa*, however, were

Table 3.1. The main physical characteristics of the sampling sites and abundance (%) of different prey taxa found within the stomach contents of *Astropecten irregularis* collected from various locations off the southern and western coasts of the British Isles.

Site		Water depth (m)	Sediment	Starfish	Stomach contents (%)[1]				
No.	Location	mean (range)	type	examined	Bivalves	Crustaceans	Echinoderms	Gastropods	Polychaetes
1	Little Sole Bank	135 (80-180)	Shell/gravel	59	75.0	0.6	10.2	13.4	0.8
2	Western Channel	55 (50-60)	Sand shell/gravel	48	62.5	0.3	16.5	20.0	0.7
3	Western Channel	35 (30-40)	Sand	108	60.5	1.3	11.9	25.3	1.0
4	Cardigan Bay	17 (15-20)	Sand	74	65.1	13.6	7.0	10.8	3.5
5	Red Wharf Bay	20 (18-20)	Sand	66	87.4	4.0	5.5	3.1	0.0
6	Colwyn Bay	17 (15-20)	Sand	59	76.8	9.3	1.2	8.0	4.7

[1] Values based on the number of all prey taxa found within those starfish stomachs at each site

Table 3.2. The most abundant (%) prey species found in the stomachs of *Astropecten irregularis* collected from various locations off the southern and western coasts of the British Isles. Samples from Little Sole Bank were collected in July 1995; those from both Western Channel sites during late October-November 1996 and those from Cardigan Bay, Red Wharf Bay and Colwyn Bay in March 1997.

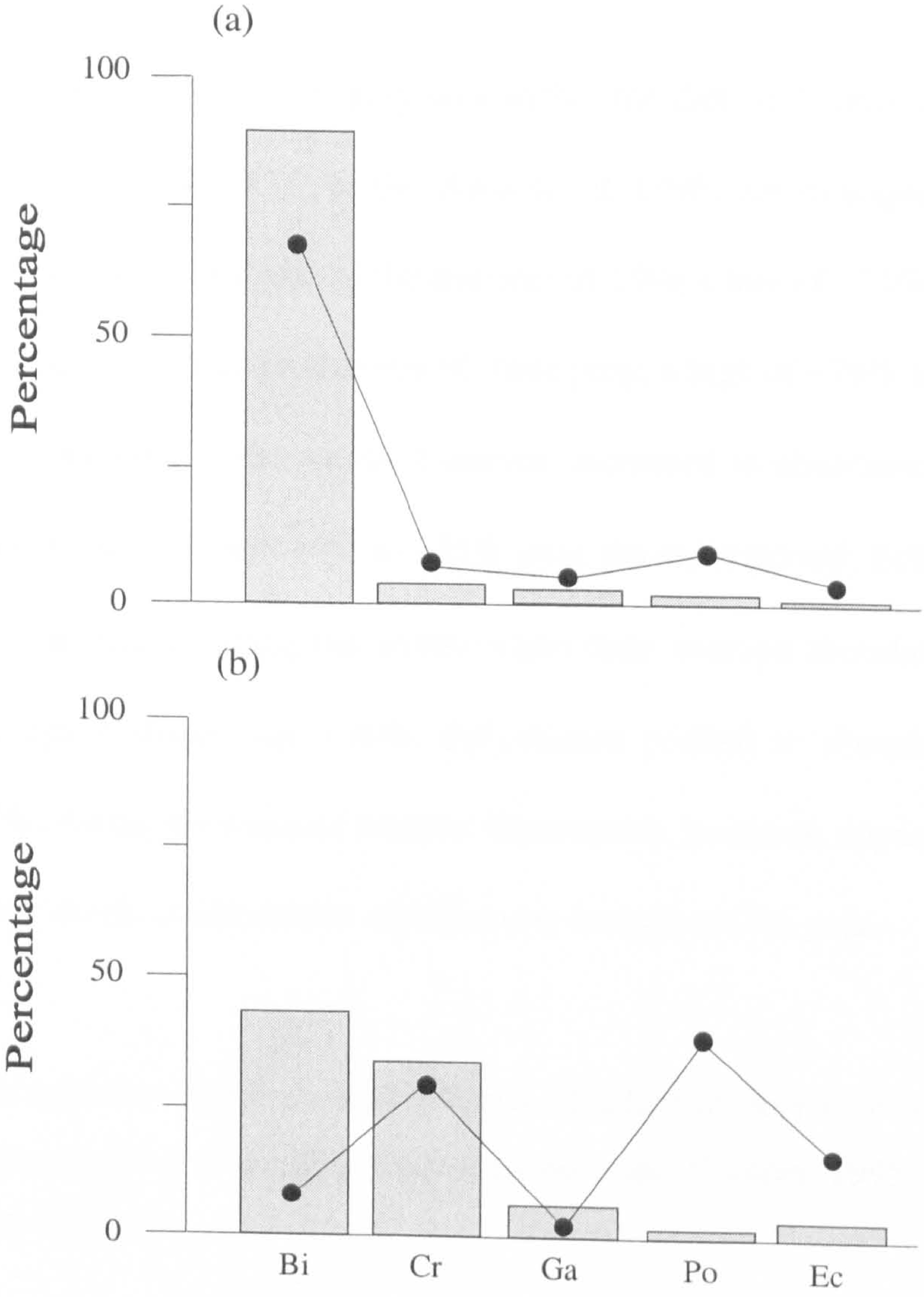
		Prey species (%)[1]							
		Bivalves			Crustaceans	Echinoderms		Gastropods	Polychaetes
Site No.	Location	*Spisula subtruncata*	*Chamellea gallina*	*Parvicardium.* *spp.*	*Diastylis rugosa*	*Echinocardium cordatum*	*Ophiura ophiura*	*Polinices polianus*	*Lagis koreni*
1	Little Sole Bank	0.0	1.2	70.2	0.0	8.2	2.0	5.0	0.0
2	Western Channel	0.0	3.2	50.6	0.0	16.5	0.0	12.0	0.5
3	Western Channel	0.0	1.5	43.2	0.0	11.9	0.0	14.0	1.0
4	Cardigan Bay	2.5	37.5	0.0	7.6	0.0	7.0	2.7	3.5
5	Red Wharf Bay	18.2	7.3	0.0	3.0	0.5	5.0	3.1	0.0
6	Colwyn Bay	17.5	0.0	0.0	5.2	0.0	1.2	3.9	4.7

[1] Values based on the number of all prey taxa found within those starfish stomachs at each site

absent from the southern locations, but occurred at all three western locations, where they ranged between ~3-18 and ~3-8% of the stomach contents, respectively. *Chamelea gallina*, was most abundant prey species in Cardigan Bay (~38%). *Echinocardium cordatum* was the most common echinoderm prey species occurring mainly at sites 1-3 (~8-17%). *Ophiura ophiura* occurred mainly at sites 4 and 5 (~5-7%) whilst the tube living polychaete, *Lagis koreni* was maximally abundant at sites 4 and 6 (~4-5%). The gastropod, *Polinices polianus* was recorded at all six study sites but was most abundant at sites 2 and 3 (12-14%).

The stomach contents of *A. irregularis* collected between October 1995 and September 1996 from the main study site (5) in Red Wharf Bay, broadly reflected the relative abundance, biomass and type of prey found within the surrounding benthos (Figure 3.2a and b). Throughout the year bivalves were the most abundant prey taxa (>90%) found in the stomachs, whereas in the benthos these taxa accounted for ~70% of all available prey. The relative biomass of bivalves was also greater within the diet of starfish (~42%) than in the surrounding benthos (~9%). Although the abundance of crustaceans within the diet of starfish (<5%) and the surrounding benthos (<10%) was low, the biomass of crustaceans within the stomachs (~32%) and the benthos (~28%) was high, suggesting that *A. irregularis* is a selective predator with a particular preference for bivalve and crustacean prey. Polychaetes contributed the most to the overall biomass of all prey taxa found within the benthos (~34%) however, the abundance and biomass of gastropods, polychaetes and echinoderms within the stomachs of starfish (<5%) and with the exception of polychaetes within the benthos (<10%) were generally low.

Figure 3.2. Prey types (□) found within the stomach contents of *Astropecten irregularis* and in benthic grab samples (-•-) collected from Red Wharf Bay between October 1995 and September 1996. (a) The relative abundance of prey, expressed as a percentage of all prey taxa, and (b) The relative biomass; samples were Bi=Bivalves; Cr=Crustaceans; Ga=Gastropods; Po=Polychaetes; Ec=Echinoderms.


(a)
100
50
0
Percentage
(b)
100
50
0
Percentage
Bi
Cr
Ga
Po
Ec

The proportion of different prey taxa within the diet of *A. irregularis* exhibited seasonal variability (Table 3.3). In the Autumn of 1995, for example, bivalve prey reached a maximum of ~96% and by the summer of 1996 a low of ~75%, a trend which was also reflected in the relative biomass of these prey, a high of ~79% in autumn and a low of ~25% in summer. Crustaceans, however, increased in abundance from ~2% to ~14% and their biomass from ~19% to ~51% over the same period. Echinoderms were generally more abundant during the winter when their average abundance was ~6.5% and their average biomass was ~26%. Polychaetes peaked in abundance (8%) and biomass (~17%) during the summer months. Gastropods, however, appeared to maintain consistently low levels of abundance and biomass throughout the year.

Table 3.3. The relative abundance and biomass of different prey taxa found within the stomachs of *Astropecten irregularis* collected between October 1995 and September 1996 from Red Wharf Bay.

	Stomach contents (%)[1]							
	Autumn 95		Winter 96		Spring 96		Summer 96	
Prey type	Abundance	Biomass	Abundance	Biomass	Abundance	Biomass	Abundance	Biomass
Bivalves	96.3	79.0	90.8	41.8	86.7	37.7	74.7	25.0
Crustaceans	1.5	18.6	1.5	31.7	6.7	47.3	14.3	50.8
Echinoderms	0.3	0.2	6.4	25.6	4.1	11.4	0.9	3.6
Gastropods	1.8	1.5	1.3	0.9	2.2	3.6	2.1	3.7
Polychaetes	0.1	0.7	0.0	0.0	0.3	0.0	8.0	16.9

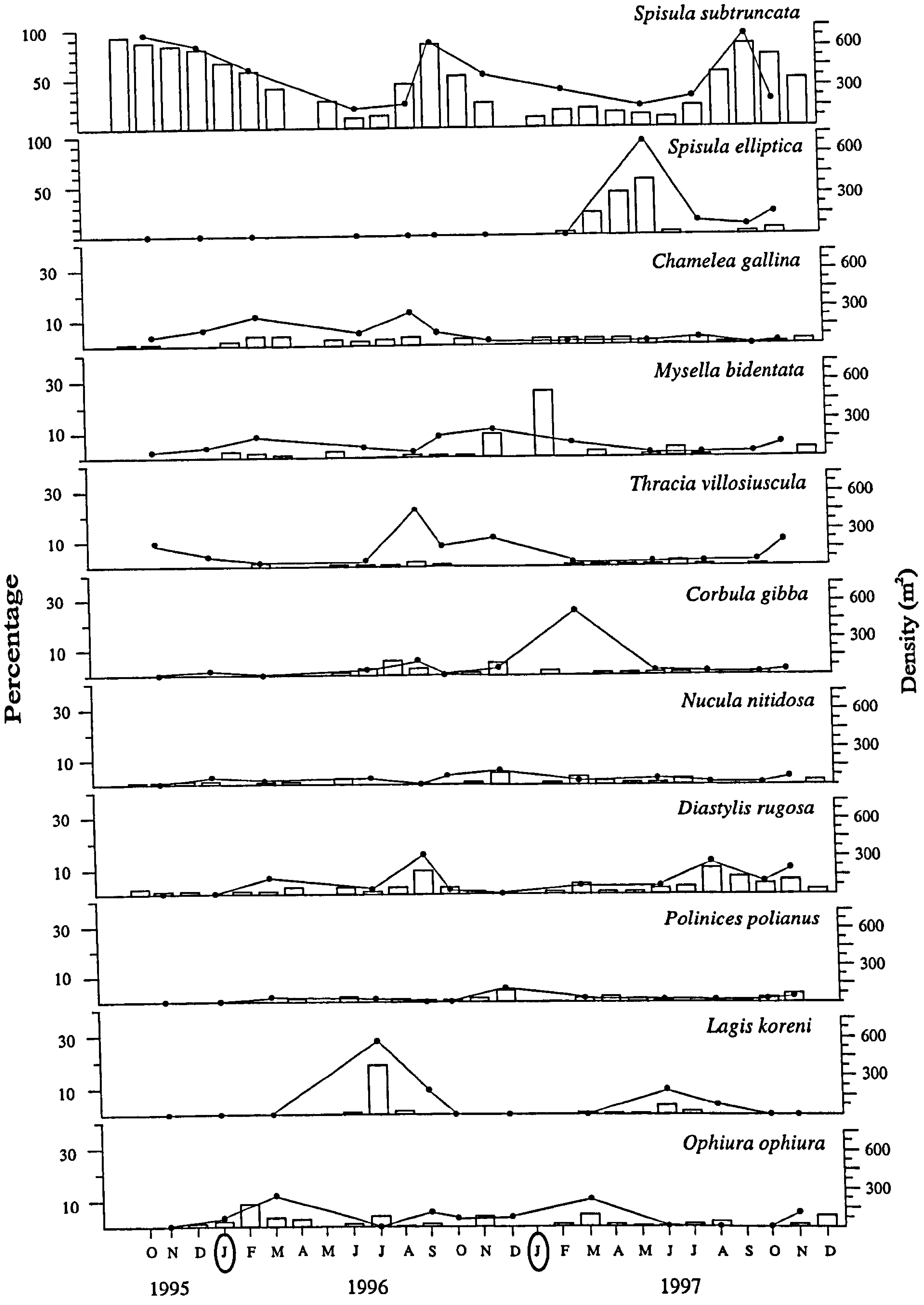
[1] Denotes pooled values for all prey taxa found in starfish stomachs during each season

The abundance of different prey species in the stomachs of *A. irregularis* and in benthic grab samples collected from Red Wharf Bay between October 1995 and

December 1997, showed marked seasonal patterns (Figure 3.3). Numerically the most abundant prey species was *S. subtruncata*, which broadly reflected its availability within the surrounding benthos. For instance, during the autumn months, when newly settled juvenile *S. subtruncata* were recorded, they account for >90% of the diet, indicating that during this period *S. subtruncata* is heavily predated by *A. irregularis*. Following this period, however, the abundance of *S. subtruncata* within the benthos gradually declined from ~700ind.m^2 in October 1995 to ~90ind.m^2 in July 1996. This trend was also reflected in the diet of the starfish, where the abundance of *S. subtruncata* declined from around 96% to <20% of all prey species over the same period. It is suggested, therefore, that *A. irregularis* feeds almost exclusively on *S. subtruncata* whenever this prey species is abundant in the benthos, and that the predation of this particular species will continue, even when prey population densities are relatively low. During spring 1997, however, when the abundance of *S. subtruncata* within the benthos was low, a settlement of juvenile *S. elliptica*, a similarly desirable prey species of *A. irregularis* was readily consumed accounting for >60% of the diet in June 1997.

A. irregularis does not always consume the most numerically abundant prey, since the bivalve *Thracia phaseolina* appeared to form only a small part of the starfish diet even though juveniles of this prey species were abundant in the benthos especially during September 1996. During this same period a settlement of juvenile *D. rugosa* also occurred and, presumably because this small crustacean is a more desirable prey species to *A. irregularis* than *T. phaseolina*, it was readily consumed. In winter 1997 a heavy settlement of juvenile *Corbula gibba* was recorded yet this bivalve was only poorly represented in the diet of *A. irregularis*. However, during the winter period starfish

Figure 3.3. The seasonal abundance of different prey species (□) within the stomach contents of *Astropecten irregularis* and in benthic grab samples (●) collected between October 1995 and December 1997 from Red Wharf Bay; percentage data based on all prey species found in the diet of starfish each month.


Spisula subtruncata
Spisula elliptica
Chamelea gallina
Mysella bidentata
Thracia villosiuscula
Corbula gibba
Nucula nitidosa
Diastylis rugosa
Polinices polianus
Lagis koreni
Ophiura ophiura
Percentage
Density (m^2)
100
50
30
10
600
300
O N D J F M A M J J A S O N D J F M A M J J A S O N D
1995
1996
1997

feeding rates are greatly reduced together with the migration of the starfish population out of the study site (see Chapter 2). In mid-summer 1996 a heavy settlement of *L. koreni*, a sedentary polychaete, was recorded and these were readily consumed by *A. irregularis*, accounting for ~15% of the diet during July 1996. However, during the summer of 1997, when another settlement of *L. koreni* occurred, these were not consumed to the same extent as in 1996 and accounted for <6% of the starfish diet. This lower level of *L. koreni* consumption coincided with a recent settlement of juvenile *S. elliptica*, a prey species preferred over *L. koreni*, and subsequently this species was more heavily predated.

Throughout the entire study period a wide range of different prey species were regularly recorded in the stomachs of *A. irregularis*. Although these species included the bivalves *Chamelea gallina* and *Nucula nitidosa* and the gastropod *Polinices polianus*, these species occurred only at a relatively low level in the benthos as well as in the diet of the starfish. The presence of other prey species or fragments of various prey items were occasionally found within the stomachs of *A. irregularis*. These included foraminiferans, shrimps, juvenile fish, hydrozoans, nemerteans, bryozoans, sipunculans, shell fragments, stones and on one occasion an areneid (spider) (see Appendix IV). Many of these organisms were, therefore, presumably consumed either because they were attached to the outer shell of a 'preferred' prey item or because they were scavenged.

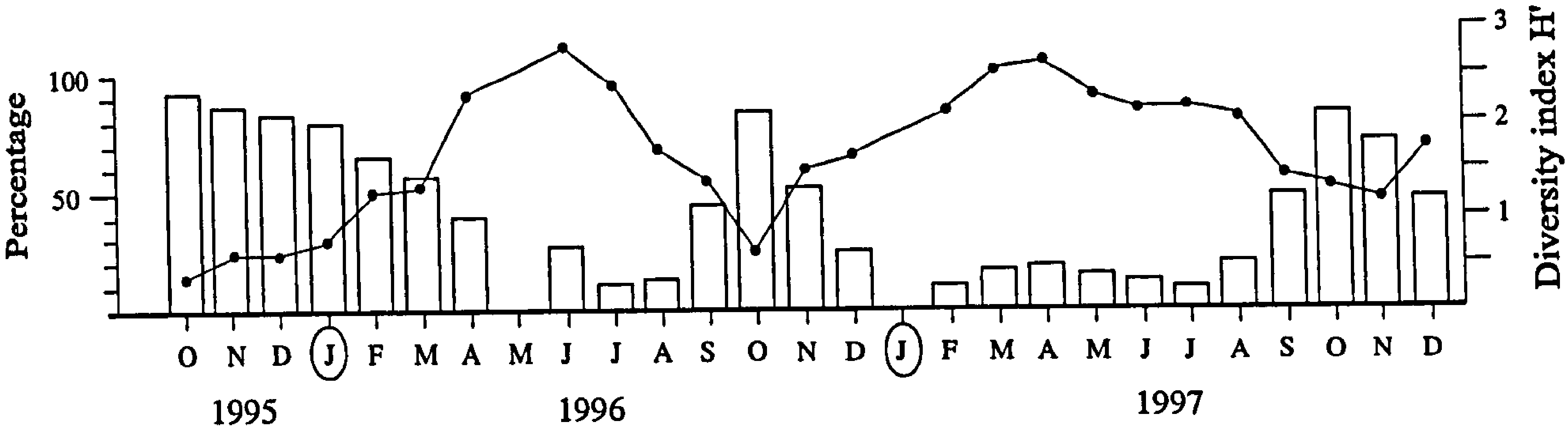
As the abundance of *S. subtruncata* in the diet of starfish declines during the autumn each year, the diversity of other prey species within the stomach contents of *A.*

irregularis increases, demonstrating that starfish feed on *S. subtruncata* preferentially whenever this species is present in the benthos (Figure 3.4). The Shannon's diversity index H', for example, increased from <0.5 during autumn 1995, a period when *S. subtruncata* was highly abundant within the benthos, to ~3.0 during the summer of 1996, when this prey species was scarce. A similar seasonal trend occurred in 1997 suggesting, therefore, that when *S. subtruncata* declines in abundance within the benthos other presumably less desirable prey are consumed; this trend is even more exaggerated when other 'preferred' prey e.g. *D. rugosa* or *S. elliptica* are unavailable. The overall abundance of all prey within the stomachs of *A. irregularis* declined from a high of ~55ind.stomach^{-1} in October 1995 to a low of <2ind.stomach^{-1} in February 1996, a period during which seawater temperatures declined from 12°C to 4°C (Figure 3.5a); this pattern was reflected over the same period in 1997. Figure 3.5b shows the occurrence of starfish with empty stomachs and indicates that these occur mainly during the colder winter months.

Cluster analysis and subsequent multi-dimensional scaling identified three major seasonal groups of prey species based on the monthly stomach content samples of *A. irregularis* collected between October 1995 to December 1997 from Red Wharf Bay (Figure 3.6a). These groups broadly represented three seasonal periods spring/summer (group 1) autumn (group 2) and winter (group 3). However, because seasonal trends in the abundance of particular prey species had a tendency to occur either later or earlier in each sample year not all the sample dates conform precisely to these three seasonal groupings. For example, December 1996 did not conform to any of the three groups, December 1995 January 1996 and August 1997 appeared within the autumn group,

Figure 3.4. Seasonal abundance of the dominant prey *Spisula subtruncata* in the stomach contents of *Astropecten irregularis* (□) and changes in the Shannon's diversity index H' of all other prey species (-●-); data collected between October 1995 and December 1997 from Red Wharf Bay.

Figure 3.5. (a) The average number of prey items (□+SD) within the stomach contents of *Astropecten irregularis* and seawater temperature (-●-) (b) The proportion of empty stomachs (□); n/d denotes no data; abs denotes starfish absent.


Percentage
100
50
Diversity index H'
3
2
1
O N D J F M A M J J A S O N D J F M A M J J A S O N D
1995
1996
1997

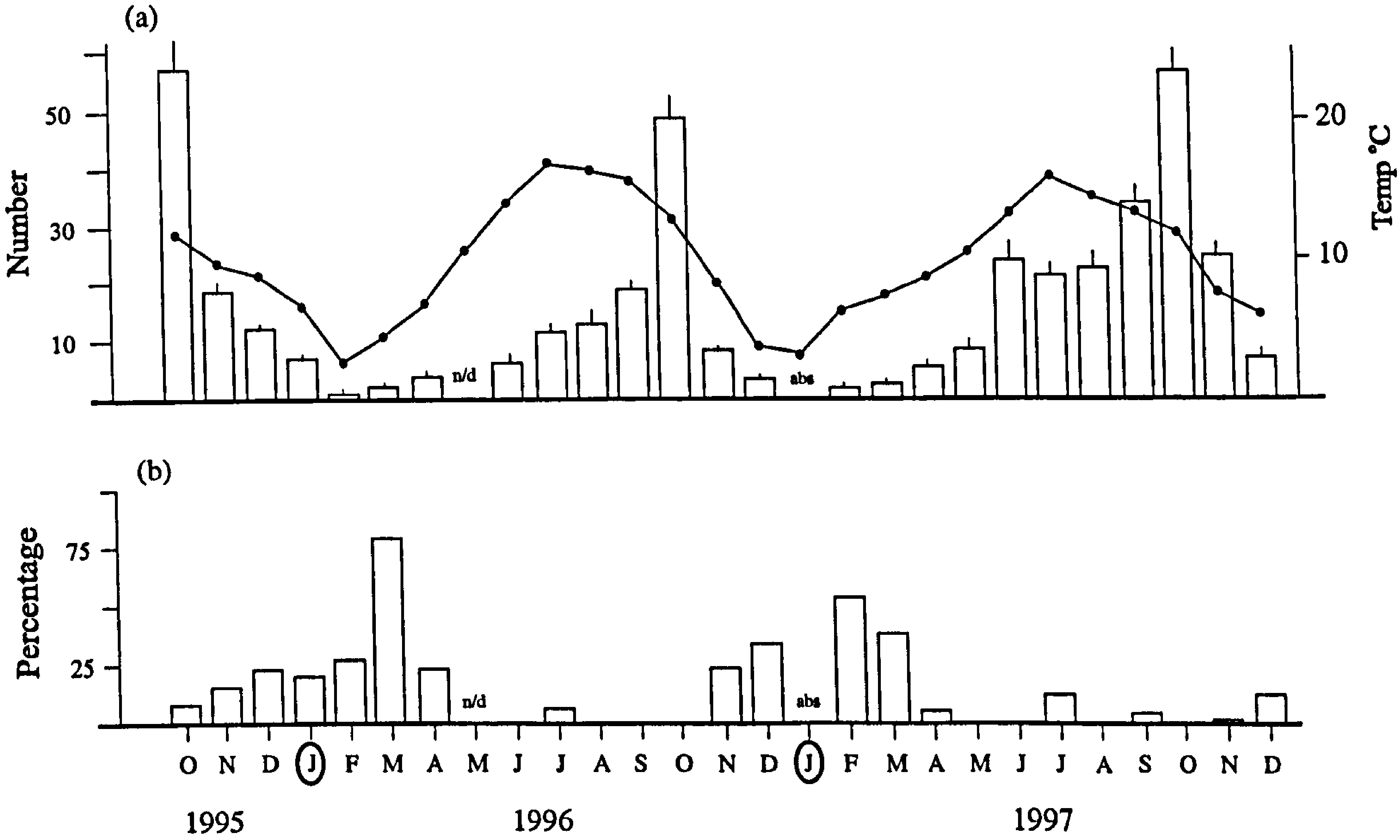
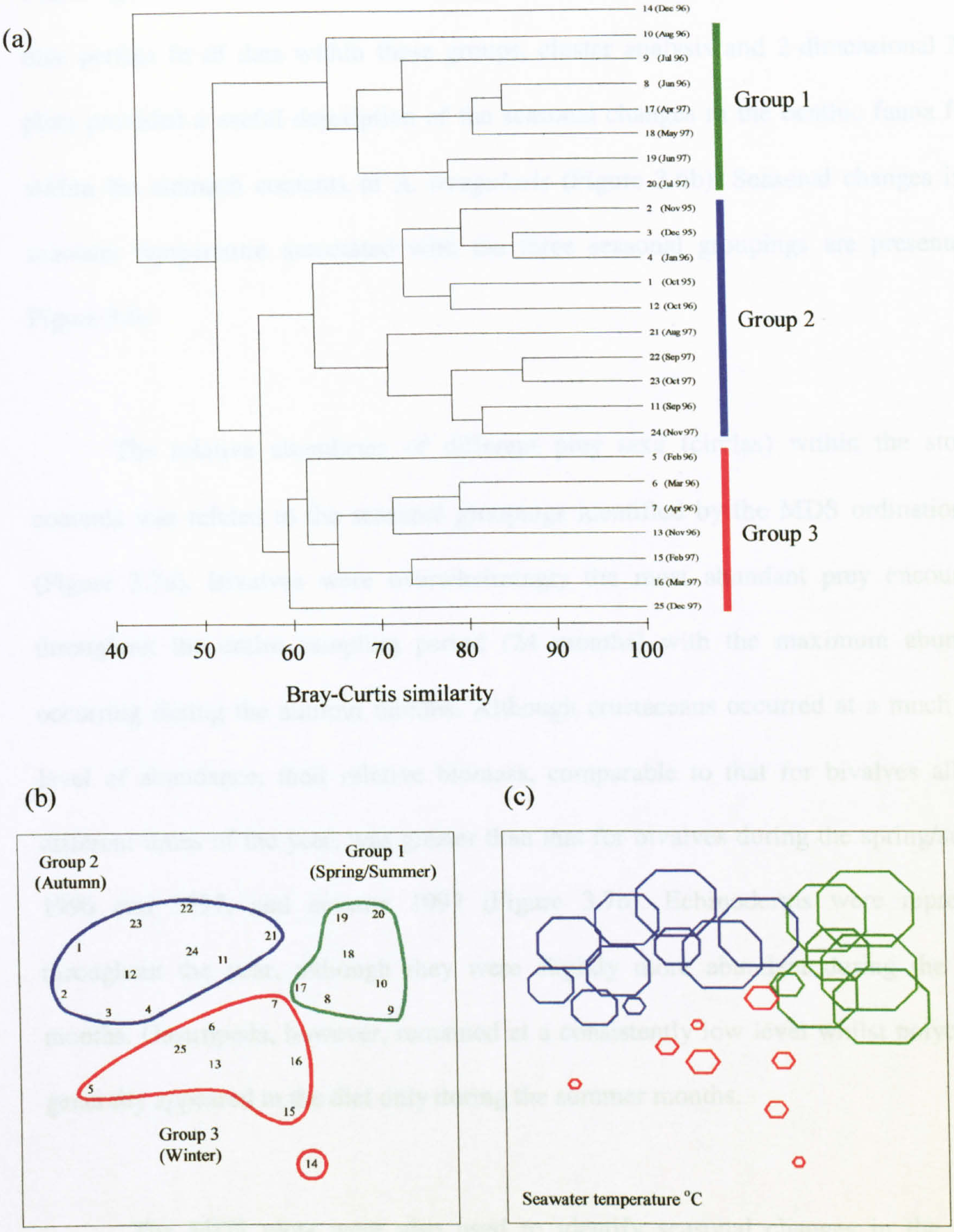

(a)
Number
50
30
10
Temp °C
20
10
n/d
abs
(b)
Percentage
75
25
n/d
abs
O N D J F M A M J J A S O N D J F M A M J J A S O N D
1995
1996
1997

Figure 3.6. (a) Cluster diagram of the stomach contents of *Astropecten irregularis* collected between October 1995 and December 1997 from Red Wharf Bay. Each month has a numerical code from 1 (October 1995) to 25 (December 1997); coloured bars represent three different groups at 63% similarity (b) A 2-dimensional MDS plot of the same monthly samples and the subsequent three groups which approximate into seasons; colours designate these seasonal groups, spring/summer (green, group 1) autumn (blue, group 2) and winter (red, group 3) (c) Seasonal changes in seawater temperature; coloured octagons denotes the relative magnitude in temperature for each seasonal group.


(a)
14 (Dec 96)
10 (Aug 96)
9 (Jul 96)
8 (Jun 96)
17 (Apr 97)
18 (May 97)
19 (Jun 97)
20 (Jul 97)
2 (Nov 95)
3 (Dec 95)
4 (Jan 96)
1 (Oct 95)
12 (Oct 96)
21 (Aug 97)
22 (Sep 97)
23 (Oct 97)
11 (Sep 96)
24 (Nov 97)
5 (Feb 96)
6 (Mar 96)
7 (Apr 96)
13 (Nov 96)
15 (Feb 97)
16 (Mar 97)
25 (Dec 97)
Group 1
Group 2
Group 3
40
50
60
70
80
90
100
Bray-Curtis similarity
(b)
(c)
Group 2
(Autumn)
Group 1
(Spring/Summer)
Group 3
(Winter)
22
23
21
1
24
11
12
2
3
4
19
20
18
17
8
10
9
7
6
25
13
16
5
15
14
Seawater temperature °C

whilst April 1996 and November 1996 appeared within the winter group. Despite a less than perfect fit of data within these groups, cluster analysis and 2-dimensional MDS plots provided a useful description of the seasonal changes in the benthic fauna found within the stomach contents of *A. irregularis* (Figure 3.6b). Seasonal changes in the seawater temperature associated with the three seasonal groupings are presented in Figure 3.6c.

The relative abundance of different prey taxa (circles) within the stomach contents was related to the seasonal groupings identified by the MDS ordination plot (Figure 3.7a). Bivalves were overwhelmingly the most abundant prey encountered throughout the entire sampling period (24 months) with the maximum abundance occurring during the autumn months. Although crustaceans occurred at a much lower level of abundance, their relative biomass, comparable to that for bivalves albeit at different times of the year, was greater than that for bivalves during the spring/summer 1996 and 1997, and autumn 1997 (Figure 3.7b). Echinoderms were represented throughout the year, although they were slightly more abundant during the winter months. Gastropods, however, remained at a consistently low level whilst polychaetes, generally appeared in the diet only during the summer months.

The MDS plots were also used to identify seasonal changes in the relative numerical abundance of different prey species in the diet of *A. irregularis* (circles) (Figure 3.8a-l). *S. subtruncata* was the most abundant prey species and clearly dominated the stomach contents during the autumn months when settlement of this species occurred. Other species such *Fabulina fabula, Astarte trianglaris, Morella*

Figure 3.7. (a) The relative abundance (coloured circles) of different prey taxa within the stomach contents of *Astropecten irregularis* related to the MDS ordination. (b) The relative biomass (coloured circles) of different prey types within the stomach contents of *A. irregularis*. Samples were collected between October 1995 and December 1998 from Red Wharf Bay (pooled data); coloured circles denote the seasonal groups corresponding to the 2-dimensional MDS plot, spring/summer (green, group 1) autumn (blue, group 2) and winter (red, group 3); circle size represents relative abundance.

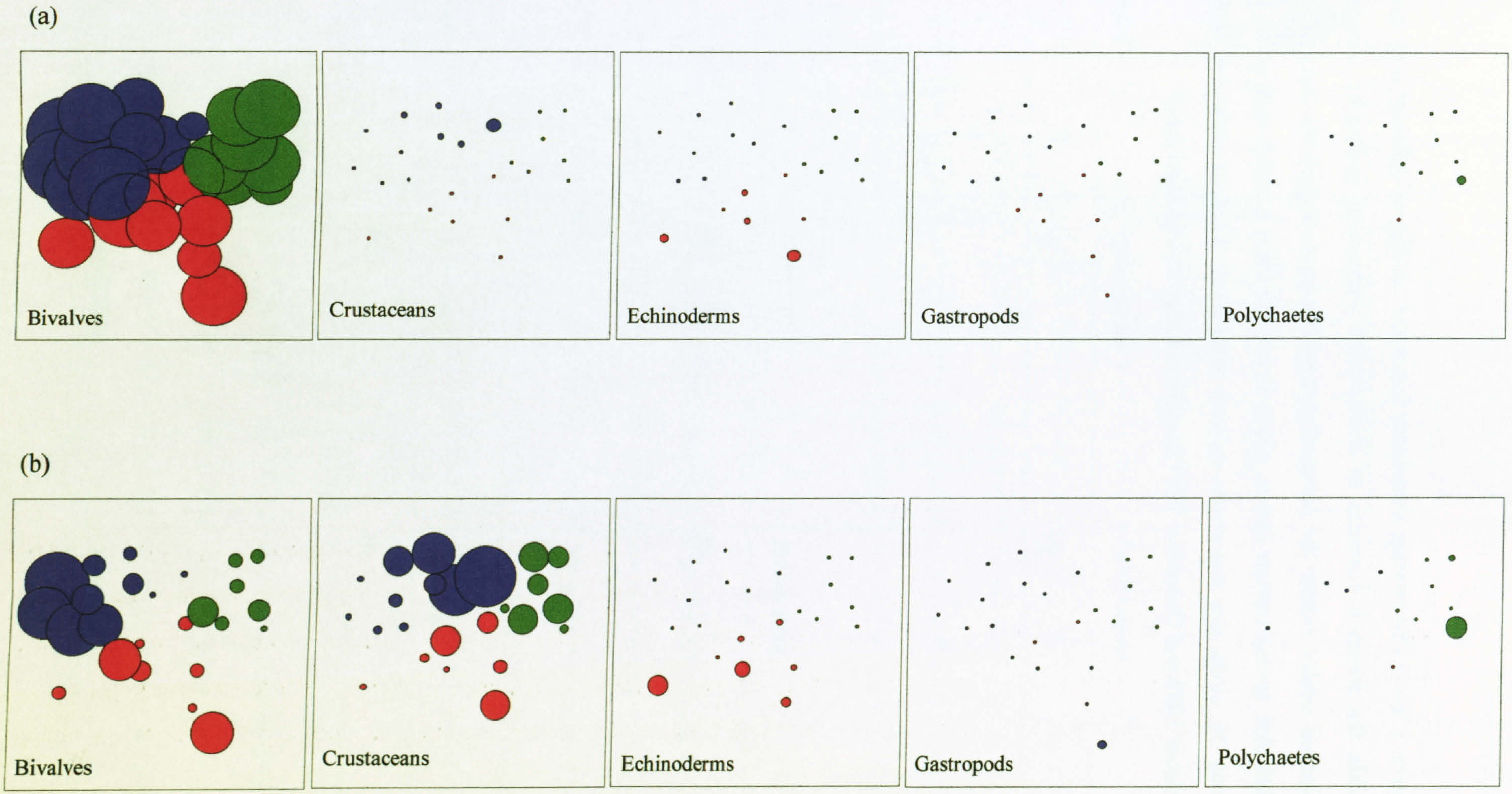
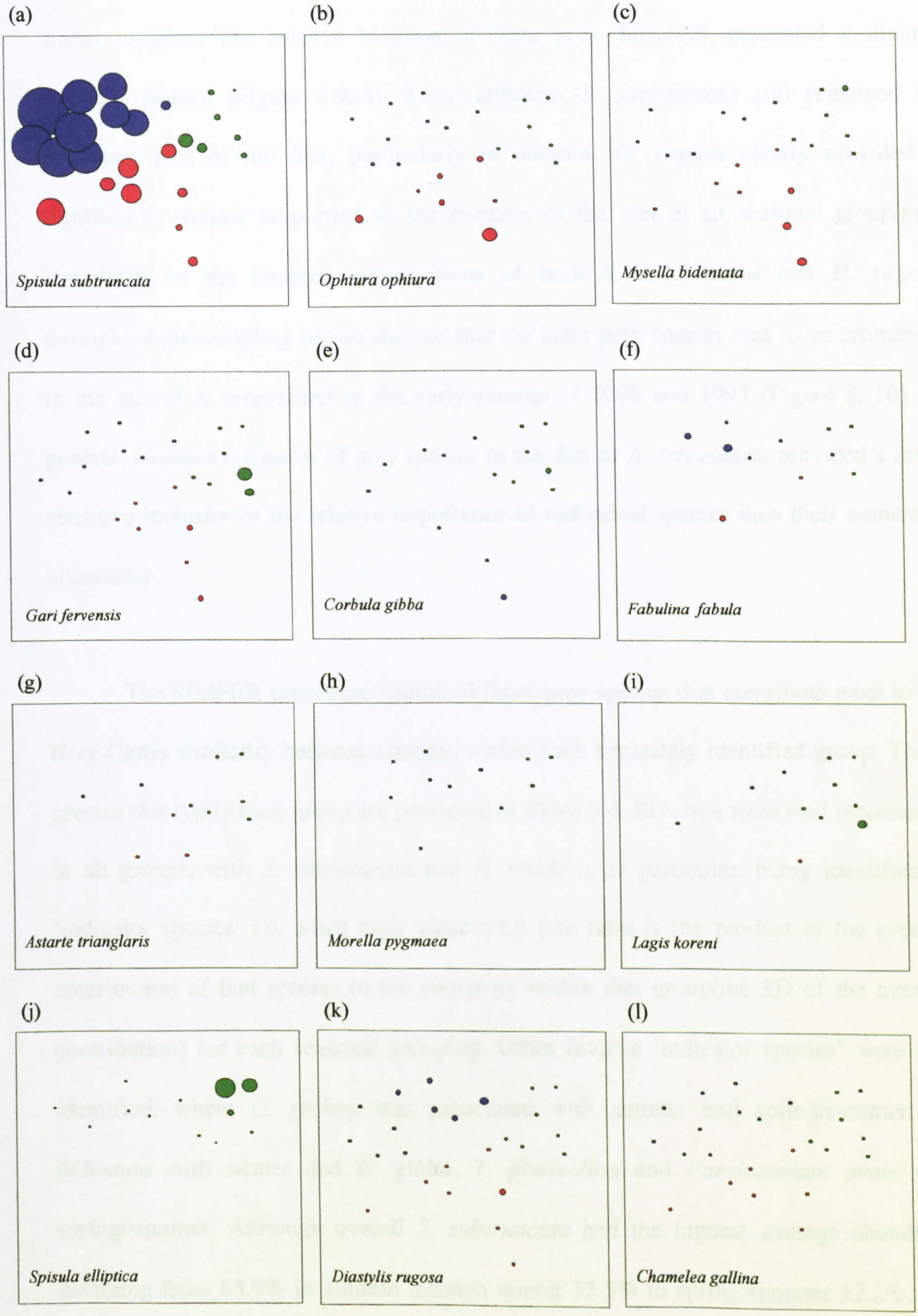

(a)
Bivalves
Crustaceans
Echinoderms
Gastropods
Polychaetes
(b)
Bivalves
Crustaceans
Echinoderms
Gastropods
Polychaetes

Figure 3.8(a-l).The relative abundance (coloured circles) of different prey species within the stomach contents of *Astropecten irregularis* (coloured octogons); coloured circles denote the seasonal groups corresponding to the 2-dimensional MDS plot, spring/summer (green, group 1) autumn (blue, group 2) and winter (red, group 3); circle size represents relative abundance. Samples collected between October 1995 and December 1997 from Red Wharf Bay (pooled data)


(a)
Spisula subtruncata
(b)
Ophiura ophiura
(c)
Mysella bidentata
(d)
Gari fervensis
(e)
Corbula gibba
(f)
Fabulina fabula
(g)
Astarte trianglaris
(h)
Morella pygmaea
(i)
Lagis koreni
(j)
Spisula elliptica
(k)
Diastylis rugosa
(l)
Chamelea gallina

pygmaea, *L. koreni* and *S. elliptica* were present in the diet mainly in the spring/summer months, whereas *O. ophiura* and *Mysella bidentata* were rather more abundant in the winter samples. The relative biomass of these prey, however, presented a slightly different picture (Figure 3.9a-l). Thus, although *S. subtruncata* still remained an important part of the diet, particularly in autumn, *D. rugosa* clearly provided a significantly greater proportion of the biomass of the diet in all seasonal groupings. Variability in the biomass contributions of both *S. subtruncata* and *D. rugosa* throughout the sampling period showed that the latter prey species was more prominent in the diet of *A. irregularis* in the early-autumn of 1998 and 1997 (Figure 3. 10). In general, biomass estimates of prey species in the diet of *A. irregularis* provided a more sensitive indicator of the relative importance of individual species than their numerical abundance.

The SIMPER procedure identified those prey species that contribute most to the Bray-Curtis similarity between samples within each separately identified group. Those species that typify each group are presented in Table 3.4. Bivalves were well represented in all groups, with *S. subtruncata* and *N. nitidosa*, in particular, being identified as 'indicator species' i.e. when ratio value >1.5 (the ratio is the product of the average contribution of that species to the similarity within that group/the SD of the average contribution) for each seasonal grouping. Other bivalve 'indicator species' were also identified, where *C. gallina* was associated with autumn and spring/summer; *M. bidentata* with winter and *C. gibba*, *T. phaseolina* and *Parvicardium ovale* with spring/summer. Although overall *S. subtruncata* had the highest average abundance declining from 63.9% in autumn through winter 32.5% to spring/summer 12.2%. The

Figure 3.9(a-l). The relative biomass (coloured circles) of different prey species within the stomach contents of *Astropecten irregularis* (coloured octogons); coloured circles denote the seasonal groups corresponding to the 2-dimensional MDS plot, spring/summer (green, group 1) autumn (blue, group 2) and winter (red, group 3); circle size represents relative biomass. Samples collected between October 1995 and December 1997 from Red Wharf Bay (pooled data).

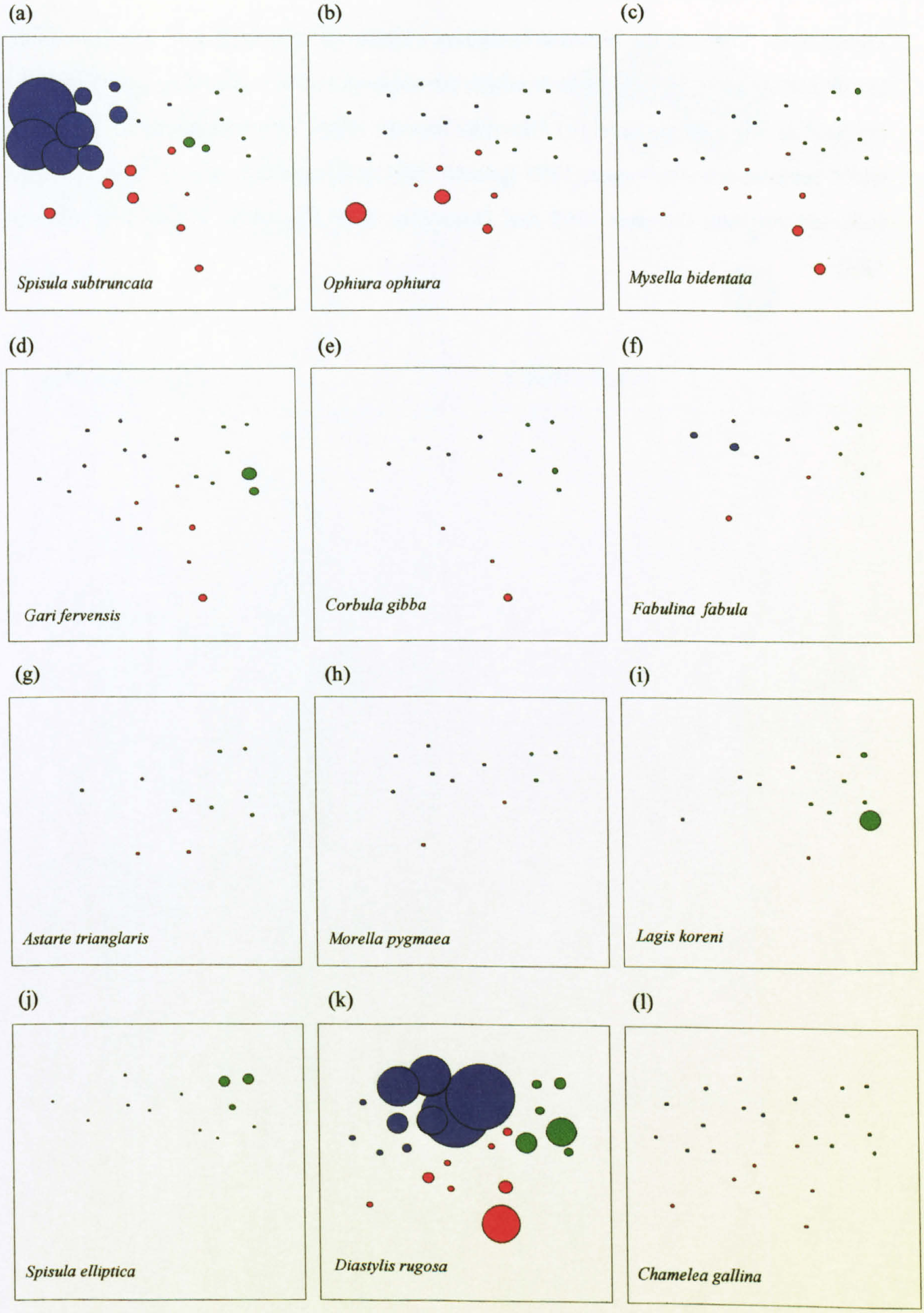

(a)
Spisula subtruncata
(b)
Ophiura ophiura
(c)
Mysella bidentata
(d)
Gari fervensis
(e)
Corbula gibba
(f)
Fabulina fabula
(g)
Astarte trianglaris
(h)
Morella pygmaea
(i)
Lagis koreni
(j)
Spisula elliptica
(k)
Diastylis rugosa
(l)
Chamelea gallina

Figure 3.10. The relative biomass (coloured circles) of two main prey species within the diet of *Astropecten irregularis* which correspond to the 2-dimensional MDS plot. (a) *Spisula subtruncata,* and (b) *Diastylis rugosa*; coloured circles denote the year in which samples were collected, 1995 (green) 1996 (red) and 1997 (blue). Samples were collected between October 1995 and December 1997 from Red Wharf Bay (pooled data).

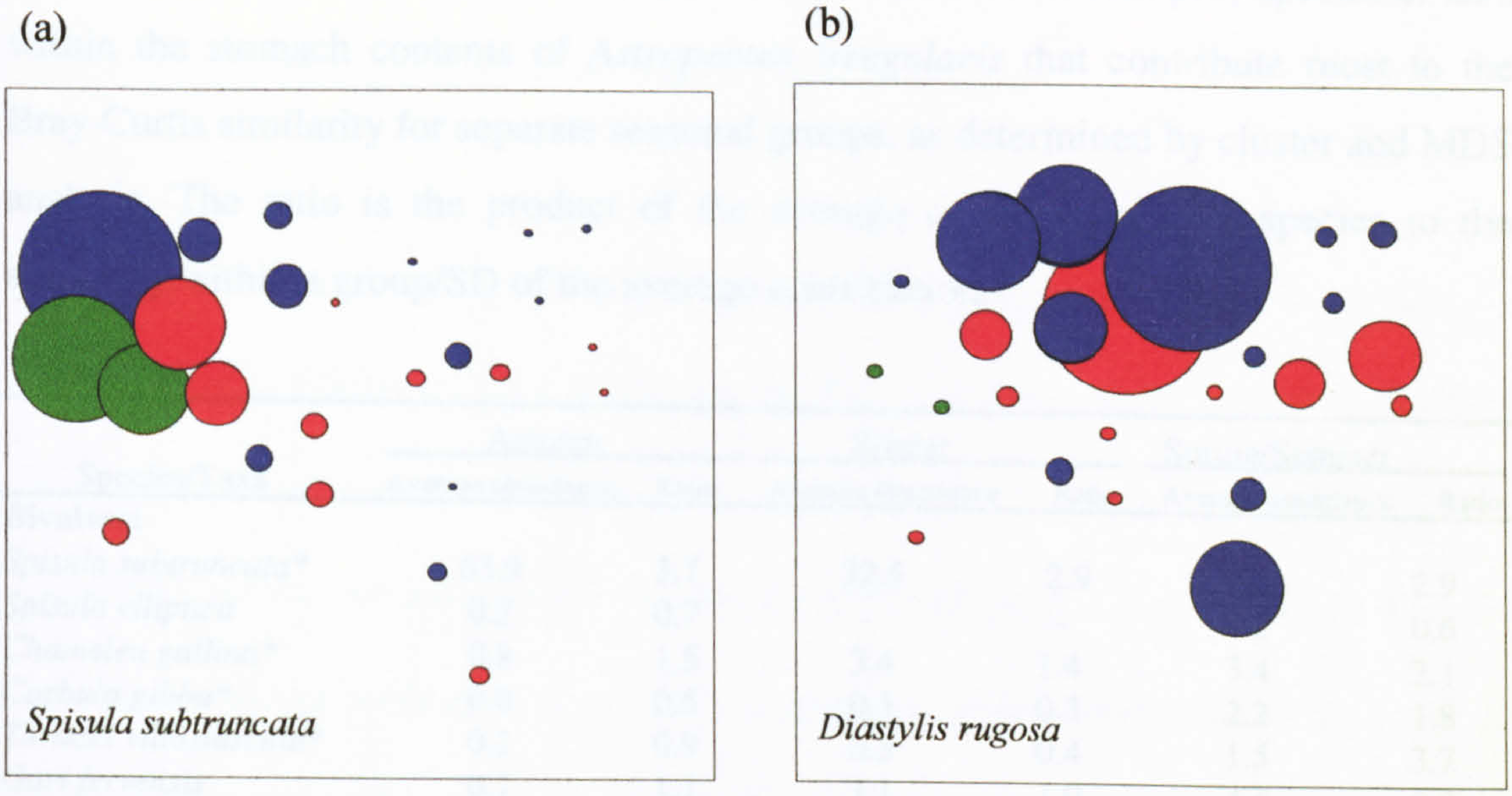

(a)
(b)
Spisula subtruncata
Diastylis rugosa

Table 3.4. The average abundance (%) and ratio value of different prey species or taxa within the stomach contents of *Astropecten irregularis* that contribute most to the Bray-Curtis similarity for separate seasonal groups, as determined by cluster and MDS analysis. The ratio is the product of the average contribution of a species to the similarity within a group/SD of the average contribution.

	Autumn		Winter		Spring/Summer	
Species/Taxa	Average abundance	Ratio	Average abundance	Ratio	Average abundance	Ratio
Bivalves:						
*Spisula subtruncata**	63.9	3.7	32.5	2.9	12.2	2.9
Spisula elliptica	0.2	0.7	-	-	6.2	0.6
*Chamelea gallina**	0.8	1.5	3.4	1.4	3.4	2.1
*Corbula gibba**	0.0	0.5	0.3	0.3	2.2	1.8
*Thracia villosiuscula**	0.2	0.9	0.3	0.4	1.5	3.7
Gari fervensis	0.7	1.1	3.1	1.0	4.4	0.8
Fabulina fabula	0.6	0.5	-	-	0.5	0.7
Gafrarium minimum	0.2	0.8	0.3	0.4	1.2	0.7
*Mysella bidentata**	0.3	0.8	5.1	1.5	2.8	1.3
*Nucula nitidosa**	0.4	2.3	2.7	1.5	1.9	1.5
Donax vittatus	0.2	0.6	0.1	0.3	-	-
Dosinia lupinus	0.0	0.4	-	-	1.2	1.0
Ensis sp.	0.1	0.4	-	-	0.1	0.6
Astarte triangularis	-	-	-	-	1.2	1.1
Laevicardium crassum	-	-	-	-	0.2	0.6
*Parvicardium ovale**	0.3	0.6	0.2	0.2	0.8	1.9
Venerupis pullastra	0.5	0.6	0.5	0.5	1.3	1.1
Crustaceans:						
*Diastylis rugosa**	4.6	1.1	2.5	2.4	3.6	5.3
Corystes cassivelaunus	0.0	0.4	-	-	1.4	1.2
Amphipods	0.1	0.5	0.1	0.2	1.1	1.4
Gastropods:						
Polinices polianus	0.7	1.0	0.9	0.7	0.9	1.1
Obtusella intersecta	0.5	0.5	0.0	0.2	0.6	0.8
Polychaetes:						
*Lagis koreni**	0.0	0.4	-	-	1.4	1.8
Echinoderms:						
Echinocardium cordatum	0.2	0.4	0.2	0.3	0.1	0.5
*Ophiura ophiura**	0.4	0.7	5.1	1.0	1.0	1.7

* 'Indicator species' when the ratio value is ≥1.5

average abundance of many other prey species e.g. *Gari fervensis*, *Gafrarium minimum* and *L. koreni* during this same period generally increased.

The Chesson's feeding preference index (α) was used to compare the 'preference' for different prey species in the diet of *A. irregularis* from Red Wharf Bay, where *S. subtruncata* is a dominant prey species in stomach contents, and Cardigan Bay, where *C. gallina* tended to dominate the stomachs (Figure 3.11a and b). In Red Wharf Bay, a significant preference (α >0.10) for prey species declined through the sequence *S. subtruncata* - *C. gallina* - *G. fervensis* - *D. rugosa* - *M. bidentata*, whereas in Cardigan Bay (α >0.09) the sequence was *C. gallina* - *T. phaseolina* - *D. rugosa* - *P. polianus* - *G. fervensis*. It appears, therefore, that in Cardigan Bay the two most abundant bivalve species within the benthos, *T. phaseolina* and *C. gallina* were also the most 'preferred' prey species. In Red Wharf Bay, although *C. gibba* was numerically the most abundant prey species, *S. subtruncata* the second most abundant was 'preferred', suggesting that marked variations in diet between these two sites generally reflect variations in the composition of prey in the benthos.

In Red Wharf Bay the Chesson's index (α) revealed that in October 1996 *A. irregularis* showed a significant preference (α >0.80) for *S. subtruncata*, when this bivalve was numerically abundant within the benthos (~50% of all prey species) (Figure 3.12a). Moreover preference appeared to be almost exclusive to this particular species. In July 1996, however, *S. subtruncata* had a much lower abundance within the benthos (~9% of all prey species) and the most 'desirable' prey at this time of year was *D.*

Figure 3.11. The Chesson's index (alpha) based on the stomach contents of *Astropecten irregularis* and benthic grab samples collected in March 1997 from; (a) Red Wharf Bay, where values above the horizontal line (alpha = 0.10) indicate a significant preference for a particular prey species, and (b) Cardigan Bay (alpha = 0.09); % density denotes the relative abundance of all prey species found in benthic grab samples.

Prey species; ● *Spisula subtruncata*; ◆ *Chamelea gallina*; ▲ *Corbula gibba*; ■ *Thracia villosiuscula*; ◉ *Gari fervensis*; ◈ *Gafrarium minimum*; ▲ *Mysella bidentata*; ▣ *Nucula nitidosa*; ○ *Venerupis pullastra*; ◇ *Abra nitida*; △ *Modiolus modiolus*; □ *Morella pygmaea*; ⊗ *Dosinia lupinus*; ◈ *Polinices polianus*; ▲ *Ophiura ophiura*; ▨ *Diastylis rugosa*.

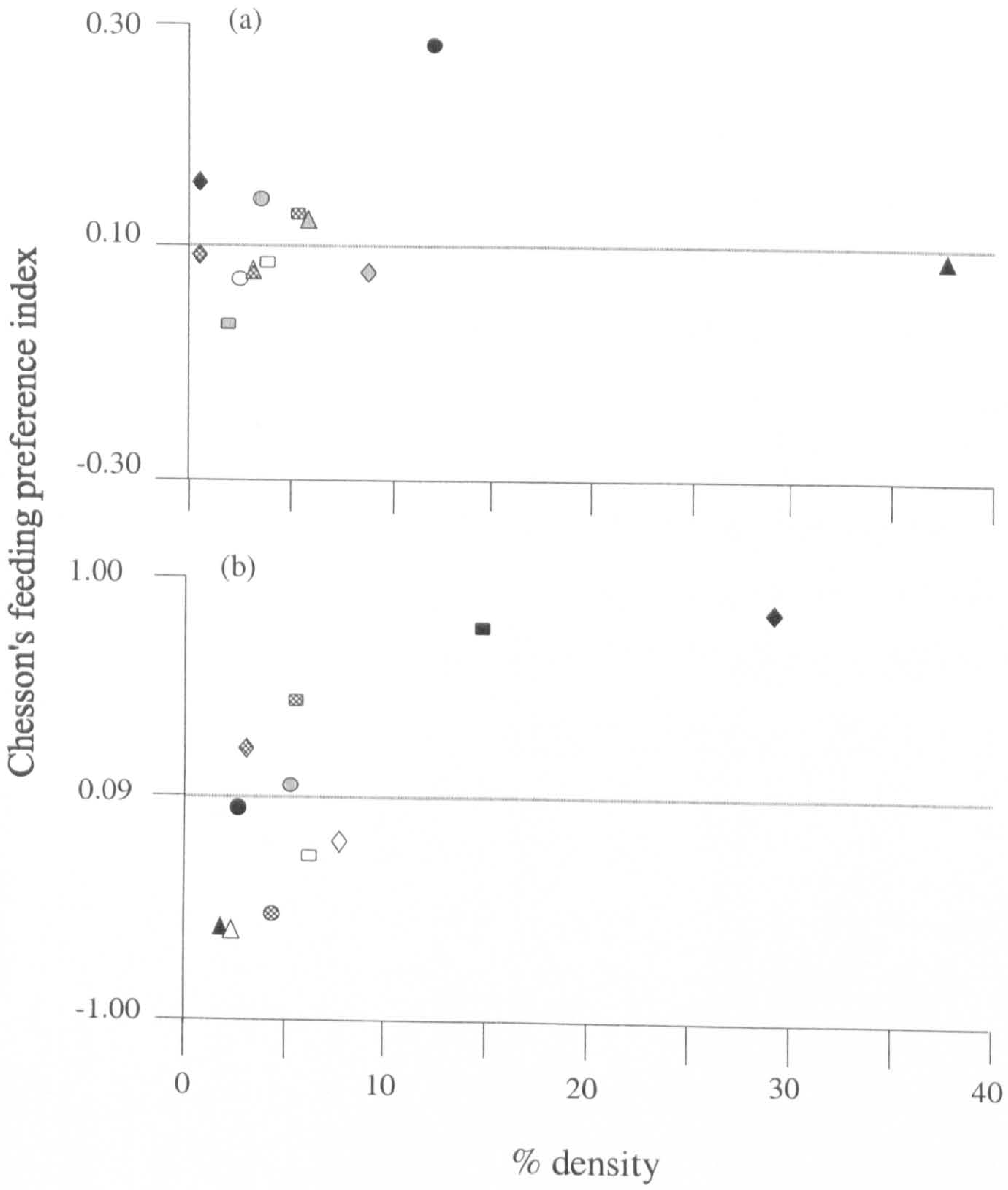
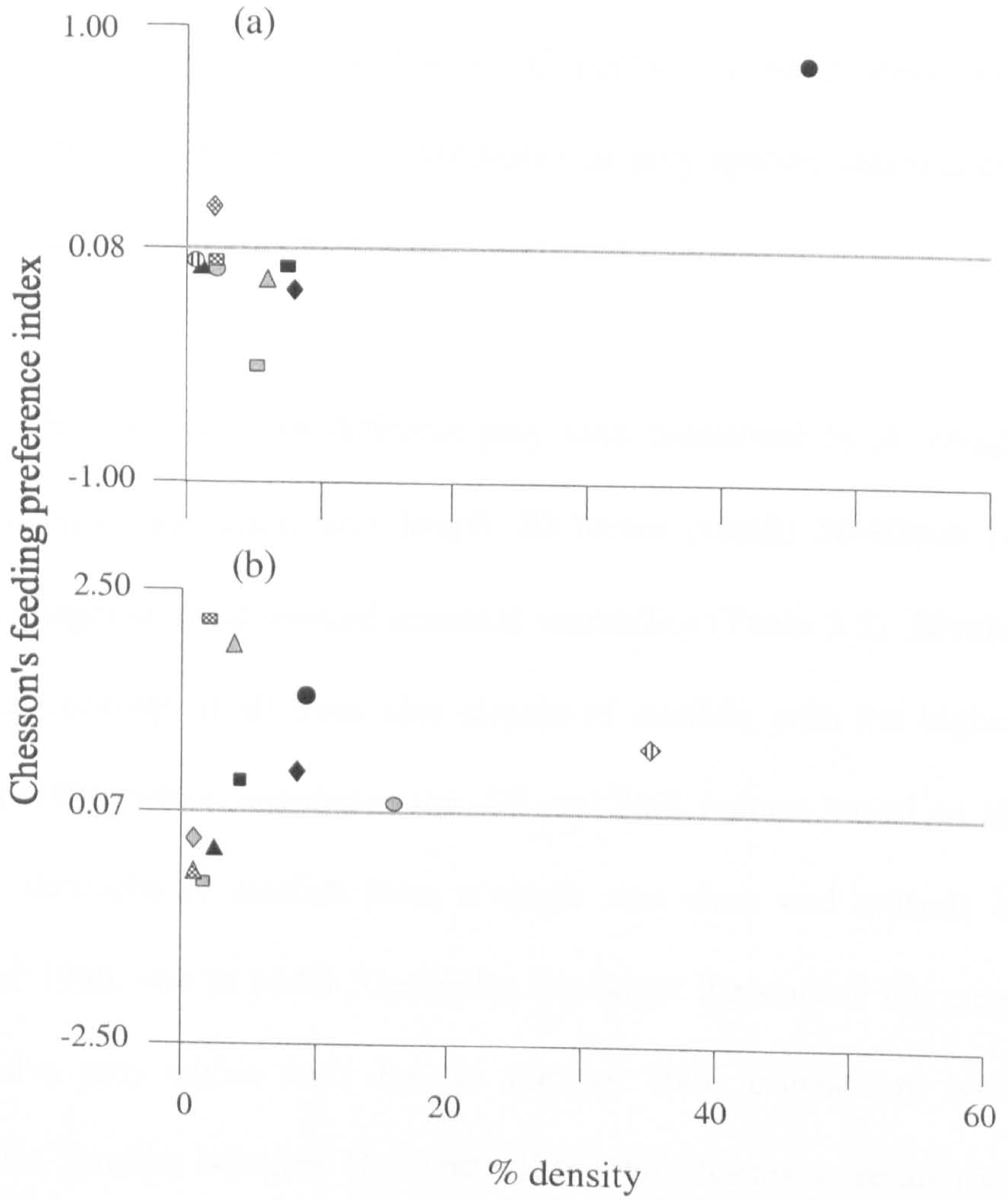

0.30
(a)
0.10
-0.30
1.00
(b)
0.09
-1.00
0
10
20
30
40
Chesson's feeding preference index
% density

Figure 3.12. The Chesson's index (alpha) based on the stomach contents of *Astropecten irregularis* and benthic grab samples collected from Red Wharf Bay; (a) Data collected in October 1996, where values above the horizontal line (alpha = 0.08) indicate a significant preference for a particular prey species, and (b) July 1996 (alpha = 0.07); % density denotes the relative abundance of all species found in benthic grab samples.

Prey species; ● *Spisula subtruncata*; ◆ *Chamelea gallina*; ▲ *Corbula gibba*; ■ *Thracia villosiuscula*; ○ *Gari fervensis*; ◇ *Gafrarium minimum*; △ *Mysella bidentata*; ▭ *Nucula nitidosa*; ◈ *Polinices polianus*; ▲ *Ophiura ophiura*; ▨ *Diastylis rugosa*; Φ *S. elliptica*; ◈ *Lagis koreni*.


(a)
1.00
0.08
-1.00
(b)
2.50
0.07
-2.50
Chesson's feeding preference index
0
20
40
60
% density

rugosa; the preference for other prey declined through the sequence, *D. rugosa* - *M. bidentata* - *S. subtruncata* - *L. koreni* - *C. gallina* - *T. phaseolina* - *G. fervensis* (Figure 3.12b). Although the preference for particular prey species varied seasonally the bivalve *N. nitidosa* was consistently the least preferred.

The abundance of different prey taxa consumed by *A. irregularis* from three different size categories; arm length 20-30mm (small) 30-40mm (medium) and 40-50mm (large) showed marked seasonal variability (Table 3.5). Bivalves dominated the stomach contents of all three size classes of starfish, with the highest contribution in autumn 1996, which accounted for ~93 and 98% (values based on all prey taxa found within stomachs of starfish from a single size class and season) and the lowest in summer 1996, ~64 to ~84%. Generally, the larger the starfish the greater the proportion of bivalve prey within their diet. In summer 1996, crustaceans were relatively more abundant, ranging between 10.0 and ~17%. Polychaetes were also well represented in summer 1996 especially in the stomachs of smaller starfish (~15%) but in all other samples they were poorly represented. Echinoderms and gastropods were present at relatively low abundance throughout the study period and neither species showed any consistent trend amongst starfish of different size.

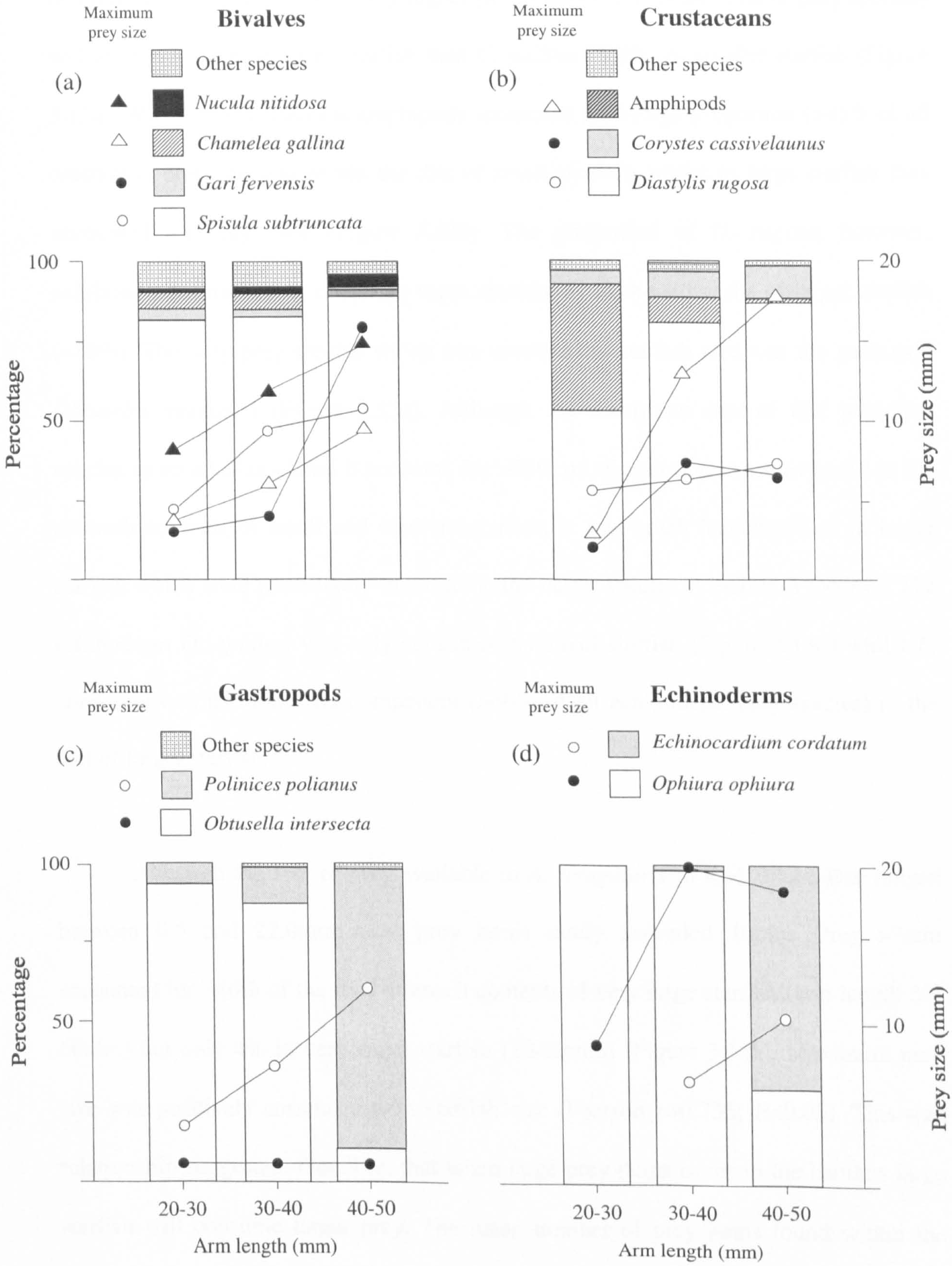
The abundance and maximum size of different prey species, which contributed to >4% of all species in the diet of *A. irregularis*, in three different size categories of starfish collected from Red Wharf Bay between October 1995 and September 1996 are presented in Figure 3.13a, b, c and d. In general, there was a strong positive relationship between the size of the predator and the size of its prey. Amongst the bivalves *S.*

Table 3.5. The abundance of different prey taxa found within the stomach contents of *Astropecten irregulars* from three different size categories, arm length 20-30mm (Small; S) 30-40mm (Medium; M) and 40-50mm (Large; L) collected from Red Wharf Bay between October 1995 and September 1996 (pooled data).

	Stomach contents (%)[1]											
	Size classes of *Astropecten irregularis*											
	Autumn 95			Winter 96			Spring 96			Summer 96		
Prey taxa	S	M	L	S	M	L	S	M	L	S	M	L
Bivalves	93.3	97.7	98.0	89.2	90.3	92.8	83.4	88.1	88.5	64.3	76.3	83.5
Crustaceans	3.1	1.0	0.3	1.6	1.4	1.5	10.8	4.5	4.6	17.2	15.6	10.0
Echinoderms	0.3	0.2	0.5	8.6	6.2	4.3	3.1	2.4	6.9	1.0	1.3	0.4
Gastropods	3.3	1.0	1.2	0.6	2.1	1.4	1.8	4.7	0	2.6	2.4	1.3
Polychaetes	0	0.1	0	0	0	0	0.9	0	0	14.9	4.4	4.8

[1] Values based on all prey taxa found within stomachs of starfish from a single size class and season

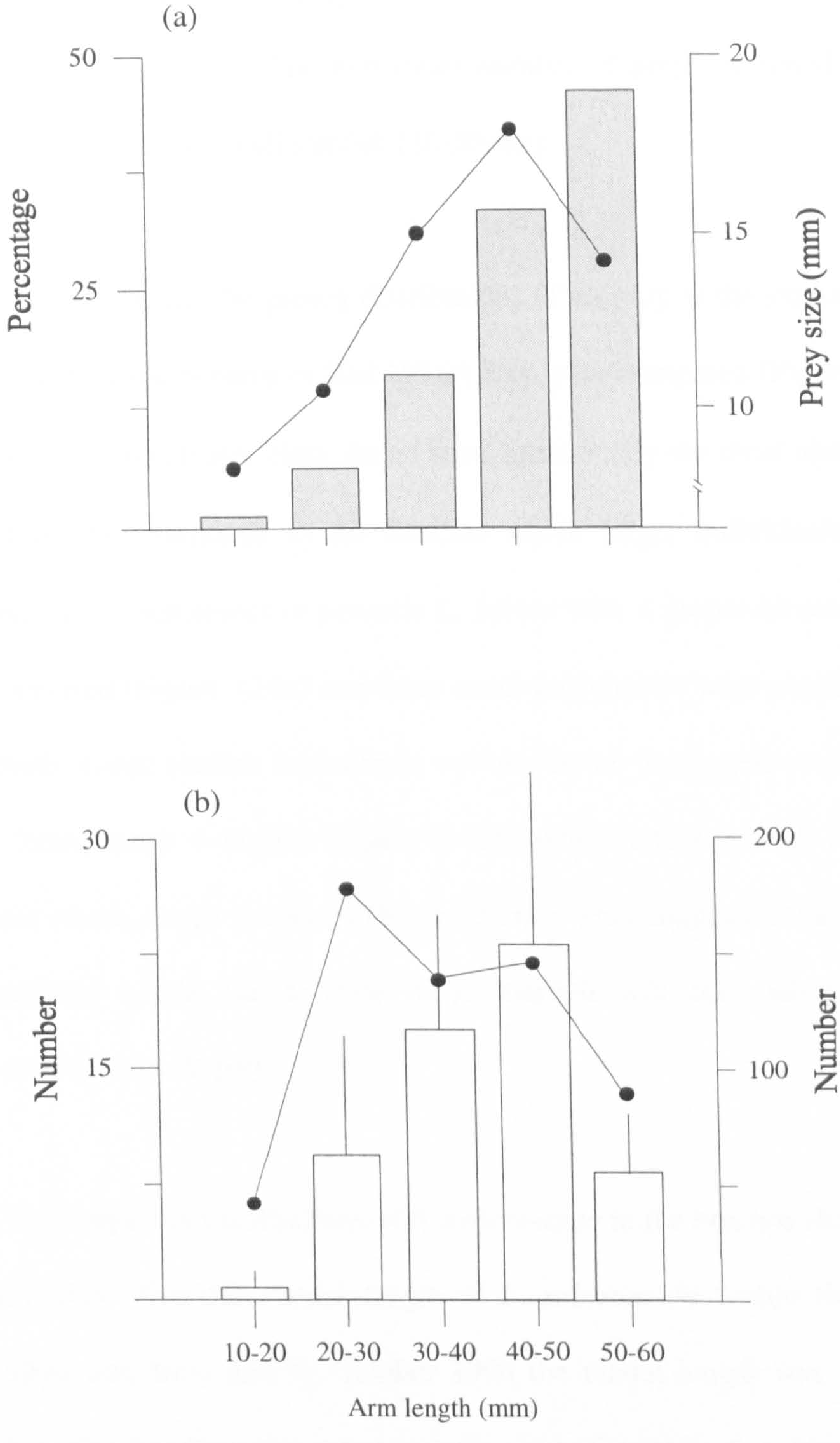
Figure 3.13. The relationship between three different size categories of *Astropecten irregularis*, arm length 20-30mm (small) 30-40mm (medium) and 40-50mm (large) and the abundance (patterned boxes) and maximum size (symbols) of different groups of prey found within the stomachs of starfish collected from Red Wharf Bay between October 1995 and September 1996 (pooled data); % data based on the all prey species within each taxa.


Maximum prey size
Bivalves
(a)
Other species
Nucula nitidosa
Chamelea gallina
Gari fervensis
Spisula subtruncata
100
50
Percentage
Maximum prey size
Crustaceans
(b)
Other species
Amphipods
Corystes cassivelaunus
Diastylis rugosa
20
10
Prey size (mm)
Maximum prey size
Gastropods
(c)
Other species
Polinices polianus
Obtusella intersecta
100
50
Percentage
20-30
30-40
40-50
Arm length (mm)
Maximum prey size
Echinoderms
(d)
Echinocardium cordatum
Ophiura ophiura
20
10
Prey size (mm)
20-30
30-40
40-50
Arm length (mm)

subtruncata dominated the stomach contents of all size categories of starfish, although *N. nitidosa* occurred in a relatively higher proportion (~5% of all bivalve prey species) within the stomachs of large starfish than *C. gallina* (5-6%) in smaller starfish (Figure 3.13a). Within the crustaceans amphipods accounted for a large proportion (>45% of all crustacean prey species) within the diet of small starfish, whilst in large starfish they accounted for only ~4% (Figure 3.13b). The proportion of *D. rugosa*, however, exhibited a reverse trend, occurring more abundantly in the stomachs of larger starfish (~80%). The only prey species which was unrelated to starfish size was the gastropod *Obtusella intersecta* (Figure 3.13c). Although the maximum size of this particular species as an adult is ~2mm it accounts for >90% of all gastropod species found in the stomach contents of small and medium starfish, it was much less abundant in larger starfish which were more likely to consume the larger species *P. polianus* (>80%). The echinoderm *O. ophiura* was only consumed by small starfish (Figure 3.13d) whilst *E. cordatum* was the dominant component (>60% of all echinoderm prey species) in the diet of larger starfish.

Although the size of prey available to *A. irregularis* in Red Wharf Bay ranged between 0.5 and 22.0mm most prey items rarely exceeded 10mm. Prey >7mm accounted for ~46% of the total stomach contents of very large starfish (arm length 50-60mm) but only 4% in very small starfish (10-20mm) (Figure 3.14a). Maximum prey size was positively correlated with starfish size (Pearson r=0.736; P<0.05). This size relationship suggested, therefore, that when large prey items occur in the benthos large starfish will consume larger prey. The mean number of prey items found within the stomachs of *A. irregularis* and the maximum number of prey are presented in Figure

Figure 3.14. (a) The abundance (%) of all prey species above the mean size of 7mm (◘) found within the stomachs of five different size categories of *Astropecten irregularis*, arm length 10-20mm (very small) 20-30mm (small) 30-40mm (medium) 40-50mm (large) and 50-60mm (very large) and the maximum prey size (-●-) found in each class. (b) The mean number of all prey species (□+SD) found within the stomachs of different sizes categories of *A. irregularis* and the maximum number of prey (-●-); starfish collected from Red Wharf Bay between October 1995 and December 1997 (pooled data).


(a)
50
25
Percentage
20
15
10
Prey size (mm)
(b)
30
15
Number
200
100
Number
10-20
20-30
30-40
40-50
50-60
Arm length (mm)

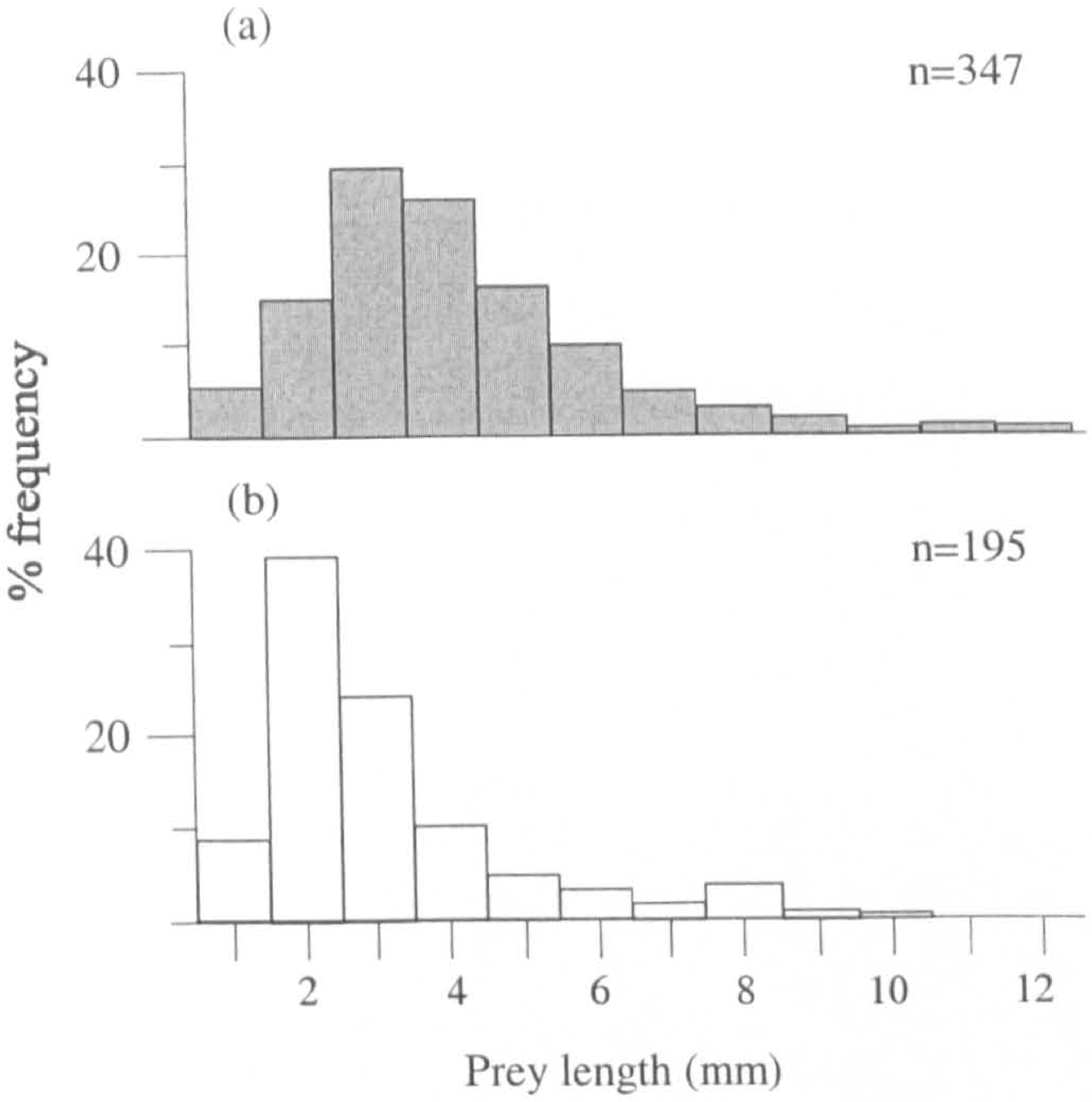
3.14b. The maximum number of prey in starfish >20mm appeared to decline with starfish size (see Figure 3.14a). The maximum number of prey consumed by starfish was greatest (>180) amongst small starfish (20-30mm).

In July 1996, the size frequency distributions of all prey in the stomach contents of starfish and within the benthos in Red Wharf Bay were compared (Figure 3.15a and b). Smaller animals (modal size class 2mm) were numerically the most abundant items within the stomachs, compared to the benthos where larger individuals dominated (3mm). During July a settlement of juvenile *L. koreni* with a preponderance of 2-4mm sized worm occurred (Figure 3.16a) and these small polychaetes were readily consumed by *A. irregularis*. Large starfish feed almost exclusively on the largest available worms (modal size 9mm, range 4-11mm) (Figure 3.16b) whilst small starfish fed on much smaller worms (4mm, range 2-10mm) (Figure 3.16c). This suggested that when larger prey are available within the benthos, large starfish will take advantage of the opportunity to feed on such prey.

The size frequency distributions of *S. subtruncata* in the benthos showed marked seasonal variability. Thus the modal length of *S. subtruncata* within the benthos in September 1996 was 3mm and by October 1996 the modal length was 1mm (Figure 3.17a and b). In October there was a heavy settlement of juvenile *S. subtruncata*, which coincided with a period when *A. irregularis* normally reached its seasonal maximum feeding rate (see Figure 3.5a). Generally, both small and large starfish consumed the smallest (1-2mm) prey (Figure 3.17c, d, e and f) which were available within the

Figure 3.15. The size frequency distributions of all prey species (a) collected from within the benthos, and (b) within the stomachs of *Astropecten irregularis*; all data collected from Red Wharf Bay in July 1996.

Figure 3.16. The size frequency distributions of (a) *Lagis koreni* found the benthos (b) *L. belgica* within the stomachs of starfish, arm length 20-30mm (small) and (c) *L. koreni* within stomachs of *Astropecten irregularis*, arm length 40-50mm (large); all data collected from Red Wharf Bay in July 1996.


(a)
n=347
40
20
% frequency
(b)
n=195
40
20
2
4
6
8
10
12
Prey length (mm)

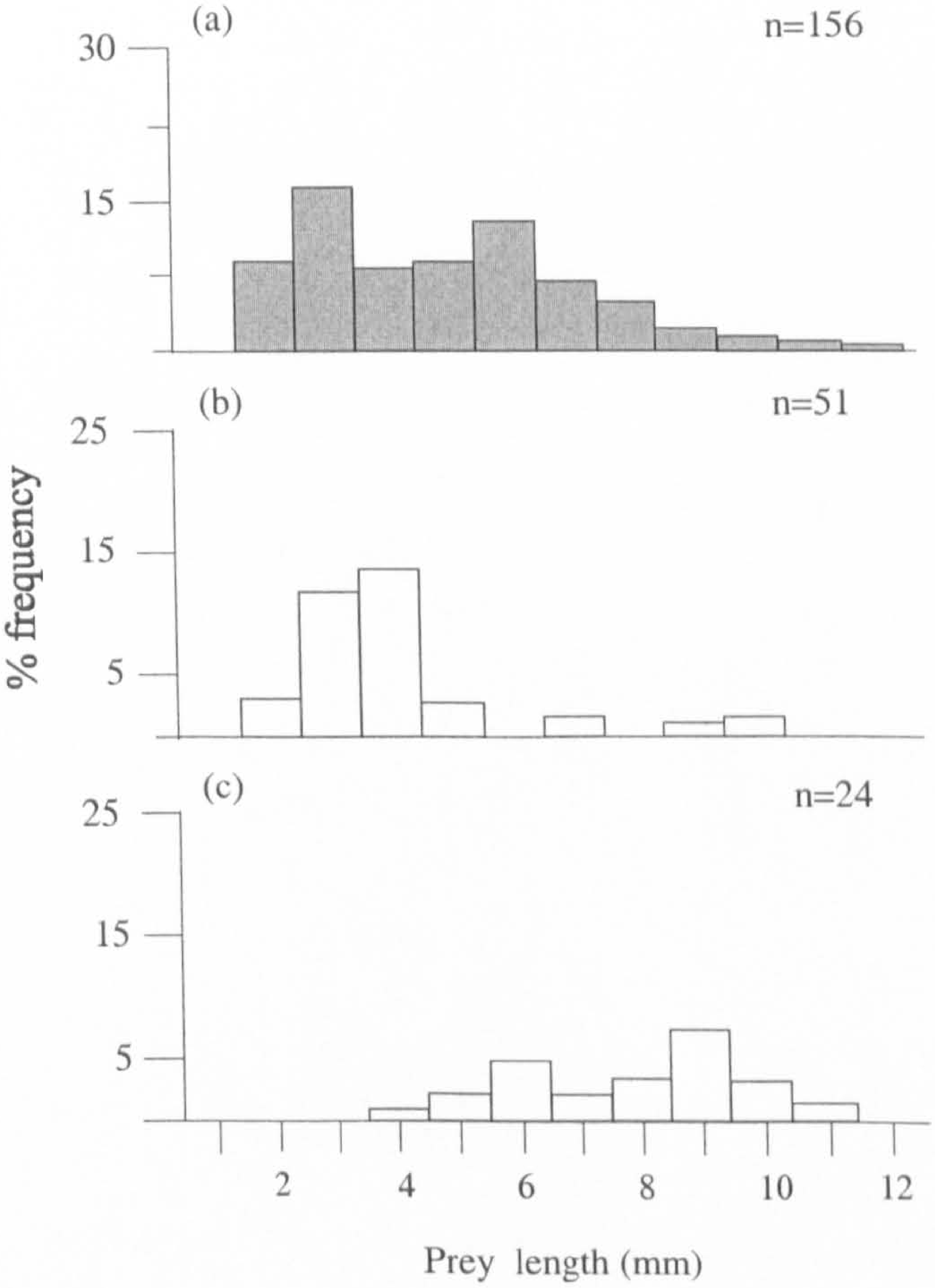
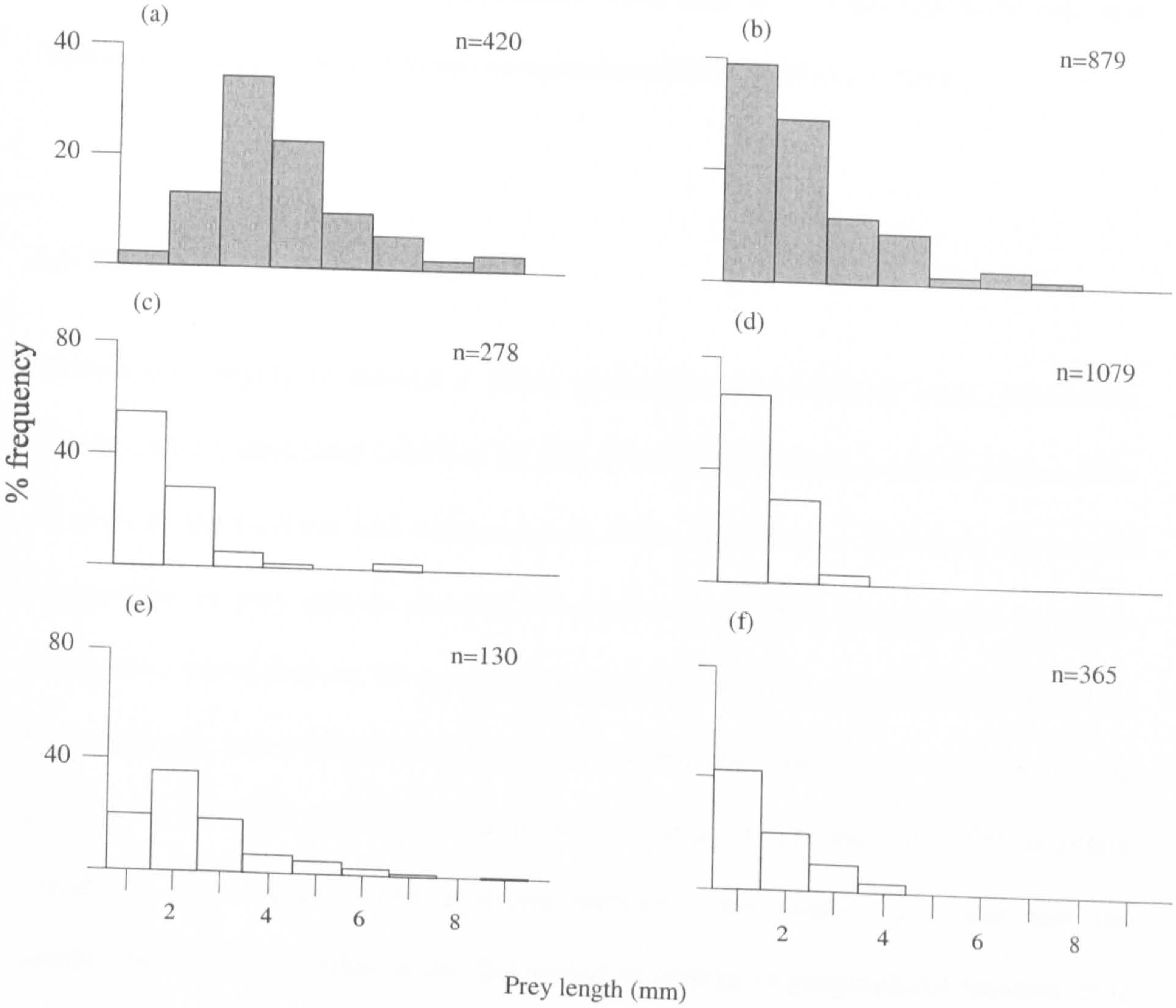

(a)
n=156
30
15
(b)
n=51
25
15
5
% frequency
(c)
n=24
25
15
5
2
4
6
8
10
12
Prey length (mm)

Figure 3.17. The size frequency distributions of *Spisula subtruncata* collected from Red Wharf Bay in September 1996 (a, c and e) and October 1996 (b, d and f). (a and b) *S. subtruncata* collected from within the benthos (■); (c and d) *S. subtruncata* collected from the stomachs of small (20-30mm) *Astropecten irregularis* (□); and (e and f) *S. subtruncata* collected from large (40-50mm) *A. irregularis* (□).


(a)
n=420
40
20
(b)
n=879
(c)
n=278
80
40
(d)
n=1079
(e)
n=130
80
40
(f)
n=365
% frequency
2
4
6
8
2
4
6
8
Prey length (mm)

surrounding benthos, although in September 1996 large starfish did appear to feed on a broader size range of prey (1-9mm) compared to smaller starfish (1-7mm).

3.4. Discussion

Astropecten irregularis showed a strong preference for molluscan prey, particularly bivalves, which dominated (>60% of all prey taxa) the stomach contents of starfish from all sites off the southern and western coasts of the British Isles. However, the overall composition of prey species changed between these different geographical locations. The bivalve *Parvicardium*, for example, was highly abundant at all southern sites (1-3) but completely absent from all western sites, whereas the clam *Spisula subtruncata* was absent from all of the former sites but present at the latter. Christensen (1970) similarly noted that *A. irregularis* had a strong preference for bivalve prey and that the composition of prey species in the diet varied according to geographical location. It is likely, therefore, that these geographical differences are in part attributed to the habitat requirements of different prey species and thus to their availability within the benthos. *Parvicardium*, for instance, inhabits greater seawater depths and a wider variety of substrates than *S. subtruncata*, a species which is generally confined to shallower inshore waters and finer sediments (see Hayward *et al.*, 1995).

The composition of other prey taxa within the diet of *A. irregularis* also showed a high degree of inter-site variability with, for example, crustaceans and polychaetes being the more abundant at all western sites. Crustaceans included a wide variety of different species including *Pagurus* spp., *Corystes cassivelaunus* and several amphipod species, although the most common species was the cumacean *Diastylis rugosa*, which accounted for ~87% of all crustaceans in the diet. Previously, however, crustaceans have not been considered to be an important prey of *Astropecten* (Christensen, 1970; Franz and Worley, 1982; Nojima, 1989) although Lemmens *et al* (1995) noted that they accounted for to >17% of the stomach contents of *A. velitaris*, a common benthic predator in the shallow waters of Northern Queensland, Australia. In the present study, polychaetes generally contributed the least to the overall diet of *A. irregularis*, accounting for ~4 and 5% of all prey taxa within the diet in Cardigan Bay and Colwyn Bay respectively and ≥1% at all three southern sites. The tube worm, *Lagis koreni*, was the most commonly occurring polychaete and accounted for >98% of all worms found in the diet of *A. irregularis*. Although *L. koreni* is an importance prey species in the diet of starfish when it is numerically abundance in the benthos during the summer months, this polychaete was completely absent from Red Wharf Bay, at the time of sampling in March 1997. Several studies have suggested that the fleshy bodies of these animals are quickly digested and so their contribution to the overall diet may be generally underestimated (Christensen, 1970; Ribi *et al*, 1977; Jangoux, 1982; Nojima, 1989).

Echinoderms and gastropods were noticeably more abundant at the southern sites, where seawater depths exceeded 30m and the sediment generally consisted of much coarser material than the shallower and finer sediments associated with the western sites. Christensen (1970) found that echinoderms and gastropods were poorly represented in the diet of *A. irregularis* from Danish waters, although on one occasion, at a site in the North Sea, juvenile *Echinocardium cordatum* were well represented.

Hunt (1925) reported that echinoderms were common prey of *A. irregularis* collected from several sites in the English Channel where the sea bed consisted of coarse sediment. Generally, echinoderms have not been considered to be important food items in *Astropecten* (Franz and Worley, 1982; Nojima, 1989; Lemmens *et al.*, 1995) with the exception of *A. aranciacus* which feeds almost exclusively on its conspecific prey, *A. jonstoni* (Pabst and Vicentini, 1978). Although at the southern sites ophiuroids were virtually absent form the diet of *A. irregularis*, and accounted for only <7% at all the western sites they, like polychaetes, appear to play an important seasonal component in the diet of starfish in Red Wharf Bay.

Few previous studies have provided information on seasonal changes in the dietary habits of *Astropecten* (Christensen, 1970; Franz and Worley, 1982). At the main study site in Red Wharf Bay the abundance and biomass of different prey types within the stomachs of *A. irregularis* showed marked seasonal variability. Bivalves, for example, generally played an increasingly important role in the diet of starfish throughout 1995-1996, from a low during the summer months (<20%) to a high during the autumn months (>90%) (see Table 3). Crustaceans, on the other hand, showed the reverse of this trend with low abundance in winter and high abundance in summer. Franz and Worley (1982) similarly noted seasonal fluctuations in the occurrence of different prey taxa within the stomachs of *A. americanus*. Here juvenile clams, *Arctica islandica* were the most abundant prey in May, but by the following November significantly fewer bivalves were collected whilst gastropods had become the most dominant prey in the diet. Nojima (1989) also noted seasonal changes in the diet of *A. latespinosus*, with echinoderms and gastropods becoming more abundant during winter.

Changes in the diversity index (H') of prey within the stomachs of *A. irregularis* identified *S. subtruncata* as one of the most important prey species; there being an inverse relationship between the abundance of this species and the diversity of other prey species in the diet. For example, there was a low diversity in October 1995 following the settlement of juvenile *S. subtruncata* which dominated the stomach contents; however, as this species became less numerically abundant in the benthos, due to heavy predation by *A. irregularis*, the diversity of other prey within the diet of starfish increased. This suggests that *A. irregularis* is a 'specialist' predator during the autumn months, when its preferred prey is abundant, and becomes increasingly a more 'generalist' predator during the spring and summer months, when its preferred prey are least abundant. Christensen (1970) also noted that *S. subtruncata* was an important prey species of *A. irregularis* and showed that when this species was unavailable, starfish would either feed on less optimal prey or stop feeding altogether and wait for more favourable conditions.

Christensen (1970) proposed that when *S. subtruncata* was highly abundant *A. irregularis* fed almost exclusively on this prey species and this predation continued until this 'preferred' prey was almost eliminated. Christensen also suggested that total elimination of *S. subtruncata* was only prevented by the timely settlement of other prey species such as the bivalve, *Montacuta* spp. and the echinoderm *E. cordatum*, which were readily consumed by *A. irregularis*. In this present study, when population densities of *S. subtruncata* were low during the summer months, this species was never totally eliminated since heavy settlements of other prey species occurred. For example, in 1996 *L. koreni* and *D. rugosa* and in 1997 *S. elliptica* and *D. rugosa*. Although it is suggested that *A. irregularis* has a 'broad' diet (when its preferred prey is unavailable) and, therefore, demonstrates an ability to switch from a preferred prey type to a much less preferred prey type, depending on their seasonal or relative numerical abundance, the dietary requirements of this important benthic predator exhibits a high degree of plasticity. This is an ideal foraging strategy in an environment where the availability of prey can often be highly unpredictable.

Although the Chesson's feeding preference index (α) confirmed that *A. irregularis* has a strong preference for bivalve prey, particularly *S. subtruncata*, the index also demonstrated a relationship between the numerical abundance of prey in the benthos and the diet. In Cardigan Bay, for example, *Chamelea gallina* was highly abundant within the benthos and similarly well represented in the stomachs of *A. irregularis*. Whilst *S. subtruncata* was the second most abundant species within the benthos in Red Wharf Bay during March 1997, it was more abundant during other periods of the year. In mid-autumn, for example, it accounted for >90% of all prey species in the diet of starfish and ~70% of all the available prey in the benthos. It appears, therefore, that prey population density is an important factor in prey selection. Support for this also comes from laboratory experiments (see Chapter 4) where a functional response to prey density by *A. irregularis* was demonstrated, whereby an increase in the availability of prey stimulated an increase in the feeding rates of starfish. This may help to explain why some prey species appear to be 'preferred' over others. Functional responses have also been documented for many other asteroid predators. Menge (1972) for example, found that *Leptasterias hexactis* increased its foraging intensity when the availability of prey increased and suggested that such a response was, in part, a result of their ability to feed on many different prey items during a single foraging bout. McClintock and Lawrence (1985) also noted that *Luidia clathrata* responded to increases in the density of its prey, *Donax vittatus*, by increasing both the time spent foraging and the number of prey ingested.

In Red Wharf Bay, high population densities of prey did not always result in high densities of that particular prey in the stomachs of *A. irregularis*. Large numbers of juvenile *Thracia phaseolina*, following a settlement during the late-summer of 1996 (see Figure 3.3.) for example, were not consumed to any great extent accounting for <4% of all prey species in the diet. Nojima (1989) similarly found that although the bivalve, *Nitidotellina iridella*, was the most abundant prey species in the benthos it was not always the most 'preferred' prey of *A. latespinosus*. In the present study, using data collected in March 1997 the Chesson's feeding index illustrated that although *S. subtruncata* was the most 'preferred' prey, it was not the most abundant species in the benthos. The settlement of *Corbula gibba* during the winter appeared to avoid intense predation by *A. irregularis*, as feeding rates of starfish during this period is greatly reduced and most starfish migrated out of the study site. Christensen (1970) also noted that other molluscan prey such as, *Mya truncata*, avoid periods of intense starfish predation by settling during the winter months when starfish are less abundant and their feeding rates are substantially reduced.

Biomass rather than the numerical abundance of prey provides a more sensitive estimate of the importance of different prey taxa/species in the diet of *A. irregularis*.

However, the numerical abundance of prey provided a clearer identification of the relationships between different seasonal groupings when performing cluster and MDS analysis. MDS plots have not previously been used to analyse seasonal changes in the stomach contents of starfish although they have been successfully used to assess dietary characteristics of hermit crabs in response to trawling disturbance (Ramsay *et al.*, 1996).

In Red Wharf Bay several important and relatively consistent seasonal trends in the diet of *A. irregularis* have been identified over the 2½ year sample period (see Figure 11). In autumn, for example, juvenile *S. subtruncata* were the primary food source, contributing both the greatest abundance and biomass to the overall diet. As the abundance of *S. subtruncata* within the surrounding benthos declines during early-winter through spring to late-summer, other prey species become more abundant in the diet of *A. irregularis*. For example, during the winter months, *Ophiura ophiura*, *D. rugosa* and *Mysella bidentata*, become increasingly more prominent in the stomach contents, whilst during the spring/summer months, when *S. subtruncata* reaches its lowest population density within the benthos, *L. koreni*, *Gari fervensis* and *S. elliptica* become more dominant. During late-summer and early-autumn, however, the crustacean *D. rugosa* becomes the most important component of the diet in terms of biomass contribution. Moreover, the contribution of *D. rugosa* to the diet of *A. irregularis* became pronounced in 1997 even though the actual population density of this cumacean species remained relatively consistent throughout this period. It is suggested, that since large starfish contain a greater proportion of *D. rugosa* in their diet, this apparent increase in the contribution of this particular species is due to the overall increase in the size of individual starfish within the population during 1997. Furthermore, since *D.*

rugosa is a relatively fast moving animal, larger starfish may be more successful in capturing such prey, as they move much faster than smaller individuals (see Chapter 5).

Polychaetes seem to contribute significantly to the diet of *A. irregularis*, but only when they are numerically abundant within the benthos and more 'preferred' prey species are unavailable. In the summer of 1996, for example, a heavy settlement of *L. koreni* was recorded and accounted for ~17% of the total biomass of prey in the starfish stomachs. Christensen (1970) also noted that juvenile *L. koreni* occurred in large numbers within the stomachs of *A. irregularis* when they were numerically abundant in the benthos; usually during the summer months. Christensen similarly noted that although polychaetes constituted part of the diet of *A. irregularis* they were usually consumed only when other more attractive prey such as bivalve molluscs were unavailable. Findings from this present study, however, suggest that *L. koreni* may have a greater seasonal importance in the diet of *A. irregularis* than previously expected.

Several prey species in the diet of *A. irregularis* have been identified as significant 'indicator species' for a particular seasonal period, based on their contribution to the average similarity within each seasonal grouping. Although, overall ten prey species have been identified as 'indicator species' including *T. phaseolina* (spring/summer) *M. bidentata* (winter) and *Nucula nitidosa* (autumn and winter) the most prominent species were *S. subtruncata*, a characteristic species throughout the year, especially during autumn, and *D. rugosa* an important species during spring/summer. In general, the number of 'indicator species' increased from autumn (3) through winter (5) to spring/summer (9).

The diet of *A. irregularis* changed with predator size. Bivalves contributed more to the diet of large starfish (arm length 40-50mm) than any other size class, whilst small starfish (20-30mm) had a greater overall diversity of prey than larger individuals. Moreover, most of crustaceans in the stomachs of small *A. irregularis* comprised juvenile amphipods rather than cumaceans which were more common in larger starfish. The small gastropod, *Obtusella intersecta*, was a more important prey species in small *A. irregularis*, than the larger gastropod *P. polianus*, which was more frequently encountered within the diet of larger starfish. Similarly, *E. cordatum* were more abundant in large starfish whereas juvenile *O. ophiura* were more dominant in smaller starfish. Presumably such size differences are associated with the ability of larger starfish either to capture faster moving prey or to swallow larger prey items than smaller individuals (see Chapter 5). Nojima (1989) reported similar differences in the diet of different size classes of *A. latespinosus*, where small starfish fed primarily on bivalves and gastropods in winter, whilst larger starfish became 'non-selective' deposit feeders and consumed mainly detrital material.

Although, many previous studies have shown that several *Astropecten* spp. appear to consume only juvenile prey (Christensen, 1970; Beddingfield and McClintock, 1993; Lemmens *et al.*, 1995) it is not clear from these studies whether large starfish consume relatively larger prey than smaller starfish or whether the composition of the diet changes with predator size. In Red Wharf Bay, prey smaller than the modal size of those available within the surrounding benthos were often consumed by all size classes of *A. irregularis* (see Figure 18) and a positive correlation between the arm length of starfish and the maximum prey size were recorded; most prey items found in the stomachs were <10.0mm, broadly reflecting the size range of prey available within the benthos. However, following a heavy settlement of *L. koreni*, in July 1996, large *A. irregularis* fed on much larger prey items than smaller starfish. Nojima (1989) similarly found a positive relationship between prey size and arm length of *A. latespinosus*. In this study, since a strong relationship exists between the size of predator and the availability of prey in the benthos, it is suggested, that resource partitioning may occur between different size classes of *A. irregularis*. Ribi *et al* (1977) documented a shift in the size of prey consumed by two Mediterranean species of *Astropecten* at sites where these predator starfish co-occurred and suggested that this was probably a response to competition for food. In Red Wharf Bay, seasonal changes in the size and availability of different prey throughout the year appears to influence the size and range of prey consumed by *A. irregularis*, suggesting that starfish shift their dietary habitats according to the availability of suitable prey.

CHAPTER 4

Bivalve Prey Selection and Energy Maximization by *Astropecten irregularis*

4.1. Introduction

Whilst some studies have suggested that *Astropecten* spp. are indiscriminate feeders consuming whatever they encounter during a foraging excursion (Kisch, 1958; Well *et al.*, 1961) others have shown that these starfish are highly selective predators, with a particular predilection for molluscan prey (Massé, 1966, 1975; Christensen, 1970; Schwartz and Porter, 1976; Ribi and Jost, 1978; Franz *et al.*, 1982; Nojima, 1989; Beddingfield and McClintock, 1993; Lemmens *et al.*, 1995; Freeman *et al.*, 1998). Although *Astropecten* spp. are not too specialized to be at risk from starvation when their preferred prey are unavailable. *A. irregularis*, for example, feeds almost exclusively on juvenile *Spisula subtruncata* during the autumn months when this prey species is numerically abundant within the benthos, but switches its feeding preference to another apparently 'attractive' prey species, juvenile *L. koreni*, during the summer months when these tube-living polychaetes become the most abundant prey species (Christensen, 1970).

Information on how predators select their prey and how they modify their feeding preferences when changes in the environment occur e.g. changes in the availability of prey and the encounter of different habitats, plays a key role in optimal foraging theory (Hughes, 1980) and promotes a better understanding of the kind of dynamics and structure of predator-prey systems (Paine, 1966). One basic prediction of optimal foraging theory under the energy maximization premise is that predators should choose those prey sizes which maximize calorific intake per unit of foraging time (Feder and Christensen, 1966; Krebs, 1978; Hughes and Burrows, 1990; Beddingfield and McClintock, 1993). Size selection, however, may be a trade-off between the ease of handling and the amount of energy returned for a given size of prey (Doi, 1976; Paine, 1976, McClintock and Robinett, 1986; Beddingfield and McClintock, 1993). Thus, when a predator is given a choice of prey species from varying size classes, it should select those which provide the greatest profitability (Beddingfield and McClintock, 1993). Although large prey individuals of any given prey species will have a higher energy content than smaller individuals of that species, these will generally require longer handling and digestion times resulting in higher energetic costs (Paine, 1976).

The ingestion of prey by intra-oral feeding asteroids such as *A. irregularis*, *A. latespinosus*, *A. articulatus* and *Luidia clathrata*, is generally constrained by the morphology and size of the oral aperture of their mouth parts, thus inhibiting the ingestion of large prey items (Fenchel, 1965; Christensen, 1970; McClintock and Lawrence, 1981; Beddingfield and McClintock, 1993). Consequently these predators have a strong preference for prey which are significantly smaller than the mean size of those which are available (Christensen, 1970; Doi, 1976; Doering, 1980; McClintock and Lawrence, 1981). Few previous studies have been able to demonstrate a predator-prey size relationship in *Astropecten* spp. i.e. where larger starfish consume larger prey (Ribi and Jost, 1978; Nojima, 1989).

Factors other than prey size seem to be important in the selection of prey by *Astropecten* spp. these include the nutritional value of the prey and their numerical abundance (Christensen, 1970; Ribi and Jost, 1978; Beddingfield and McClintock, 1993). Christensen (1970) noted that the retention period of different prey species within the stomach of *A. irregularis* was a key factor in prey selection; prey species with short retention times were generally the most 'preferred'. *Spisula subtruncata,* for example, had a significantly shorter retention time than *Chamelea* (=*Venus*) *gallina* a somewhat less 'preferred' prey species. The precise mechanism underlying prey selection by *A. irregularis* are largely unknown and no single model of prey selection which would predict the outcome of multiple species encounters, comprising of different prey sizes, has been proposed.

In this study prey selection by *A. irregularis* based on prey species, size, their individual retention times within the starfish stomach and their numerical abundance is evaluated with respect to the energy maximization premise.

4.2. Materials and methods

In laboratory experiments (unless otherwise stated) *Astropecten irregularis* were maintained individually in aquaria (area 450cm^2 30x15cm) filled with sand to a depth of 5cm and supplied with running seawater at ambient temperature (~10°C). Two experiments were undertaken to determine whether *A. irregularis* exhibited a preference for different molluscan prey species. In the first experiment five species of bivalves (shell length 6-8mm) *viz. Spisula subtruncata, Gari fervensis, Chamelea gallina, Nucula nitidosa* and *Cerastoderma edule*, and one gastropod, *Polinices polianus*, were offered as species pairs to a total of eighty-eight medium-sized starfish (arm length 30-40mm); prey were replaced when eaten in order to maintain constant prey availability. Over a period of five days each starfish was offered five individuals of each prey species and the number of individuals consumed recorded. In the second experiment groups of ten individuals from each prey species (6-8mm) were offered separately to each of thirty-six medium-sized starfish. The number of prey ingested daily over a period of eight days was recorded and prey were replaced when eaten.

The locally abundant intertidal cockle, *C. edule* was offered as prey to determine whether prey selection by *A. irregularis* was size dependent. Although cockles are not normally part of the natural diet of *A. irregularis*, they are readily consumed by starfish and the large numbers of prey, which were required for these experiments, could be obtained. Eight starfish from each of the following size categories; arm length 20-25mm (small) 35-40mm (medium) and 50-55mm (large) were each presented with six *C. edule* from five different size classes; shell length 2-4, 8-10, 14-16, 20-22 and 26-28mm. The experiment was continued over a period of four days and individual prey items were replaced when eaten. Size selection was quantified using the Chesson's feeding preference index (α) (see Chapter 3) by substituting p_i for the total number of prey type i offered during the experiment, and r_i for the total number of i consumed.

The retention times of prey within the stomach of *A. irregularis* were examined for those species used in the prey preference experiments. Five different size classes of each prey species; 3-5, 7-9, 11-13, 15-17 and 19-21mm were offered separately to each of the thirty-eight medium-sized *A. irregularis* and the time between ingestion and ejection of empty shells was observed. Since a range of prey species from different size classes were unavailable the experimental procedure was repeated offering *C. edule* to three size classes of starfish; 20-30mm (small) 35-45mm (medium) and 50-60mm (large) and the time between ingestion and ejection of empty shells was again recorded.

To investigate why the survival times of different prey species in the stomach of *A. irregularis* were variable, a laboratory experiment was undertaken to simulate the anaerobic conditions within the stomach. Six 500ml Kilner jars fitted with oxygen probes were filled with seawater and placed in a constant temperature bath at 12°C. A supply of oxygen free nitrogen gas was then used to saturate seawater. Six individuals from those prey species used in the prey preference experiment *viz. S. subtruncata, G. fervensis, C. gallina, N. nitidosa, C. edule,* and *P. polianus* were then placed into each jar and allowed to acclimate to the conditions over a period of one hour. The experiment was concluded once these prey species had died.

X-ray radiography was used to determine the survival and retention times of bivalve prey within the stomach of *A. irregularis*. Ten starfish (40-50mm) maintained individually in aquaria (area 325cm^2 25x13cm) filled with sand to a depth of 2cm and kept at a seawater temperature of 10°C were each offered fifteen *C. edule* (12-14mm). To identify each prey item on the x-ray film, individuals were marked with iron-filings super-glued to each of the valves. Once a single or several prey items were observed being ingested a single x-ray film cassette, protected against moisture, was placed immediately beneath the aquarium. An x-ray machine (Chirana KOM 5) was then positioned directly over the aquarium, at a vertical distance of 30cm, and a single exposure was taken at a shutter speed of 0.4sec. This protocol was then repeated every 30mins until the empty shell valves were eventually ejected. Film cassettes were loaded with x-ray film (CUROX RP1, 18 x 24cm) and developed in a darkroom following the protocol outlined in appendix VI.

To determine the optimal prey size for a medium-sized *A. irregularis* (30-40mm) the profitability of different prey species *viz. S. subtruncata, C. gallina, N. nitidosa, C. edule,* and *P. polianus* from a range of size classes (shell length 4, 8, 12, 16 and 20mm) was calculated using the calorific value of each prey species and their individual retention times within the starfish stomach. Calorific values of each prey species was determined using a balistic bomb calorimeter (see Appendix VII). In order to evaluate the optimal prey size for three different size classes of starfish; arm length 20-25mm (small) 35-40mm (medium) and 50-55mm (larger) the profitability of different size classes of *C. edule*; shell length 4, 8, 12, 16 and 20mm was calculated.

To predict the potential profitability (energy value of prey/retention time) of starfish filling their stomach to maximum packing capacity three different size classes of plastic beads; diameter 4, 8 and 12mm, which closely resembled the globular shape of *C. edule* were used. A total of ninety freshly dissected starfish stomachs from a range of size categories; arm length 15, 20, 25, 30, 35, 40, 45, 50 and 55mm, were each packed carefully with one size class of bead until the stomach was fully distended; the total number of beads was then noted.

To determine the feeding response of *A. irregularis* to increases in prey density, twenty-four medium-sized starfish (30-40mm) were each offered different numbers of small (4-6mm) *C. edule* ranging from 10 individuals (~field density of $300m^2$) 20 individuals (~$600m^2$) and 30 individuals (~$900m^2$). Numbers were maintained by replacing individual prey items as eaten and the total number of prey consumed by each starfish recorded over a seven day period.

4.3. Results

In the laboratory *Astropecten irregularis* demonstrated a clear preference for particular molluscan prey in which species offered as species pairs were selected through the sequence *Cerastoderma edule* - *Spisula subtruncata* - *Gari fervensis* - *Chamelea gallina* - *Polinices polianus* - *Nucula nitidosa*. (Table 4.1a). The same preference was observed when *A. irregularis* was fed on these prey species separately; *C. edule* was again the most frequently consumed species ($5.8\pm1.0 ind.d^{-1}$) whilst in *N. nitidosa* was the least consumed prey ($1.0\pm0.8 ind.d^{-1}$) (Table 4.1b).

Table 4.1. (a) The ratio of prey (species a : species b) (shell length 8mm) ingested by medium-sized *Astropecten irregularis* (arm length 30-40mm) when offered in pairs, and (b) prey (4mm) consumption rate by medium-sized starfish (30-40mm) when offered separately; n/d = no data.

(a)

	Prey species b				
Prey species a	*S. subtruncata*	*G. fervensis*	*C. gallina*	*P. polianus*	*N. nitidosa*
C. edule	1.4:1	2.2:1	2.9:1	3.6:1	4.4:1
S. subtruncata		n/d	0.3:1	4.1:1	3.7:1
G. fervensis			n/d	n/d	n/d
C. gallina				1.7:1	1.9:1
P. polianus					0.3:1

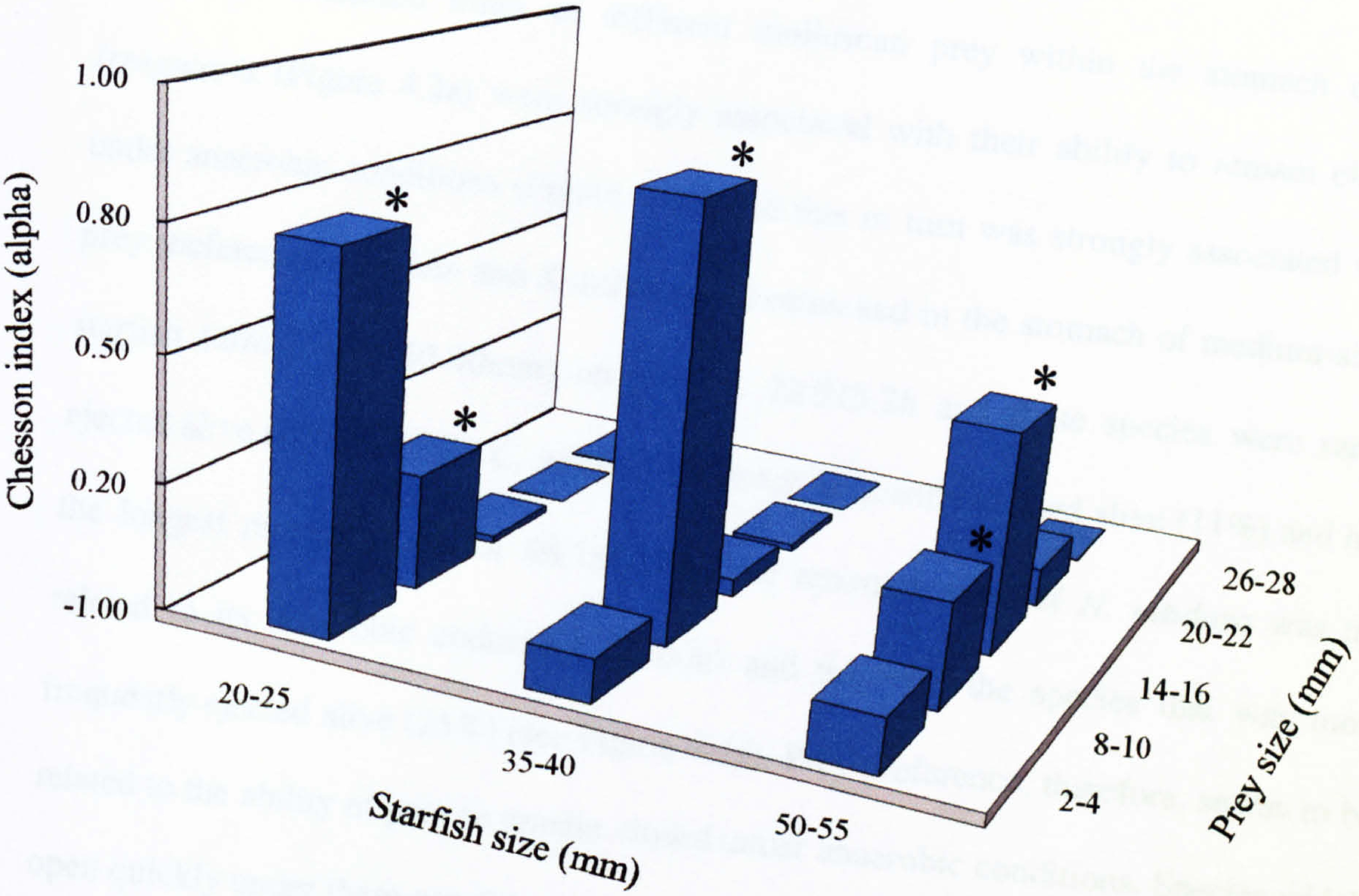
(b)

	Astropecten irregularis	
	Consumption rate (ind.d^{-1})	
Prey species	Mean[a]	n
C. edule	5.8 (1.0)	6
S. subtruncata	5.2 (1.1)	6
G. fervensis	2.9 (0.4)	6
C. gallina	2.5 (0.7)	6
P. polianus	1.3 (0.6)	6
N. nitidosa	1.0 (0.8)	6

[a]Values are mean (± SD)

Although *C. edule* is an intertidal species and not normally available to *A. irregularis*, selection of other prey species broadly reflected the feeding preferences (see Chapter 3) of starfish collected from Red Wharf Bay. When offered different size classes of *C. edule A. irregularis* revealed a strong predator-prey size relationship, where the larger starfish (arm length, 50-55mm) showed a significant preference (Chesson's feeding preference index α >0.2) for larger prey (shell length, 14-16mm) medium starfish (35-40mm) preferred (α >0.2) smaller prey (8-10mm) whilst the smallest starfish (20-25mm) preferred the smallest prey (2-4mm) (Figure 4.1). The maximum size range of *C. edule* consumed by any starfish was 20-22mm, although in general prey larger than 14-16mm were rarely consumed by medium and small starfish. These observations perhaps suggest that some physical constraint or energetic advantage may be controlling prey size selection. Occasionally, however, when starfish have been starved for a prolonged period (up to 8 weeks) they are able to ingest extremely large prey items, exceeding those sizes predicted and usually causing the body wall of the starfish to become highly extended.

Figure 4.1. Size preference (Chesson's index) by *Astropecten irregularis* when offered a size range of *Cerastoderma edule*; * denotes values which are $>1/n_i$ indicating a significant preference for those particular size categories of prey.


Chesson index (alpha)
1.00
0.80
0.50
0.20
-1.00
*
*
*
*
*
20-25
35-40
50-55
Starfish size (mm)
26-28
20-22
14-16
8-10
2-4
Prey size (mm)

The retention times of different molluscan prey within the stomach of *A. irregularis* (Figure 4.2a) were strongly associated with their ability to remain closed under anaerobic conditions (Figure 4.2b) and this in turn was strongly associated with prey preference. *C. edule* and *S. subtruncata* remained in the stomach of medium-sized starfish (arm length 30-40mm) on average 22.5±3.2h and these species were rarely ejected alive (<3%). Whilst *C. gallina* was more frequently ejected alive (11%) and had the longest retention time of 86.7±12.7h. The retention time of *N. nitidosa* was not related to its anaerobic endurance (>200h) and this was the species that was most frequently ejected alive (23%) (see Figure 4.2a). Prey preference, therefore, seems to be related to the ability of prey to remain closed under anaerobic conditions. Species which open quickly under these conditions were generally 'preferred' to those which were able to endure these conditions for longer periods. Retention time in *N. nitidosa*, the least preferred prey and the one most frequently ejected alive may suggests that particularly species is unpalatable to *A. irregularis*. The retention times of different size classes of prey showed considerable inter-species variability, although all species showed a positive relationship with increases in prey size (Table 4.2a and b). In general, the retention times of these prey species followed the same sequence as that previously reported in Figure 4.2a. The smallest prey (4mm) of *P. polianus* and *N. nitidosa*, however, had longer retention times than any other prey species, and larger (>4mm) *C. gallina* generally had the longest overall retention times. *C. edule*, on the other hand, had a shorter retention time (47.8h) than even the smallest *P. polianus* (49.2h) suggesting that large individuals of this species would be preferred by *A. irregularis* over smaller prey items of another species with a longer retention period.

Figure 4.2. (a) Retention periods (±SD) of different prey species (shell length 8.0±0.9mm) in the stomach of medium-sized *Astropecten irregularis* (arm length 30-40mm); solid circles denote the percentage of prey ejected alive following ingestion, and (b) Survival times (!SD) of different prey species (8±1.3mm) under anerobic conditions. Abbreviations denote prey species; *Ce=Cerastoderma edule*; *Ss=Spisula subtruncata*; *Gf=Gari fervensis*; *Pp=Polinices polianus*; *Cg=Chamelea gallina* and *Nn=Nucula nitidosa.*

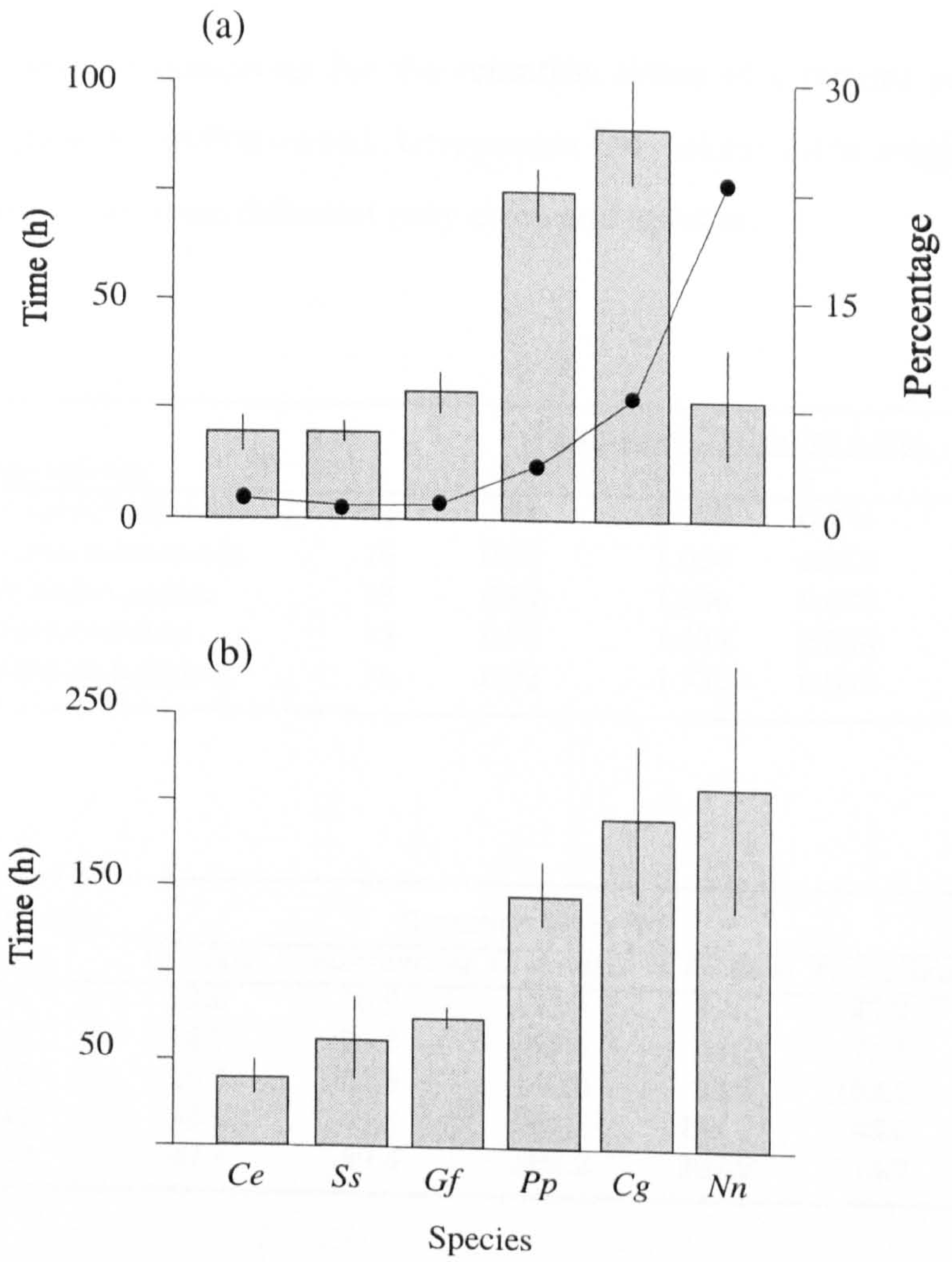

(a)
100
50
0
Time (h)
30
15
0
Percentage
(b)
250
150
50
Time (h)
Ce
Ss
Gf
Pp
Cg
Nn
Species

Table 4.2. (a) Regression equations for the retention times of different prey sizes and species in the stomach of medium-sized *Astropecten irregularis* (arm length 30-40mm). (b) Retention times (h) of these different prey sizes and species.

(a)

		Regression * prey size (mm)		
Prey species	n	r^2	a	b
Cerastoderma edule	30	0.74	0.999	0.034
Spisula subtruncata	16	0.99	1.094	0.034
Chamelea gallina	28	0.89	1.306	0.070
Nucula nitidosa	13	0.93	1.438	0.044
Polinices polianus	16	0.92	1.532	0.040

(b)

Prey size (mm)	Retention times (h)				
	C. edule	*S. subtruncata*	*C. gallina*	*N. nitidosa*	*P. polianus*
4	13.6	16.9	38.5	41.1	49.2
8	18.7	23.3	73.5	61.7	71.1
12	25.5	31.8	140.0	92.5	102.8
16	34.9	43.5	266.7	138.7	148.6
20	47.8	59.4	508.2	207.9	214.7

The retention times of *C. edule* from five different size classes exhibited a negative relationship with increases in predator size (Table 4.3a and b) where the smallest prey (4mm) was retained within the stomach of small starfish (20-25mm) for ~16h, whilst in larger starfish prey were retained for only ~8h. Although in all size classes of starfish the retention times of prey between 12 and 16mm were relatively similar, the overall time differences across the range of different prey species was lower as starfish size increased. Extrapolation of the retention times for large prey (>16mm) consumed by small starfish (<25mm) should be viewed with caution, as these starfish are unlikely to consume prey >16mm. Moreover, when small prey (<4mm) are consumed by any size of starfish their retention times do not continue to decrease as might be predicted; since a minimal time period of ~6h appears to be required by starfish to process such prey items.

Table 4.3. (a) Regression equations for the retention times of different size classes of *Cerastoderma edule* in the stomach of medium-sized *Astropecten irregularis* (arm length 30-40mm). (b) The retention times of different size classes of *C. edule* by starfish of different sizes; 20-25mm (small) 35-40mm (medium) and 50-55mm (large).

(a)

Shell length (mm)	n	r^2	Regression * starfish size (mm)	
			y	x
4	13	0.66	1.414	-0.010
8	25	0.85	1.627	-0.009
12	20	0.79	1.749	-0.007
16	21	0.82	1.799	-0.008
20	16	0.78	1.798	-0.006

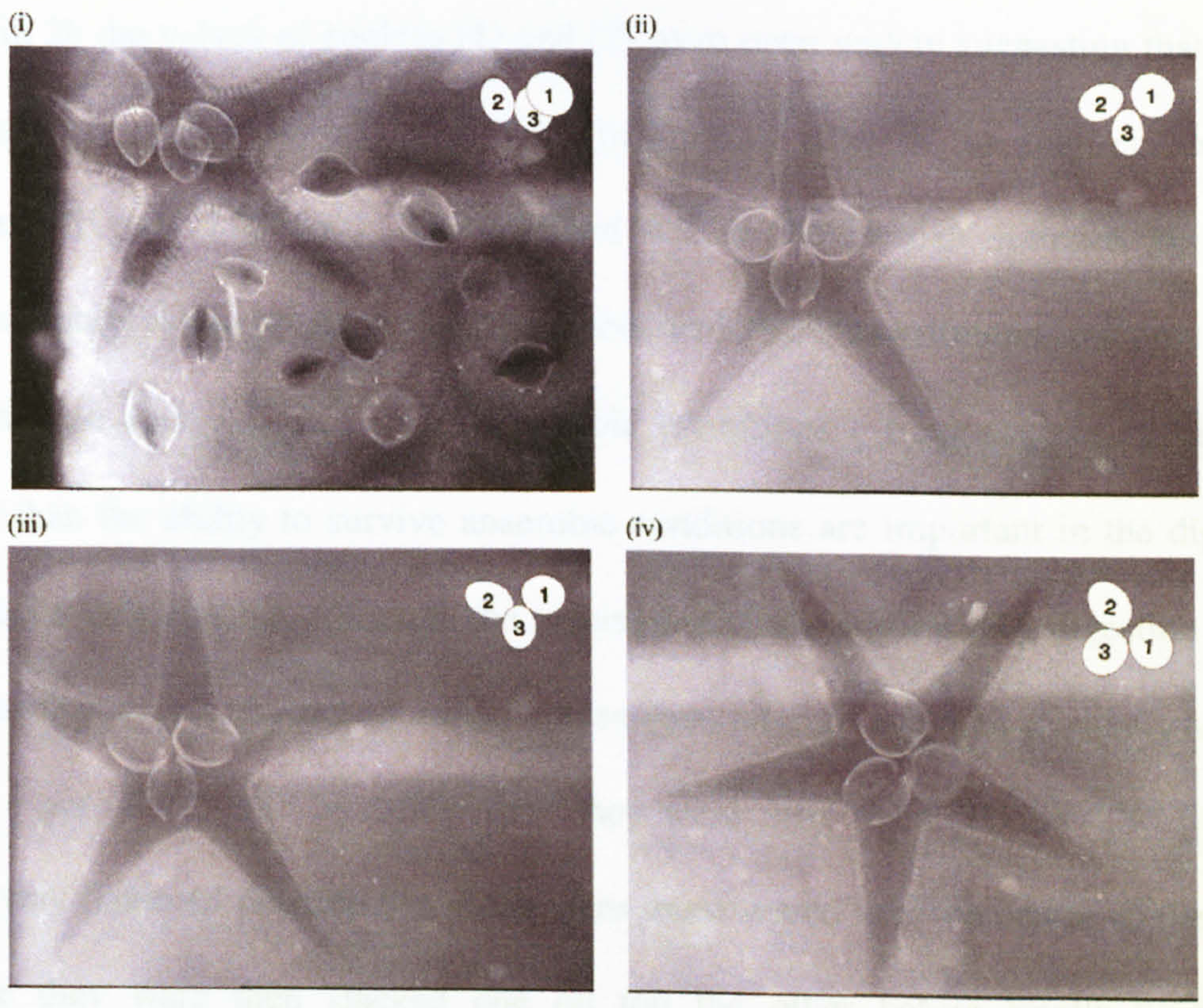
(b)

Shell length (mm)	Retention times (h)		
	Small	Medium	Large
4	15.5	10.9	7.7
8	26.6	19.5	14.3
12	39.0	30.7	24.1
16	41.6	31.6	23.9
20	46.0	37.4	30.4

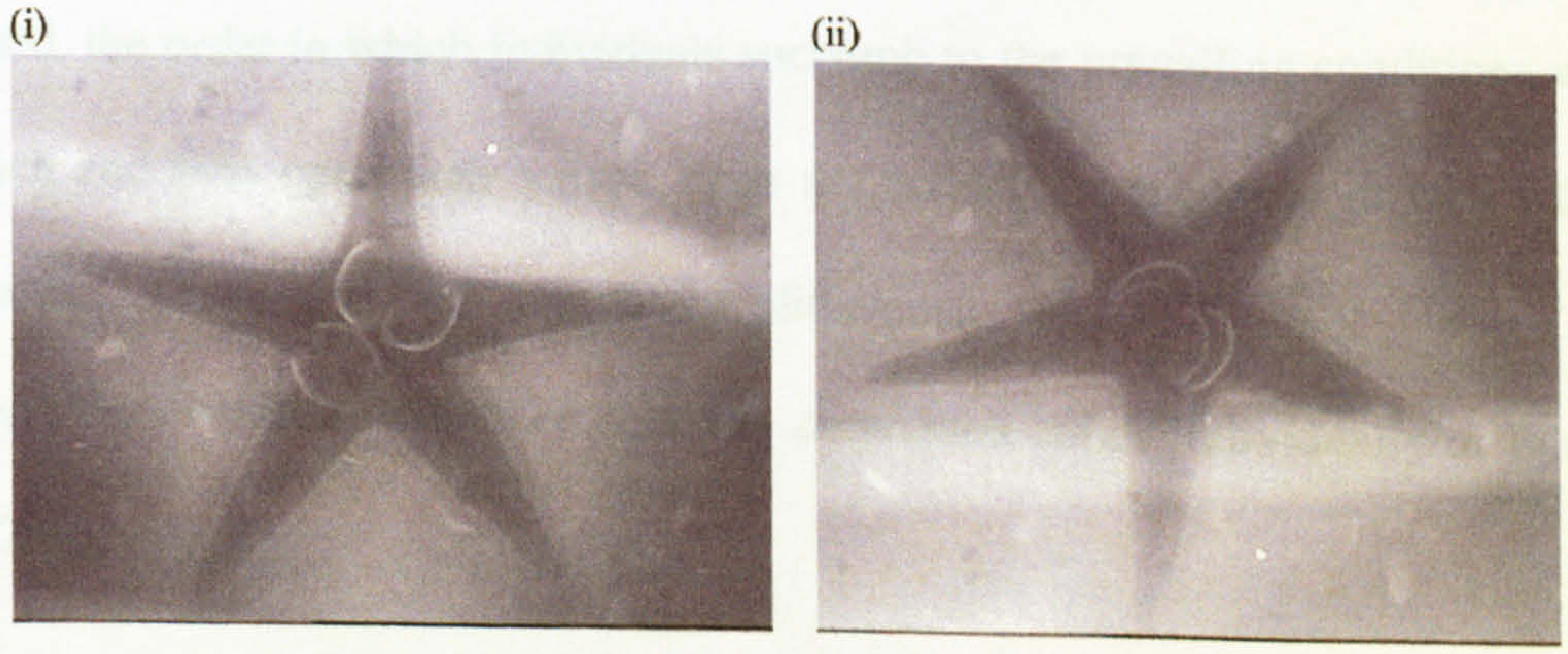
X-ray radiographs taken during periods when *C. edule* were retained within the stomach of *A. irregularis* revealed that prey survive for ~2h before they gape open and are, presumably, being digested by the starfish (Table 4.4). In Figure 4.3a(i) prey were ingested one at a time and positioned into the stomach pouches [Figure 4.3a(ii)]

Figure 4.3. X-ray radiographs of *Cerastoderma edule* within the stomach of *Astropecten irregularis* (a) the sequence of ingestion and valve opening of prey: (i) three ingested cockles (~5min); (ii) prey positioned into separate lobes of the stomach (after 30min); (iii) prey valves open indicating that digestion is taking place (after 2h), and (iv) prey valves extended; numbered symbols denote the order in which prey were ingested (after 2.5h). (b) The ejection of prey from the stomach: (i) prey valves laying fully extended and in the process of being manipulated for stacking (after 21h), and (ii) prey stacked one on top of the other and ready for simultaneous ejection through the mouth (after 22.5h).

(a)



(b)



presumably to maximize the space between prey so increasing digestion efficiency. Within 2h the valves of cockles (1) and (2) were open widely suggesting that digestion was already taking place [Figure 4.3a (iii)] whilst after 3h the final cockle (3) was opened [Figure 4.3a (iv)]. Prey survival within the starfish stomach is, therefore, considerably shorter than those times observed from experiments on prey retention (~24h) and survival rates under anaerobic conditions (~62h) suggesting that factors other than the ability to survive anaerobic conditions are important in the digestion of particular prey species. Although the precise time for complete prey digestion could not be established it is obvious that shell valves open after 2h and then gradually open wider over a period of ~18h by which time they were fully open [Figure 4.3b (i)]. In this relatively flattened position the shells were maneuvered into the centre of the stomach, where they were then stacked one on top the other before finally being ejected simultaneously, as a group, through the mouth [Figure 4.3b(ii)]. When several prey are ingested, the order in which individuals succumb to the prevailing conditions within the stomach and thus open their valves, does not reflect the sequence in which they were consumed. There was no significant difference (Mann-Whitney U=164, $P>0.05$) between the retention periods of *C. edule* consumed either individually or in multiples (~22-28h).

Table 4.4. The mean survival and retention times of *Cerastoderma edule* in the stomach of *Astropecten irregularis* (arm length) determined by x-ray radiography; time measured as the period between ingestion and when the valves are opened. *C. edule* survival times (h) under anaerobic conditions are also presented.

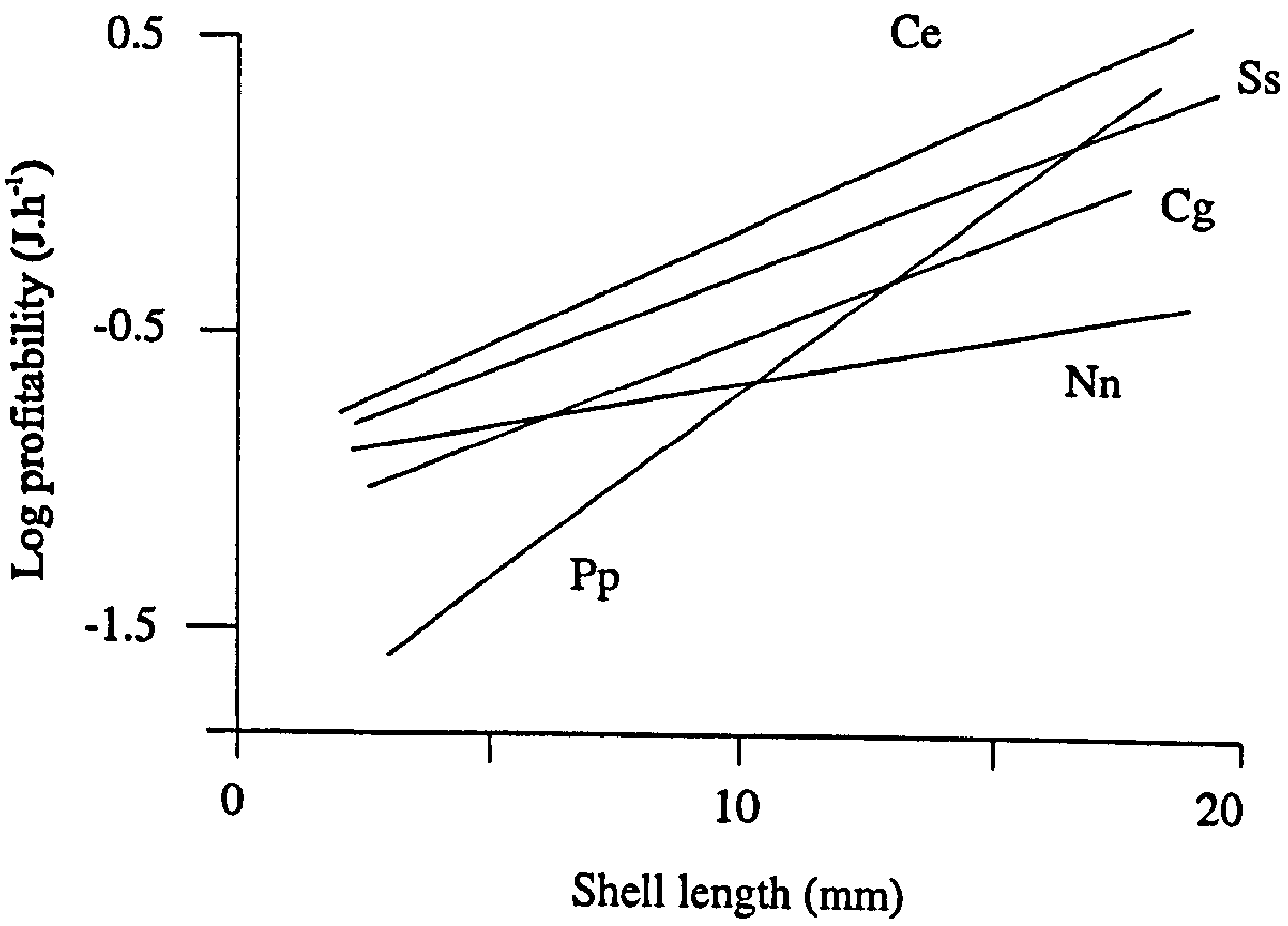
	A. irregularis	*C. edule*	Valves open		Retention		Anaerobic survival	
n	Arm length[a] (mm)	Prey length[a] (mm)	Time[a] (h)	Range	Time[a] (h)	Range	Time[a] (h)	Range
14	54.3 (4.4)	12.9 (0.5)	2.11 (0.6)	1.5-3.5	24.0 (1.1)	22.9-26.1	62.3 (4.3)	54.2-68.7

[a] Values are mean (±SD)

Prey profitability based on their retention times within the stomach of a medium-sized starfish (30-40mm) for *C. edule*, *S. subtruncata*, *G. fervensis*, *C. gallina*, *N. nitidosa* and *P. polianus* were positively related to prey size (Figure 4.4). This suggests that larger prey provide a greater source of energy and, therefore, the optimal prey size for starfish when prey are offered individually. By contrast, it is predicated that when starfish can pack the stomach with smaller prey items, such prey become more profitable (Figure 4.5). The maximum number of small beads of a similar size to *C. edule* that could be packed into the stomach of a large starfish (55mm) during this investigation was 260 (Table 4.5). This suggests that when small prey items are available at sufficiently high densities to enable starfish to fill their stomach, small rather than large prey become the optimal prey size. Prey profitability, however, was also found to be dependent on predator size, since the retention times for prey of the same size are shorter amongst larger starfish (Figure 4.6). In the prey size experiments (see Figure 4.1) where a range of different size classes of *C. edule* were offered simultaneously to starfish, the profitability of those prey consumed by each starfish generally showed that optimally sized prey were ingested (Table 4.6). For instance, the

Figure 4.4. Profitability ($J.h^{-1}$) of different prey species based on the regression of their retention time in the stomach of a medium-sized *Astropecten irregularis* (arm length 30-40mm); Abbreviations denote prey species; *Ce=Cerastoderma edule*; *Ss=Spisula subtruncata*; *Cg=Chamelea gallina; Nn=Nucula nitidosa* and

Figure 4.5. Predicted profitability ($J.h^{-1}$) of three different size groups of bivalve prey based on the regression of the maximum number of prey required to fill the stomach of different size classes of *Astropecten irregularis* and their prey retention times; predicted profitability of prey based on the following bead sizes; 4mm, 8mm and 12mm which closely resemble the globular shape of *C. edule*.


0.5
-0.5
-1.5
Log profitability (J.h^{-1})
Ce
Ss
Cg
Nn
Pp
0
10
20
Shell length (mm)

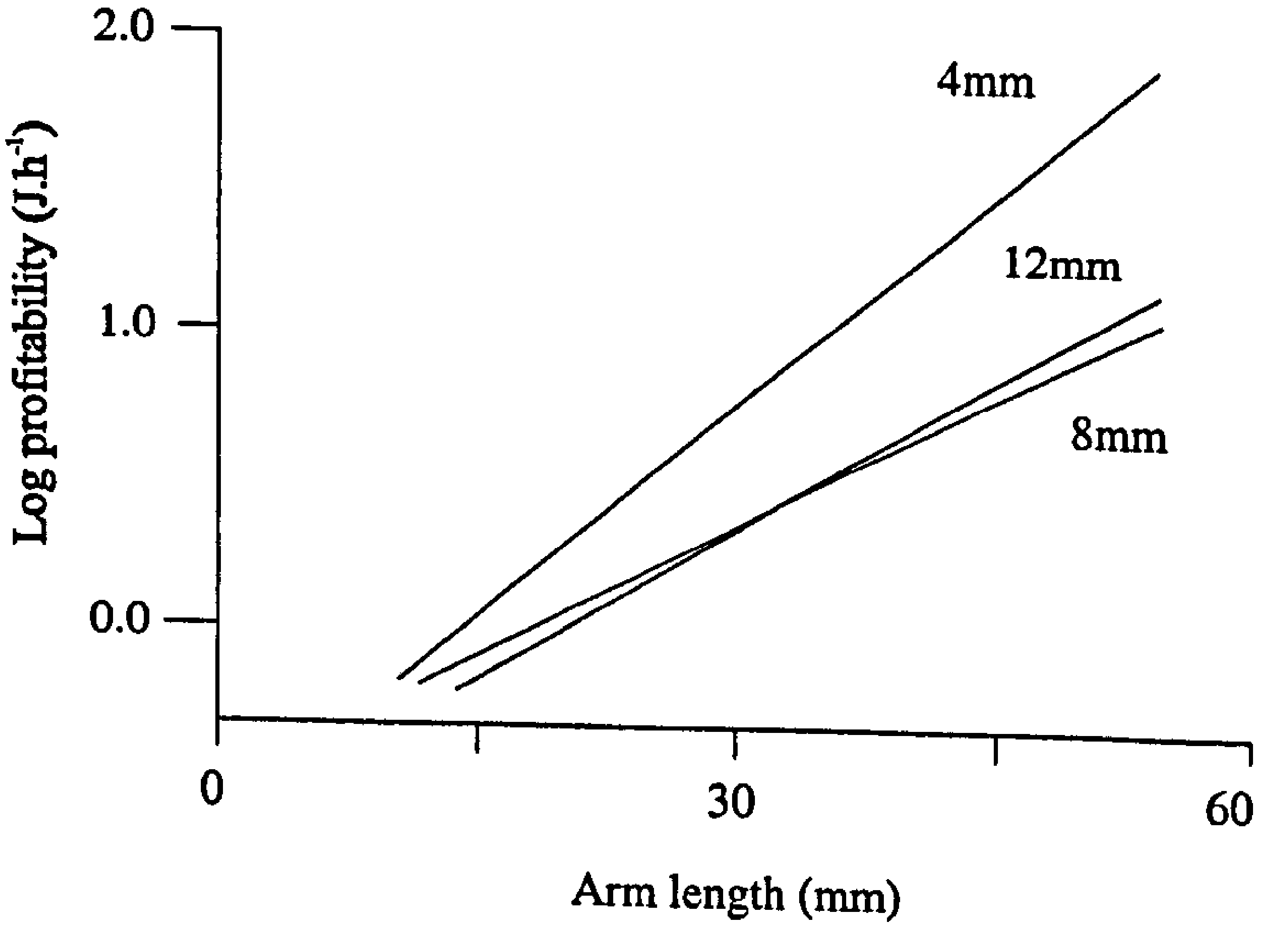
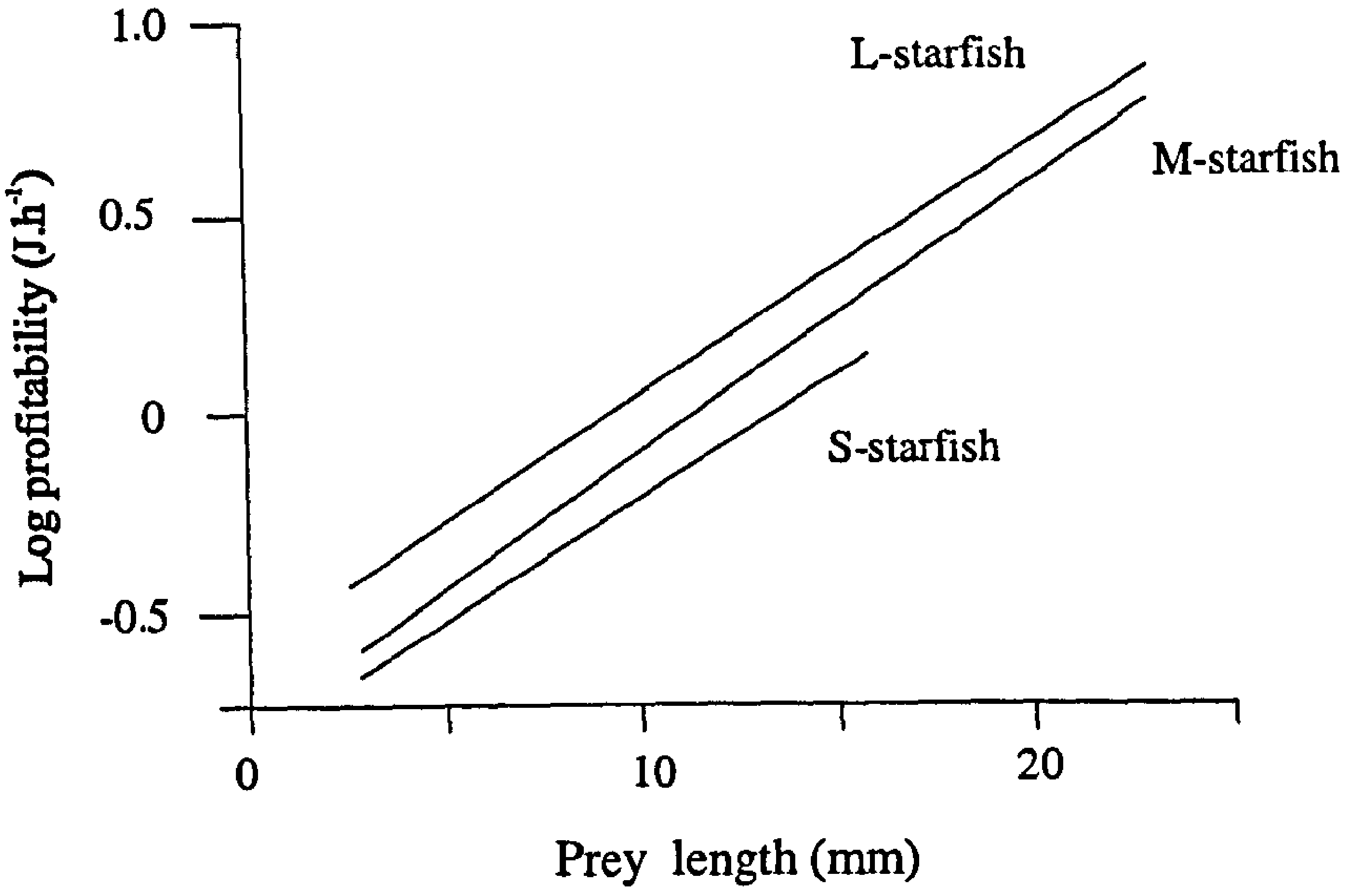
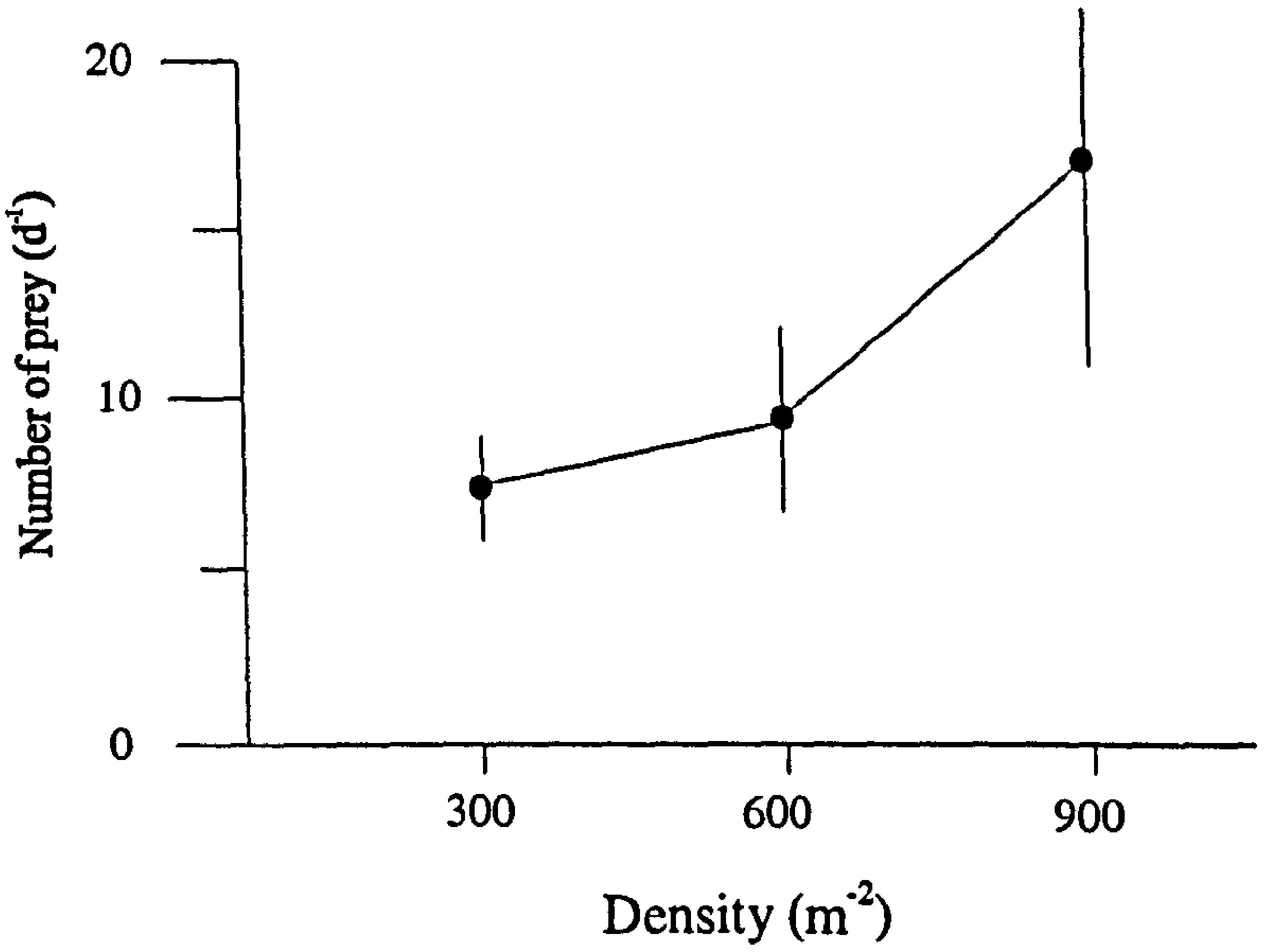

2.0
1.0
0.0
Log profitability (J.h^{-1})
4mm
12mm
8mm
0
30
60
Arm length (mm)

Figure 4.6. Profitability curves ($J.h^{-1}$) of different size classes of *Cerastoderma edule* based on the regression of their retention times in different size classes of *Astropecten irregularis;* abbreviations denote size classes of starfish; arm length, Small (20-25mm) Medium (35-40mm) and Large (50-55mm).

Figure 4.7. Functional relationship between the number of *Cerastoderma edule* (mean ±SD) consumed by *Astropecten irregularis* with increasing prey density.


1.0
0.5
0
-0.5
Log profitability (J.h^{-1})
0
10
20
Prey length (mm)
L-starfish
M-starfish
S-starfish


20
10
0
Number of prey (d^{-1})
300
600
900
Density (m^{-2})

profitability of prey consumed by larger starfish was optimal (6.49J.starfish.h^{-1}) when feeding on large prey (14-16mm) compared to prey consumed by smaller starfish, which was optimal (0.69J.starfish.h^{-1}) when feeding on smaller prey items (2-4mm).

A. irregularis responded to three different increases in *C. edule* densities by increasing its feeding rate (Figure 4.7). At the highest prey density, 900ind.m^{-2}, the number of prey consumed was approximately two and a half times greater than at the lower prey density, 300ind.m^{-2}, suggesting that the numerical abundance of prey is an important factor in controlling the consumption of bivalves by *A. irregularis.*

Table 4.5. The maximum number of beads from three size classes, bead diameter 4mm, 8mm and 12mm, required to pack the stomachs of different *Astropecten irregularis* of different sizes.

Bead size	*Astropecten irregularis* size classes (mm)									
(mm)	10	15	20	25	30	35	40	45	50	55
4	4	7	10	16	24	36	56	85	131	260
8	2	3	4	6	8	12	16	23	33	46
12	1	1	2	2	3	4	5	6	8	11

Table 4.6. Prey size selection experiment showing the rate at which *Cerastoderma edule* were consumed by *Astropecten irregularis* (ind.day^{-1}) and the profitability (J.h^{-1}) values for each amount consumed; starfish size classes, 20-25mm (small) 35-40mm (medium) and 50-55mm (large).

Prey size	Mean[a] consumption rate (ind.day^{-1})			Profitability (J.h^{-1})		
class (mm)	Small	Medium	Large	Small	Medium	Large
2-4	2.6 (0.4)	1.2 (0.7)	1.7 (0.3)	0.69	0.45	0.90
8-10	0.7 (0.3)	5.0 (1.2)	4.3 (0.8)	0.32	2.74	3.22
14-16	0.2 (1.1)	0.6 (0.5)	2.2 (0.2)	0.34	1.34	6.49
20-22	-	0.1 (0.3)	0.3 (0.3)	-	0.55	2.01
26-28	-	-	-	-	-	-

[a] Values are mean (±SD)

4.4. Discussion

Astropecten irregularis exhibits a distinct preference for certain molluscan prey (see Table 4.1a and b) with *Spisula subtruncata* and *Cerastoderma edule* being the most preferred species. In Chapter 3 it has been shown that *A. irregularis* feeds almost exclusively on *S. subtruncata* when this species is abundant within the benthos. Although *C. edule* is essentially an intertidal species and does not normally occur in the same habitat as *A. irregularis*, it is closely related to the subtidal cockle, *Parvicardium ovale* which was occasionally found within the diet of starfish in Red Wharf Bay. *Nucula nitidosa* was the species which was most likely to be ejected alive and on many occasions was avoided altogether by starfish during laboratory feeding experiments. Although *Polinices polianus* appeared to be equally unattractive, this species was rarely ejected alive once it had been ingested. Christensen (1970) similarly found that *S. subtruncata* and *C. edule* were clearly the most 'preferred' prey of *A. irregularis* in specimens collected from Danish waters and that *N. nitidosa* was only rarely consumed. Christensen also suggested that the higher than anticipated preference for *P. polianus* in laboratory experiments may have reflected the success rate of capturing these slow moving gastropods within the confines of an aquarium. In chapter 5, however, laboratory observations show that *A. irregularis* captures *P. polianus* very quickly, by responding to vibrations caused when this gastropod burrows into the sediment. It is suggested, therefore, that the low preference for this species shown by this study was not based on capture success, but on a combination of the time spent pursuing prey and the long retention period of this species within the stomach. Perhaps the ability of *P. polianus* to withstand long periods within the starfish stomach by maintaining a sealed operculum, is a mechanism that has evolved as a defense against starfish predation, especially since there appears to be no explanation for this gastropod to possess a high anaerobic endurance (*Pers. comms.* R. H. Emson). The selection of prey species by *A. irregularis* is not greatly influenced by their respective handling times, as most molluscan prey are captured and ingested quickly (see Chapter 5). The mechanism underlying the ability of starfish to differentiate between prey species must, therefore, depend on factors other than prey handling.

Prey size is probably one such factor in determining prey selection, particularly since *A. irregularis* is an intra-oral feeder and the size of the mouth restricts the size of prey that can be accommodated (Fenchel, 1965; Christensen, 1970; Doi, 1976; McClintock and Lawrence, 1981; Nojima, 1989; Beddingfield and McClintock, 1993). In this study size selection experiments revealed that small starfish usually selected small *C. edule*, whereas larger starfish consumed larger individuals, although the maximum size range of cockles consumed by any of the experimental starfish (arm length 25-55mm) was 20-22mm. In Red Wharf Bay, where most of the available prey was <10mm in length (see Chapter 3) the maximum size of prey found in the stomach contents of *A. irregularis* was positively correlated with starfish size, although the overall trend indicated that starfish generally consumed small prey. It appears that the maximum prey size is determined by the diameter of the mouth. Field and laboratory data, however, show that starfish on occasion are able to ingest extremely large prey items, exceeding those prey sizes predicted. In such cases, the ingestion of large bivalve prey, for example, often causes the body wall of the starfish to be become highly distended. When Beddingfield and McClintock (1993) presented large edible prey models (diameter 15mm) to *A. articulatus* (arm length 57.7±19.2mm) 23% were consumed, indicating that starfish can handle such prey. The Mediterranean species, *A. aranciacus* and *A. bispinosus*, frequently ingest larger prey items, particularly when small prey items are unavailable (Ribi and Jost, 1978). The impact of predation by *A. irregularis* on the population structure of its prey will also change with predator size, since a broader range of prey sizes and species will become increasingly more vulnerable to attack by larger starfish.

Christensen (1970) showed that a relationship existed between the retention period of molluscan prey within the stomach of *A. irregularis* following ingestion and their ability to survive anaerobic conditions. Findings from the present study support this observation although *N. nitidosa* was unusual in that it was able to survive long periods of anaerobic conditions and yet was more likely to be ejected alive than any of the other molluscan species, suggesting that this bivalve is particularly unpalatable to *A. irregularis* (Figure 4.2a and b). The 'preferred' prey of *A. irregularis* appear to be those species with lower resistance to anaerobic conditions and have the shortest retention times e.g. *S. subtruncata* and *C. edule*. Prey preference, however, is complicated by prey size, since a positive correlation exists between prey retention times and size, although there is considerable inter-species variability. Small (shell length 4mm) *C. gallina*, for example, had a shorter retention time (38.5h) than *P. polianus* (49.2h) but for individuals >8mm in length, the retention times of *P. polianus* is shorter than for *C. gallina*. Christensen (1970) similarly noted a change in prey preference by *A. irregularis* with increases in prey size; juvenile *C. gallina* (<4mm) for instance, were 'preferred' over juvenile *N. nitidosa*, but this preference was reversed when starfish were presented with larger (>15mm) individuals. These results it is suggest that the profitability of different size prey will alter during the lifetime of a predator, since larger starfish consume larger prey items, presumably as a result of an increase in mouth diameter.

A negative relationship existed between the retention period of bivalve prey and starfish size, with small prey being retained in the stomachs of large starfish for a shorter period of time than in smaller starfish (see Table 3b). The retention of prey within the starfish stomach can be divided into several stages i.e. (i) the ability to survival the period between ingestion and the start of digestion (ii) the time required for complete digestion of all flesh, and (iii) the ejection of empty shells from the cardiac stomach by the stomach wall muscles. Although the complete digestion of all flesh (stage iii) could not be precisely determined, each of these stages will vary between prey species and that bivalve prey, regardless of starfish size, will be retained for a minimum period of ~6h. Christensen (1970) similarly noted that the shells of small *S. subtruncata,* which generally have a short retention period, were retained in the stomach of all size classes of *A. irregularis* for a minimum period of 7h. It is predicted, therefore, prey preference by *A. irregularis* should switch between species depending on their relative size and thus their ability to survive the anaerobic conditions of the stomach. Such preferences, however, will vary according to predator size.

Although there is a strong relationship between prey retention and their survival under anaerobic conditions, x-ray radiography has revealed that the survival time of *C. edule* following ingestion is considerably shorter than that expected from experimental trials on anaerobic survival. This would suggest, therefore, that factors other than anaerobic endurance influence prey survival once ingested by the starfish. Christensen (1970) noted that once prey were ingested by *A. irregularis* they were not bathed in a pool of digestive enzymes, enabling prey to prolong survival providing both shell valves were closed tightly. Christensen speculated that prey may open their valves several times before death, since the lobes of the stomach could not penetrate a gap <1mm wide. In general, asteroids digest their prey only at the site where contact between the stomach wall and prey tissue occurs (Anderson, 1959). In this present study the premature ejection of bivalve prey following ingestion e.g. *C. gallina* suggests that in some individuals valves may remain closed sufficiently long enough to be discarded in favour of a less 'robust' individual, although this is presumably when other prey are available. The precise mechanism used by *A. irregularis* to 'determine' whether to eject or withhold a 'robust' prey still remains unclear. In the sea hare *Aphysia daetylomela* a free-back mechanism exists whereby changes in the blood-glucose level may determine its preference for a particular prey species, although this mechanism has yet to be fully demonstrated (Carefoot, 1991). It is plausible, therefore, that a similar mechanism may exist in *A. irregularis* during prey selection.

X-ray radiography has shown that when several prey items are ingested by *A. irregularis* they are pushed by the stomach muscles into separate pouches of the stomach, thereby providing a greater surface area for contact between the stomach wall and each prey item. Moreover, x-ray radiography confirmed that prey are digested simultaneously, an observation supported by the occurrence of >50 partially digested juvenile prey species within the stomach of a single *A. irregularis* collected from Red Wharf Bay (see Chapter 3). In Danish waters, Christensen (1970) found ~500 juvenile *S.*

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subtruncata (<3mm) within the stomach of a single *A. irregularis*, most of which were partially digested, thus suggesting that large numbers of prey can be simultaneously digested.

Previous studies have shown that *Astropecten* spp. choose those prey sizes which maximize net energy intake per unit foraging time (Doi, 1976; Beddingfield and McClintock, 1993). Beddingfield and McClintock, (1993) reported that *A. articulatus* was able to distinguish between edible prey models of different calorific value and when a size range of models were offered to starfish the smallest models were consumed. The authors concluded that small prey models were easier to handle and ingest by starfish, thereby maximizing the amount of food ingested per unit time. In this present study, the retention times of different size classes of prey show that the profitability of prey per unit time and prey preference becomes increasingly more dependent on prey size. It is predicted that when *A. irregularis* is confronted with a choice of prey items of different size, preference will be given to the smallest size range but only when these are in sufficient numbers to enable starfish to pack their stomachs. This preference should change, however, when larger prey are encountered at lower population densities. Although, these two cases represent extreme ends of size selection by *A. irregularis*, profitability of prey based on different size classes and retention times, indicate that smaller prey are more profitable when the stomach is packed to its maximum capacity, whereas larger prey become more profitable if these are ingested singly. Field data from Red Wharf Bay support these predictions since several hundred juvenile bivalve prey have been found in a single starfish stomach during a period of heavy prey settlement.

At other times of the year when population densities of prey are low, single large prey items occur more frequently in the stomach of *A. irregularis*.

In the laboratory, *A. irregularis* exhibited a functional response to an increase in prey density where feeding rates showed a four-fold increase at the highest prey density ($900m^{-2}$). At this high prey density starfish were observed ingesting prey until their stomachs became highly distended; this usually involved 'gorging' after which starfish burrowed into the sediment and remained quiescent for up to two days. This suggests that a threshold prey density may be needed before the starfish ingest prey at these high population densities. Such prey, however, must be small enough to enable maximum stomach packing. Increases in the consumption of prey were also shown in *A. aranciacus* when provided with a surplus of food (Ribi and Jost, 1978).

Since optimal foraging theory predicts that predators should rank their prey in order of profitability (Charnov, 1976) predators must be able to recognize certain prey characteristics which optimize the potential energy yield per unit foraging time (Hughes, 1980). Prey selection by *A. irregularis* must, therefore, involve the differentiation of prey based on information related to prey size, retention 'endurance', prey density and palatability. Such information may become confounded when the starfish simultaneously encounter different prey species, which may also vary in size, suggesting that the 'decision' whether to ingest or ignore prey must be re-evaluated by the starfish during each foraging excursion. Since *A. irregularis* is a non-visual predator the recognition of prey must presumably involve a combination of manipulation by the tube feet and olfactory stimuli in order to elicit a response to either attack or reject the prey.

To evaluate prey selection based on these factors would require a multivariate analysis using a log-linear model to establish the most important criteria influencing prey selection. Some progress has already been made in this area but requires further work which is outside the time-scale of the present thesis.

CHAPTER 5

Prey Capture and Locomotory Activity of *Astropecten irregularis*

5.1. Introduction

Although many previous studies have examined the capture and ingestion of prey by starfish (Chia and Amerongen, 1975; O'Brien, 1976; Anger *et al.*, 1977; Dearborn, 1977; Scheibling, 1980b) these have generally focused on extra-oral feeding mechanisms. The starfish *Stylasterias forreri*, for example, has prey-catching pedicellariae armed with formidable jaws which are raised when prey settle on its aboral surface (Chia and Amerongen, 1975) whilst *Asterias rubens,* as well as feeding extensively on bivalves, is capable of catching 'fast-swimming' isopods on the suckers of their tube feet (Anger *et al.*, 1977). The seizure and ingestion of prey by *Astropecten irregularis* is generally poorly documented, although several studies which have described the capture of molluscan prey by *A. aranciacus* and *A. irregularis* have generally only presented details of the excavation of prey from the sediment and prey ingestion (Power, 1857; Mangold, 1908; Christensen, 1970).

Starfish are generally considered to be slow-moving creatures that lie in/on or cling to the substratum for most of the time moving only intermittently to search for food or to avoid some physical stress (Feder and Christensen, 1966). The rate of locomotion in asteroids, however, generally depends on whether the ends of the tube feet have suckers. The slowest moving species such as, *Asterias rubens* (Romanes and

Ewart, 1881) *A. forbesi* (Loosanoff, 1958) and *Acanthaster planci* (Goreau, 1964) are those possessing suckers, whereas the fastest moving starfish, which include species of *Astropecten* and *Luidia*, are those which lack suckers (Feder and Christensen, 1966). There are exception, however, the starfish *Pycnopodia* spp., for example, which feeding on other asteroid species has suckers on its tube feet yet is capable of fast locomotory movement (Sloan and Robinson, 1988). Ferlin (1973) noted that a large (arm length 65mm) *A. auranciacus* moves at an average velocity of 20cm.min^{-1}, although several individuals of a similar size showed instantaneous velocities ranging between 50 and 140cm.min^{-1}. Many of these estimates, however, are probably maximum speeds which occur only when starfish scented food or needed to avoid immediate danger (Feder and Christensen, 1966). Information regarding the locomotory rates of *A. irregularis* when foraging have not previously been documented.

The locomotory activities of many marine invertebrates are synchronized by exposure to exogenous environmental variables such as diel and tidal cycles, and in constant laboratory conditions they can often be free-running, which are under endogenous physiological control (Bolt and Naylor, 1985). Although endogenously controlled behaviour in asteroids has previously been documented (Fenchel, 1965; Thain, 1971) most information relates to other echinoderm groups, including holothurians and echinoids (Yamanouti, 1939; Sinclair, 1959; Magnus, 1963; Berrill, 1966). *Asterias rubens* exhibits diurnal migrations moving to the upper surfaces of rocks at dusk and then to the undersurfaces at dawn. In subtidal asteroids such as *Astropecten*, diurnal patterns of locomotory activity have been reported (Power, 1857; Mori and Matutani, 1952; Burla *et al.*, 1972; Ferlin-Lubini and Ribi, 1978; Nojima, 1981). Mori and Matutani (1952) showed that *A. polyacanthus* exhibits a daily rhythmic behaviour entrained by light and which continues for several days under constant laboratory conditions. Ferlin-Lubini and Ribi (1978) similarly reported that light was an important factor governing locomotory activity patterns in *A. aranciacus, A. bispinosus* and *A. jonstoni*, although several other factors including seawater temperature, oxygen consumption and hydrogen ion changes within the body, and the availability of food also influenced activity, albeit to a lesser extent.

In this study the capture of different prey species by *A. irregularis* and the locomotory activity patterns of this starfish at different water velocities, and under different light regimes are examined. In addition, the speed and duration at which starfish move when foraging have been investigated with reference to predator size and prey availability.

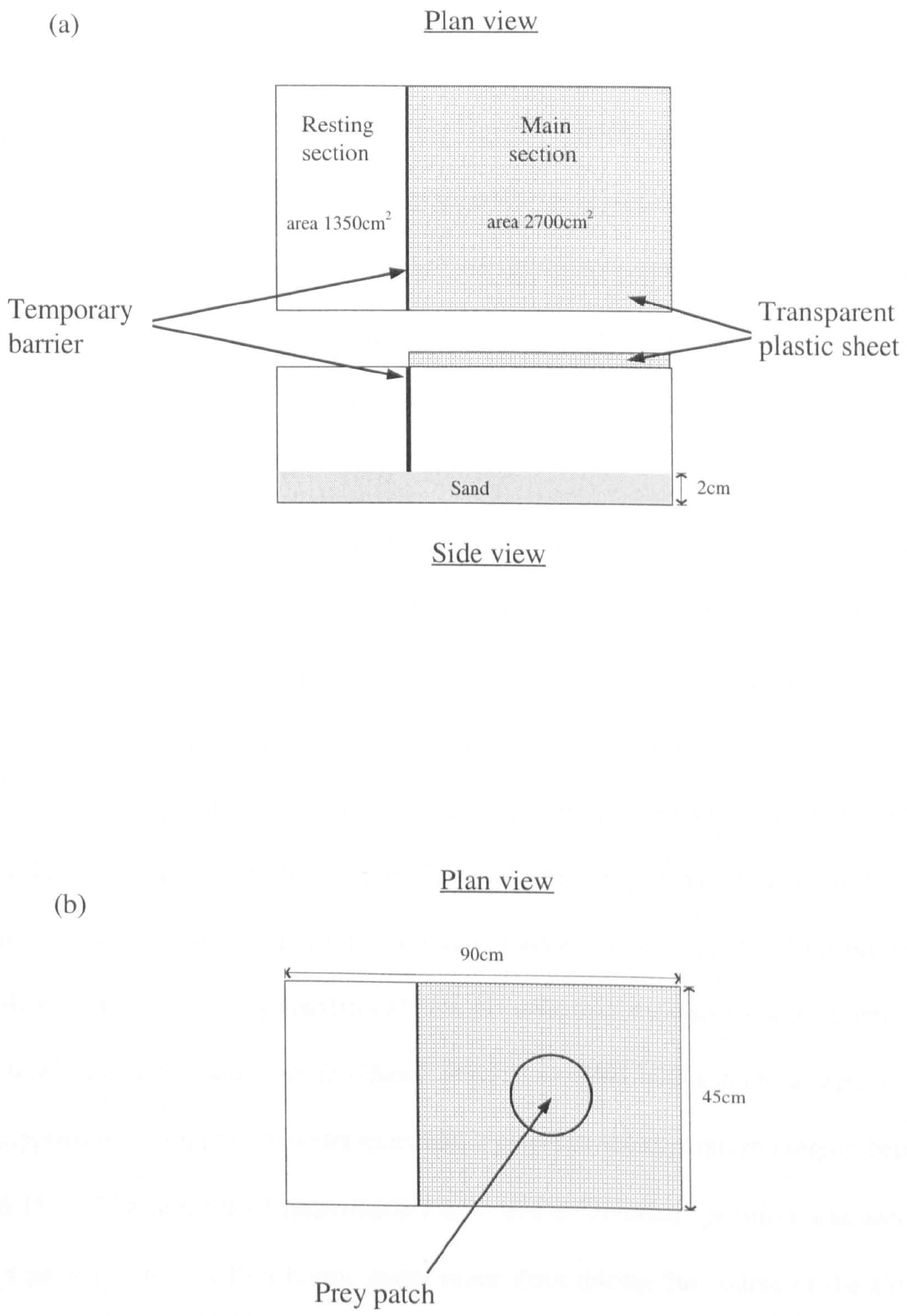
5.2. Material and methods

The ability and technique used by *Astropecten irregularis* to capture different kinds of prey were examined in the laboratory using a video camera and a time-lapse video recorder, and direct visual observations. A total of twenty starfish (arm length 35-50mm) were kept individually in aquaria (area 450cm^2 30x15cm) filled with sand to a depth of 5cm and supplied with running seawater at ambient temperature (10°C). Individual starfish were then presented with each of the following prey species, *Cerastoderma edule* (shell length 5-8mm) *Polinices polianus* (shell length 6-10mm)

Ophiura ophiura (disc diameter 5-10mm) and *Diastylis rugosa* (body length 6-10mm) and the techniques used to capture these prey identified.

Two laboratory experiments were undertaken (i) to determine the average locomotory speed of *A. irregularis* from three different size categories; arm length 20-25mm (small) 35-40mm (medium) and 50-55mm (large) and (ii) to estimate the speed of locomotion exhibited by *A. irregularis* moving over open sand, moving over a prey patch, and when pursuing mobile prey. A total of sixty-five starfish were used in these experiments and individual speed trials were conducted in a single aquarium (4000cm^2 80x50cm) filled with sand to a depth of 2cm and maintained at an ambient seawater temperature of 10°C (Figure 5.1a). The tank was divided into two sections a resting area and the main area, which were both separated by a temporary barrier, so that starfish could be isolated from the main section (3325cm^2 95x35cm) of the aquarium. A transparent plastic sheet marked with a series of grid squares (1cm^2) was placed over the top of the main section. Before the start of each experiment six starfish were placed within the resting area and allowed to burrow into the sediment. In the first experiment speed trials were conducted using six starfish from each of the three size classes, but only a single individual which had emerged 'naturally' from the sediment was released into the main section during each trial. The time and distance covered by each starfish was recorded by marking the position of the start and finish of each movement interval. Recordings were stopped once starfish touched the side of the aquarium. In the second experiment medium-sized starfish were offered ten *C. edule* (4-6mm) which were placed at the centre of the main section of the aquarium and were designated as a 'prey patch' (Figure 5.1b). Speed trials commenced once a starfish was released from the resting area into

Figure 5.1. Diagramatic representation of the aquaria experimental protocol to assess (a) The locomotory speed of *Astropecten irregularis* from three different size classes; arm size 20-25mm (small) 35-40mm (medium) and 50-55mm (large) were examined. (b) The speed of starfish when presented with a dense patch of *Cerastoderma edule.*


(a)
Plan view
Resting section
area 1350cm^2
Main section
area 2700cm^2
Temporary barrier
Transparent plastic sheet
Sand
2cm
Side view
(b)
Plan view
90cm
45cm
Prey patch

the main section of the aquarium and the time and distance covered by each individual, before, during and after prey were encountered within the 'prey patch' were recorded. The speed of the starfish when pursuing highly mobile prey was determined by simulating moving prey; this was achieved by vibrating a piece of plastic cord, back and forth within the sediment, just in front of an arm tip. In preliminary trials such vibrations induced starfish to chase the cord, providing the vibrations were sufficiently frequent to reinforce pursuit. Recordings ceased when starfish touched the side of the aquarium.

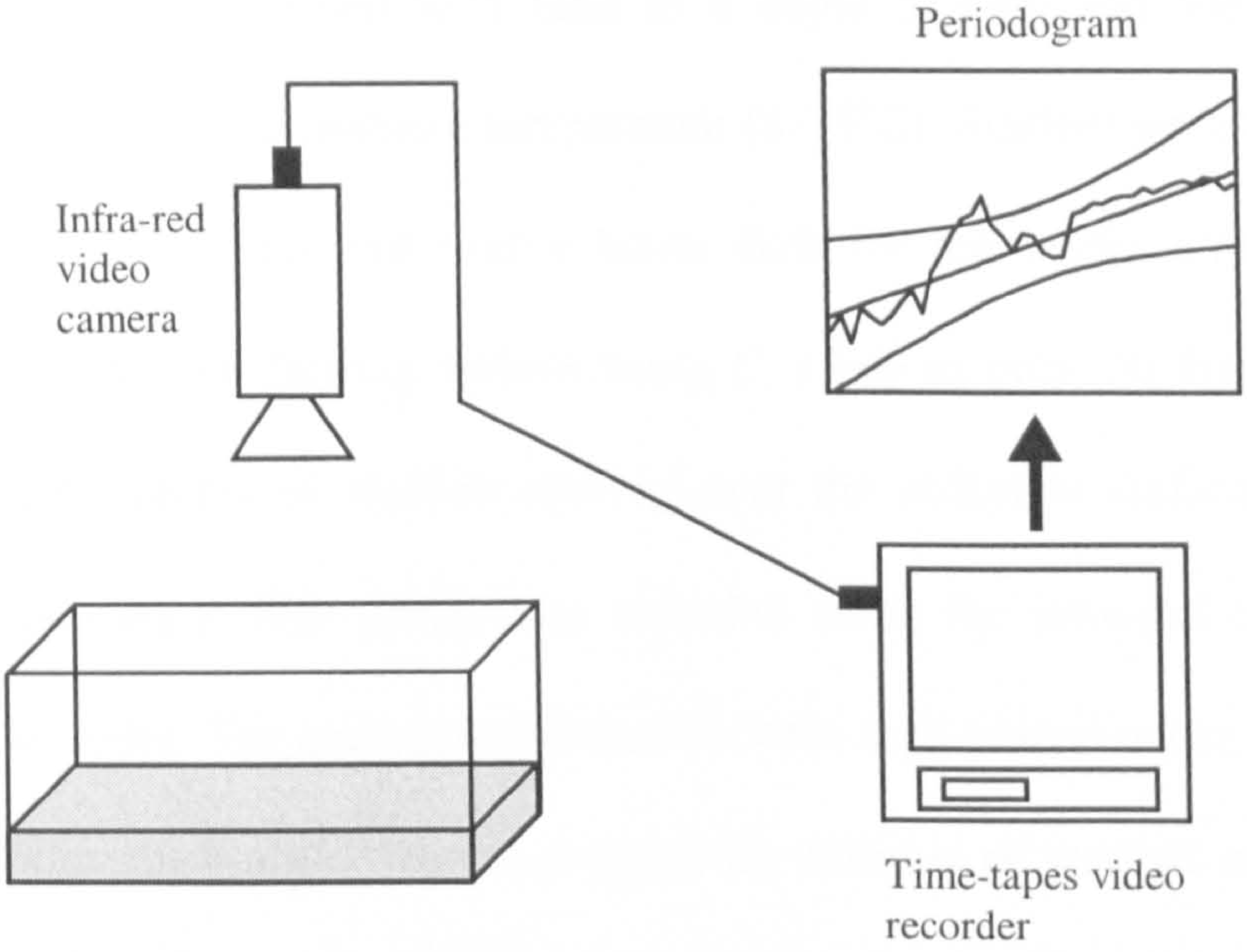
Preliminary laboratory observations indicated that starved *A. irregularis* could occasionally be found lying upside down with their mouth uppermost and their arms curled underneath the body, a position which supports the body clear of the sediment. Since starfish can remain in this 'inverted' position for up to two hours before turning over and burrowing into the sediment, and since ciliary-feeding associated with the mouth has been reported in *A. irregularis* (Gemmill, 1915) an experiment was conducted to determine whether this unusual behaviour was associated with prolonged periods of starvation. Thirty starfish (25-50mm) were left without food for a period of eight weeks in a large aquarium (3325cm^2, 95x35cm) filled with sand to a depth of 5cm and supplied with running seawater maintained at ambient temperature ranging between 8 and 10°C. The number of individuals found in the 'inverted' position was recorded over a period of twenty-four hours, every seven days during the course of the fifty-six day experiment. The same experimental protocol conducted to act as the control with starfish receiving a daily supply of *C. edule.*

Since illumination is considered to be an important factor in controlling the locomotory behaviour of *Astropecten* (Mori and Matutani, 1952) a light meter (LI-COR underwater quantum sensor) lowered off the Research Vessel the Prince Madog was used to record the attenuation of light at various depths at the main study site in Red Wharf Bay. A laboratory experiments was conducted to examine whether changes in light and dark would affected the daily locomotory activity patterns of *A. irregularis.* In March 1998 locomotory activity of thirty freshly caught starfish (35-50mm) collected from Red Wharf Bay was investigated in an aquarium (4000cm^2, 80x50cm) filled to a depth of 6cm with sand, supplied with gently running seawater (10°C) and maintained under constant darkness. Locomotory activity was recorded continuously for five days using an infra-red camera and time-lapse video recorder, and the number of starfish moving on the sediment surface at 15min intervals were recorded from the tapes and this data subjected to periodogram analysis (see Bolt and Naylor, 1985).

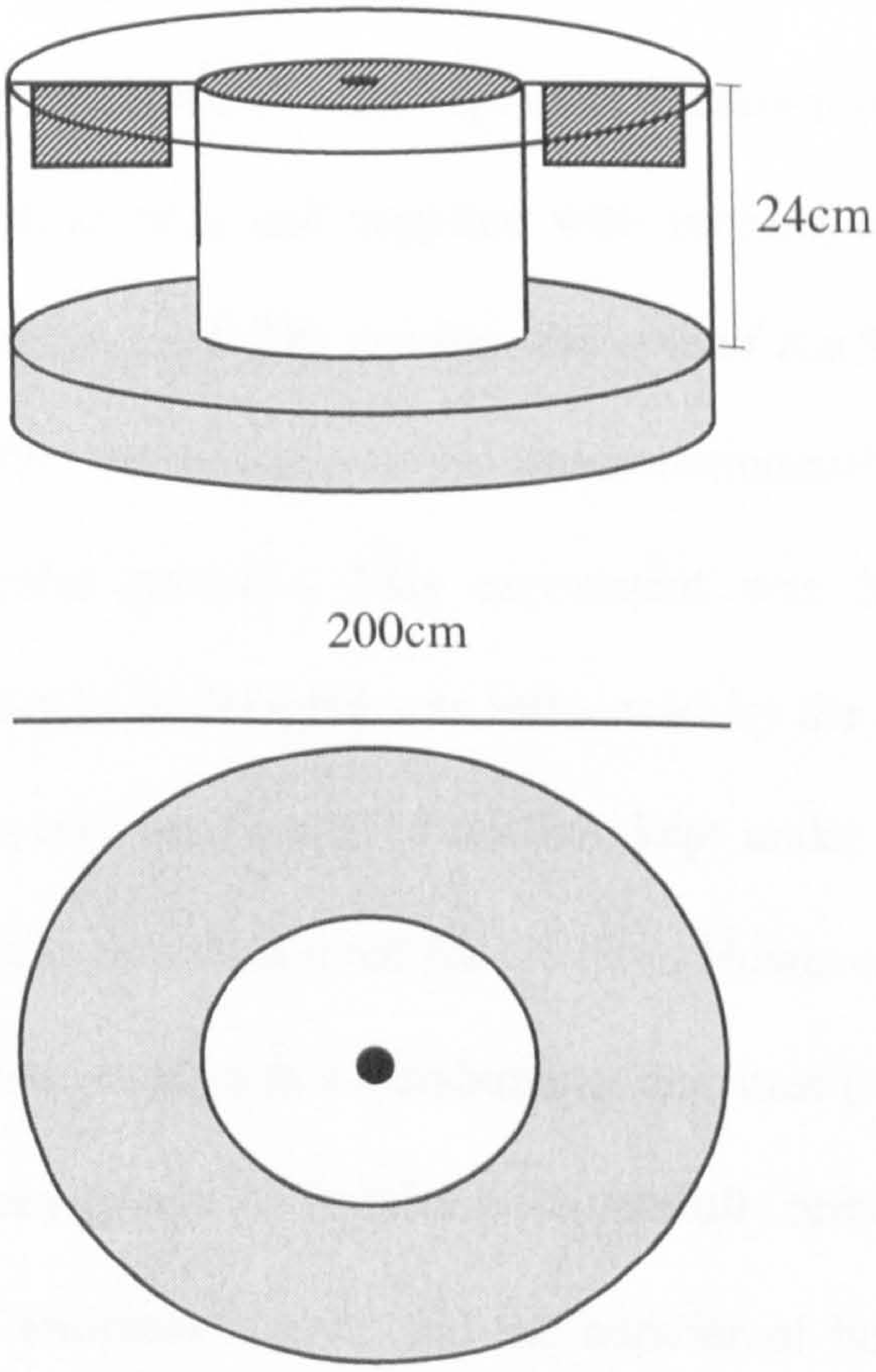
Following the results of these observations, two experiments were conducted to determine whether (i) locomotory activity could be altered by changes in different water velocities, and (ii) the locomotory activity could be entrained to a diurnal cycle of light and dark. In the first experiment the activity patterns of twenty starfish (36-44mm) at different water velocities were studied in a circular flume (5500cm^2, 100x55cm) (Figure 5.2). Starfish were initially placed in water at zero velocity for a period of one hour thus simulating slack water conditions, and then exposed to hourly changes in water velocity from 0.17 through 0.30 to 0.57m.s^{-1} before returning to zero velocity over the same hourly regime. The number of starfish moving over the sediment surface and their relative position was recorded every 15mins over a twenty-four hour period. In the

Figure 5.2. Diagramic representation of the experimental protocal to assess (a) The locomortory activity of *Astropecten irregularis* using an infra-red camera, time-lapse video recorder and periodogram analysis, and (b) The locomotory activity of *A. irregularis* with changes in water velocity within a circular flume.

(a)


Periodogram
Infra-red video camera
Time-tapes video recorder

(b)


24cm
200cm

second experiment a total of forty starfish (20-60mm) were placed into two large aquaria (4000cm^2, 80x50cm) filled with sand to a depth of 6cm and supplied with running seawater maintained at ambient temperature (8-10°C). Starfish were kept under a regime of twelve hours light and twelve hours dark for ten weeks without being disturbed, apart from regular feeding periods using *C. edule* as prey. At the end of the ten week period the number of starfish moving over the sediment surface at 15min intervals over a forty-eight hour period was recorded using the intra-red camera and time-lapse video recorder. The experimental starfish were then placed under continuous darkness for a further forty-eight hours and again the number of starfish moving was recorded; all data were subjected to periodogram analysis.

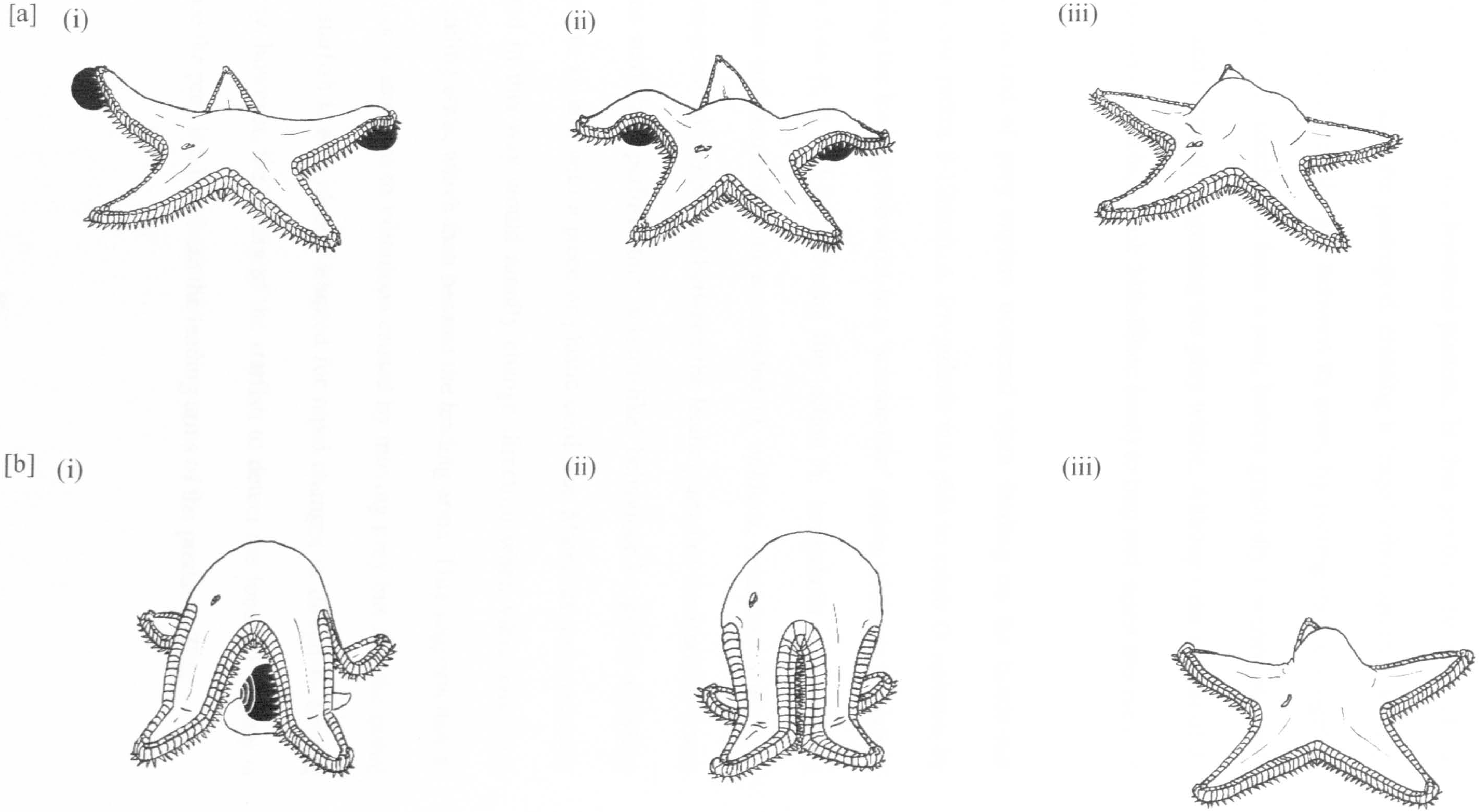
A further laboratory experiment was conducted to determine whether different size classes of *A. irregularis* exhibited different periods of locomotory activity. A total of forty small, medium and large starfish were kept in an aquarium (4000cm^2, 80x50cm) filled with sand to a depth of 6cm and supplied with running seawater at ambient temperature (10°C) but without food. The number and size of starfish moving over the sediment surface during a five day period were recorded continuously using the infra-red camera and time-lapse video recorder. This experiment was further expanded to determine whether the duration of foraging was influenced by the availability of food. The foraging activity of twenty medium-sized starfish, kept under the same conditions as in the previous experiment, was monitored for ten days. However, on the fifth day *C. edule* were presented to these starfish at superabundant densities (~600m^2) for a period of three days after which any remaining cockles were carefully removed. The number of starfish moving over the sediment surface and the number of burrowing attempts to locate prey were recorded every hour over a twenty-four hour period, prior to, during and post introduction of prey.

5.3. Results

In laboratory aquaria four different methods used by *Astropecten irregularis* to capture prey were identified. Each method was triggered either by direct contact with the prey or by the vibrations caused when the prey were moving or attempting to escape; usually such vibrations only elicited a response from the starfish and are detected when the starfish is within 2cm of the prey item. The first method of prey capture involved the multiple entrapment of *Cerastoderma edule* when *A. irregularis* encountered a dense patch of prey. Using an 'arm-curling' technique starfish were able to gather several prey items, providing they were within reach of two or more outstretched arms [Figure 5.3a (i, ii and iii)]. During this technique the tube feet assisted in the excavation of prey, enabling each prey item to be passed beneath the arms towards the mouth, where they were then ingested. Up to three *C. edule* (shell length 5-6mm) could be observed being handled simultaneously in this manner. The entire process from seizure of prey to ingestion took 140±34sec (n=18).

The second method of prey capture involved another molluscan prey, the gastropod *Polinices polianus* (shell length 6-9mm). Since this species is more mobile it was captured in a very different way [Figure 5.3b (i, ii and iii)]. As *P. polianus* attempted to escape from an attacking starfish, usually by burrowing rapidly into the

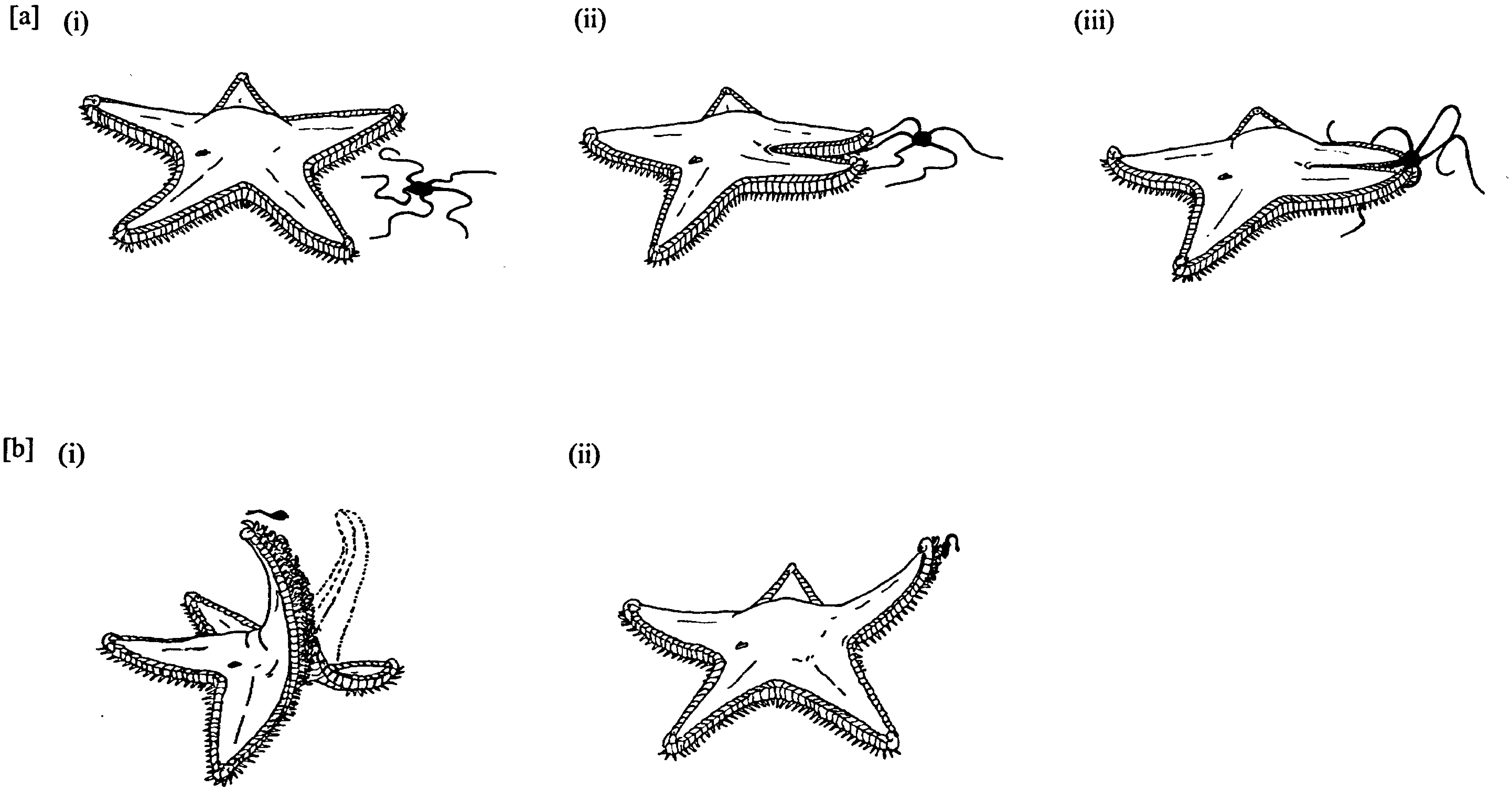
Figure 5.3. Prey capture by *Astropecten irregularis* [a] (i) simultaneous capture of two *Cerastoderma edule* using the ‘arm curling’ technique (ii) The prey being passed forwards to the mouth of the starfish using the tube feet (iii) prey ingestion. [b] (i) the hunched body posture of *A. irregularis* which creates a ‘cage’ with its arms surrounding *Polinices polianus* thus preventing escape (ii) the arms are quickly brought together trapping the gastropod (iii) the starfish lowers its body over the prey and ingests it whole.


[a]
(i)
(ii)
(iii)
[b]
(i)
(ii)
(iii)

sediment, the escape was prevented when the starfish moved into a position directly over the prey placing its body in a hunched posture. In this position the arms of the starfish effectively surrounded the gastropod, creating a 'cage' effect around the prey. The starfish then rapidly closed the gap between its arms, by pulling its arms together until their marginal-spines touch and form a seal, before gradually lowering its body over the gastropod and eventually ingesting the prey whole. Although the pursuit of *P. polianus* by starfish was variable, it took 240±89sec (n=8) to trap and ingest this prey.

The third method of prey capture occurred when feeding on the brittle-star *Ophiura ophiura* (disc radius 8-12mm). *A. irregularis* was able to catch *O. ophiura* by opening and closing the leading two arms in a 'scissor-like' action whilst in pursuit of the prey [Figure 5.4a (i, ii and iii)]. During this action *A. irregularis* could sustain forward acceleration and frequently out accelerated *O. ophiura*, resulting in the prey being quickly over-powered and pinned between the leading arms of the starfish. It was possible to induce starfish to perform this 'scissor-like' behaviour by gently vibrating the sediment close to an arm with a piece of plastic cord (see Materials and methods). Starfish stimulated in this way would rapidly change direction when vibrations were presented to the trailing arms, which then became the leading arms. This suggests that *A. irregularis* is not only sensitive to vibrations caused by moving prey but that the radial symmetry of the starfish is also ideally adapted for rapid changes in direction. During the pursuit of prey, however, the ability of the starfish to detect the location of prey is generally lost once the prey is >1cm from the leading arms of the predator. This

Figure 5.4. Prey capture by *Astropecten irregularis* [a] (i) starfish approaching *Ophiura ophiura* (ii) *O. ophiura* attempts to escape but the starfish responds by chasing prey, opening and closing its two leading arms in a ‘scissor-like’ action (iii) the starfish accelerates, capturing the prey by holding it between closed arms. [b] (i) *Diastylis rugosa* attempts to escape as *A. irregularis* ‘swipes’ its leading arm from side-to-side (ii) a single *D. rugosa* is caught as the arm makes contact and the tube feet exert a suction force which prevents the prey from escaping.


[a]
(i)
(ii)
(iii)
[b]
(i)
(ii)

suggests that *A. irregularis* has a rather poor olfactory sense and that starfish rely more on tactile stimuli than chemical cues when locating their prey.

A fourth method of prey capture involved another fast-moving prey, the cumacean, *Diastylis rugosa* (carapace length 6-10mm). When starfish detected *D. rugosa*, a swarming response by this prey species occurred and starfish quickly raise a single arm, swiping it from side to side in an attempt to catch the prey; this arm action can be maintained at forward speed. Once a single *D. rugosa* was touched by the arm the tube feet appeared to become 'sticky' and able to hold prey firmly [Figure 5.4b (i and ii)]. It is suggested, therefore, that the tube feet only become 'sticky' in response to feeding on mobile. As the arm was rapidly lowered to the sediment surface the tube feet passed the struggling cumacean towards the mouth where it was quickly ingested. The time taken to ingest prey once captured took 67±35sec (n=3).

In the laboratory a positive correlation was detected between starfish size and the speed of movement across the sediment surface when foraging (Pearson r=0.795, P<0.05) (Table 5.1a). The overall locomotory speed of starfish was highly variable; small starfish (20-25mm) moved at an average speed of 33.6±16.8cm.min^{-1}, whereas the largest starfish (50-55mm) moved at 73.2±22.8cm.min^{-1}. When medium-sized starfish were studied, however, three different speeds of movement were identified (Table 5.1b) (i) 'creeping speed' (19.2±3.0cm.min^{-1}) when a patch of *C. edule* was encountered, here the starfish moved very slowly passing its arms over each prey item before 'deciding' to feed (ii) 'searching speed' (45.6±4.2cm.min^{-1}) when starfish moved outside of the prey patch on open sand, and (iii) 'chasing speed (108.6±4.2cm. min^{-1}) when starfish were pursuing a piece of plastic cord which simulated mobile prey.

When *A. irregularis* remained unfed for ten weeks the number of starfish moving across the sediment surface showed a noticeable decline from ~12±4ind.d^{-1} after six weeks to ~5±3ind.d^{-1} after eight weeks (Figure 5.5a). The incidence of starfish found in the 'inverted' position (Figure 5.5b) gradually increased after four weeks with values ranging from ~8% to ~20%. The 'inverted' position is adopted by *A. irregularis* shortly after emerging from the sediment and is maintained for up to two hours before the starfish turn over and burrow back into the sediment. Since *A. irregularis* rarely 'foraged' during periods when the 'inverted' position was adopted, it is suggested, that starfish are feeding by trapping detritus and particulate material in mucus on their tube feet.

Table 5.1. (a) The relationship between arm length of *Astropecten irregularis* and the locomotory speed when moving across sand. (b) The speed and different types of movement displayed by medium size *A. irregularis*.

(a)

Size class	Arm length (mm)		Speed (cm.min^{-1})		Pearson correlation
	Mean^{a}	n	Mean^{a}	Range	
Small	22.0 (1.2)	19	33.6 (16.8)	14.4-66.6	*r* =0.795*
Medium	37.9 (2.1)	19	58.2 (9.0)	45.0-69.0	
Large	53.3 (1.6)	17	73.2 (22.8)	46.8-98.4	

(b)

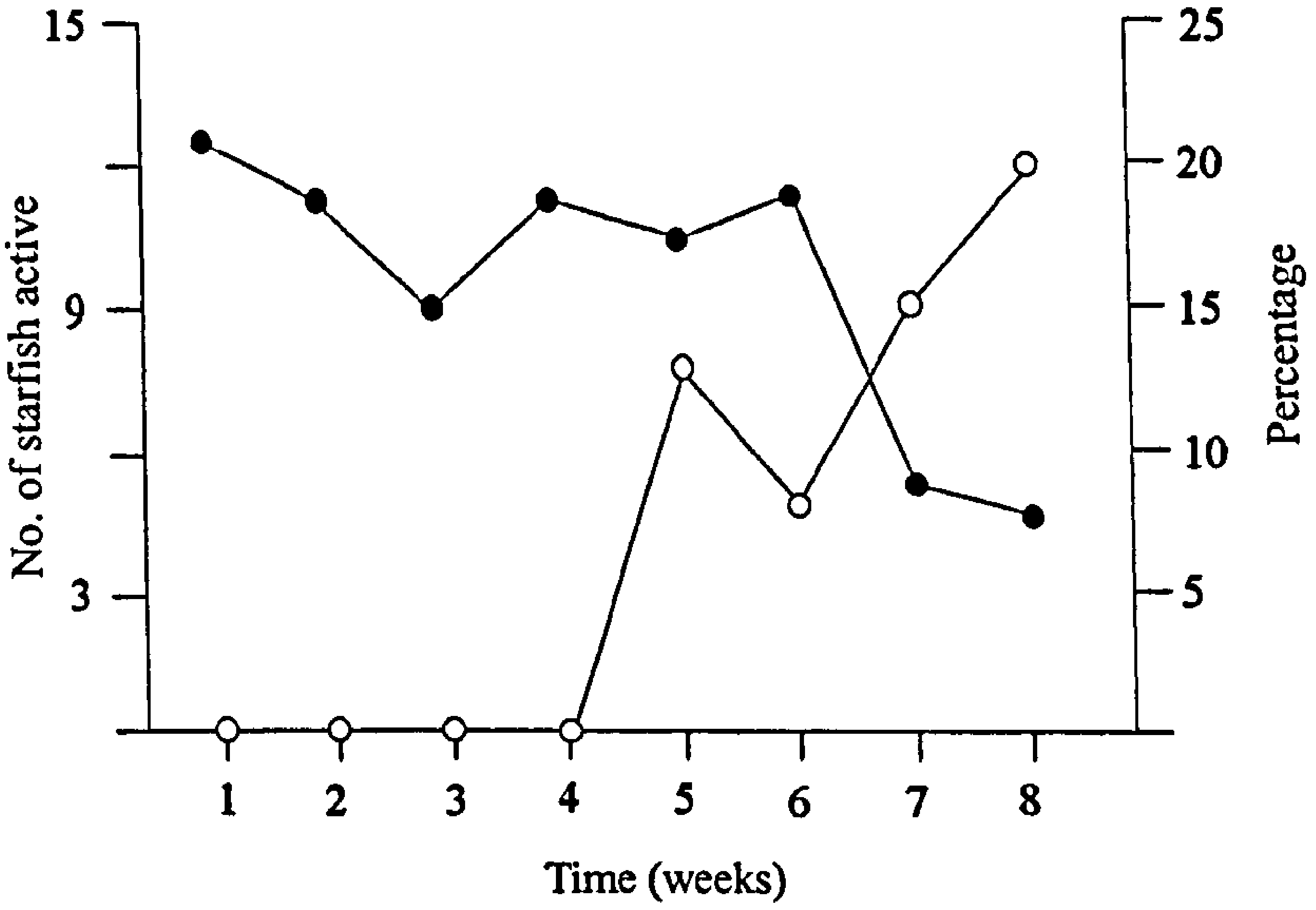
Type of movement	n	Speed (cm.min^{-1})	
		Mean^{a}	Range
'Creeping' across a prey patch	20	19.2 (3.0)	15.6-24.0
'Searching' pre/post prey patch	20	45.6 (4.2)	37.8-51.0
'Chasing' simulated mobile prey	20	108.6 (4.2)	100.8-114

^{a} Values in brackets denote ±standard deviation

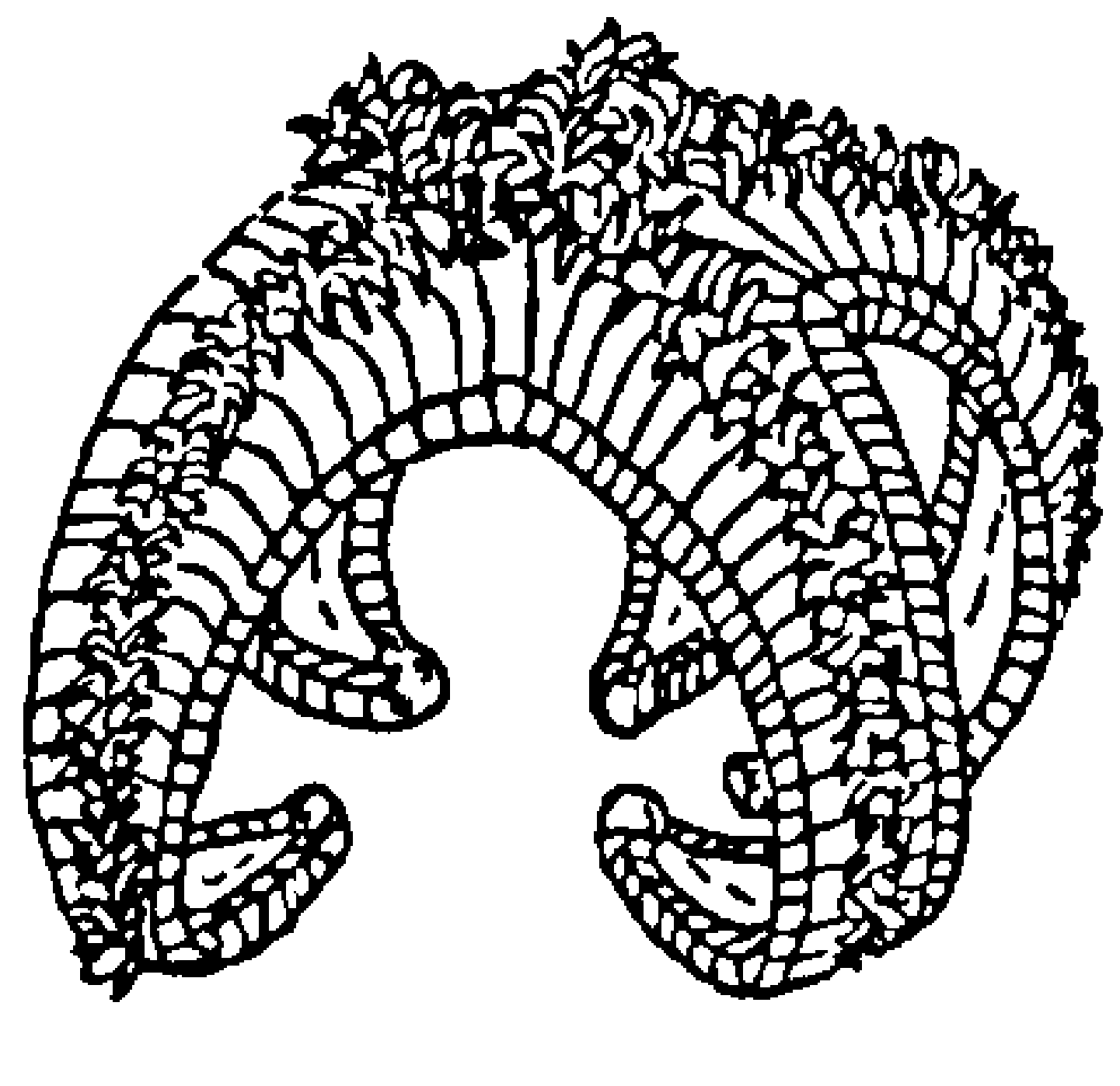
* *P*=<0.05

Figure 5.5. (a) The number of *Astropecten irregularis* moving across the sediment surface (solid circles) and the percentage of starfish in the ‘inverted’ position (open circles) during a ten week period of prolonged starvation. (b) The ‘inverted’ feeding position adopted by *A. irregularis* when starved for prolonged peirods.

(a)


15
9
3
No. of starfish active
25
20
15
10
5
Percentage
1
2
3
4
5
6
7
8
Time (weeks)

[b]



An approximate quadri-diurnal locomotory activity pattern that persisted for twenty-two hours was observed in freshly caught starfish maintained in constant darkness, with peak activity at times of slack water during predicted periods of high and low tide (Figure 5.6a). Periodogram analysis of these data indicated an approximate six hour activity pattern (Figure 5.6c). Figure 5.6b illustrates the locomotory activity pattern of starfish when subjected to cyclic changes in water velocity in a circular laboratory flume. During simulated slack water most starfish were either moving over the sediment surface or partially burrowed, but as water velocity increased ($0.17 m.s^{-1}$) they burrowed into the sediment, often forming aggregations below the surface. In the field, however, it is unlikely that such aggregations will occur as starfish tend to be more widely distributed from each other. At the higher water velocities starfish within these aggregations overlapped or interlocked their arms to increase their stability. An arm tip or an elevated part of the upper central body, which resembles a 'cone' in shape, always maintained contact with the sediment surface. Once water velocity declined starfish again became active and when simulated slack water conditions were re-established starfish began to emerge and roam over the sediment surface.

Although freshly caught *A. irregularis* from Red Wharf Bay did not exhibit an endogenously controlled diurnal locomotory pattern associated with a daily dawn and dusk photo-period (see Figure 5.6a) when starfish were maintained under a light and dark regime for eight weeks they showed a clear diurnal pattern of activity (Figure 5.7a). Two main periods of locomotory activity occurred at around the onset of darkness and again twelve hours later shortly before the beginning of the light phase. Although

Figure 5.6. (a) The number of freshly caught *Astropecten irregularis* moving over the sediment surface in continuous darkness under constant laboratory conditions; arrows denote the time of slack water at predicated high and low tides in Red Wharf Bay. (b) The number of *A. irregularis* moving over the sediment surface in the laboratory flume at different water velocity (stippled); inset, actual water velocities (m.s^{-1}); (●) denotes the percentage of starfish on the sediment surface, and (c) Periodagram analysis of freshly caught *A. irregularis* placed in constant laboratory conditions.

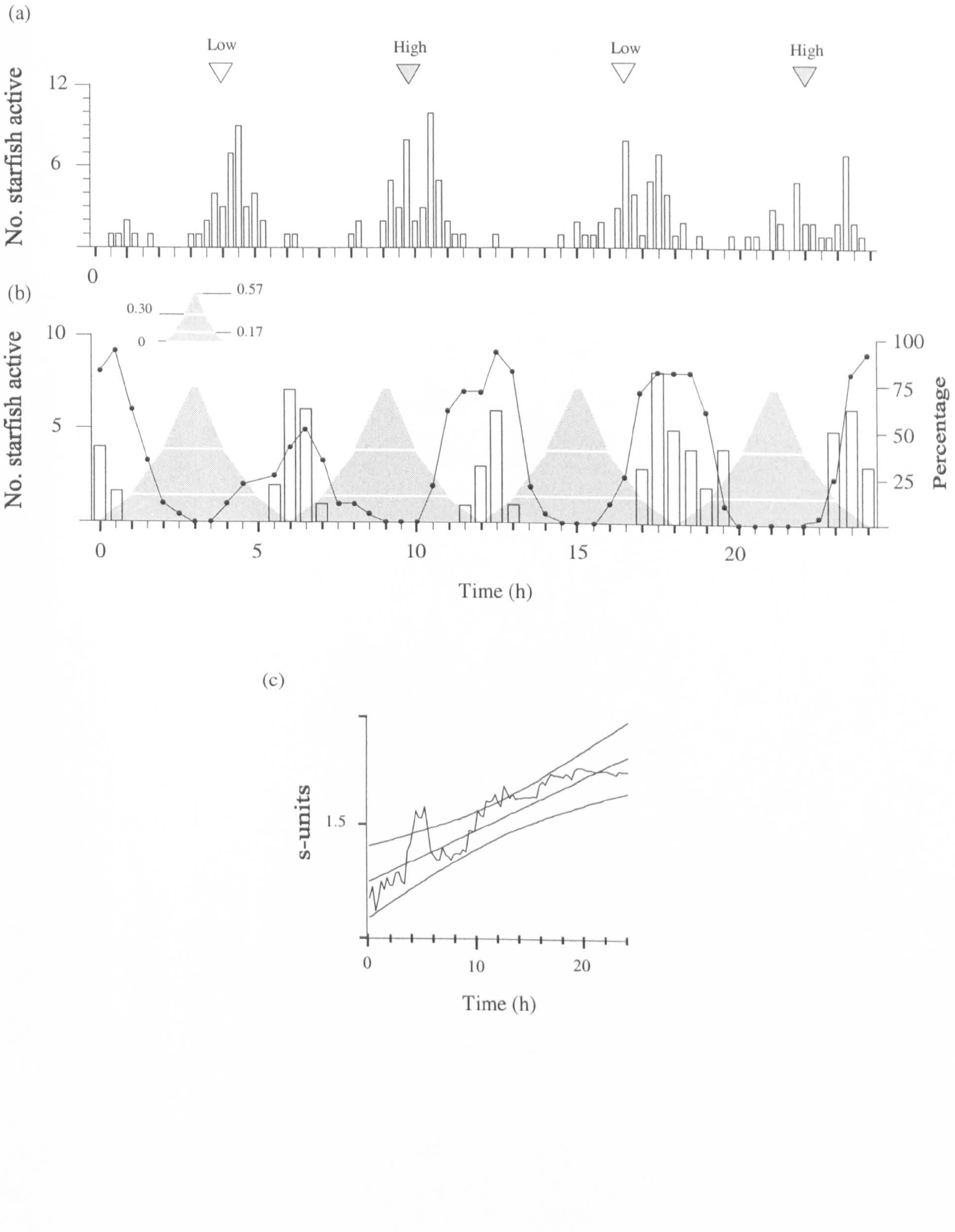
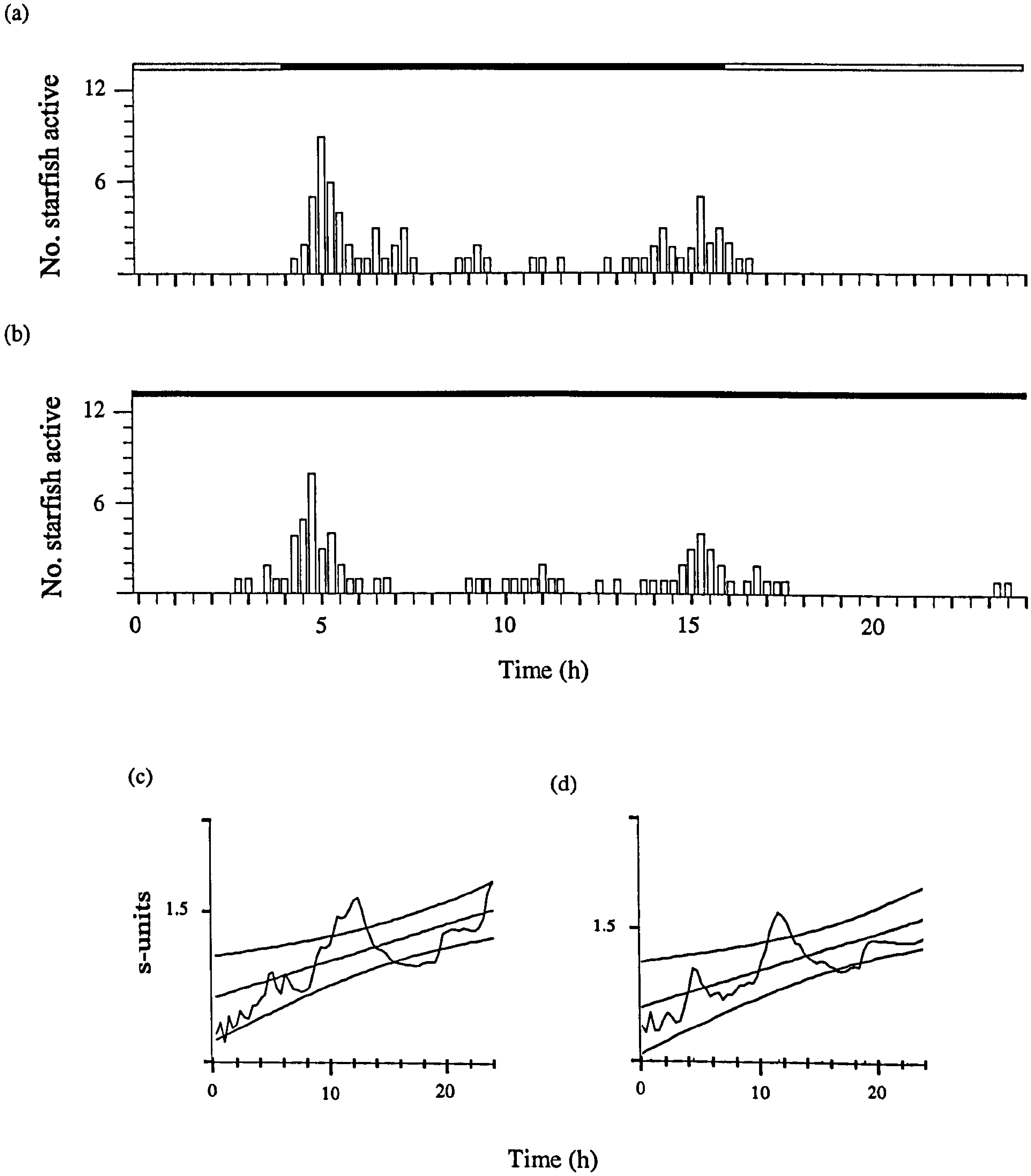

(a)
Low
High
Low
High
No. starfish active
12
6
0
(b)
0.57
0.30
0.17
0
No. starfish active
10
5
0
5
10
15
20
Time (h)
100
75
50
25
Percentage
(c)
s-units
1.5
0
10
20
Time (h)

Figure 5.7. The number of *Astropecten irregularis* moving over the sediment surface under laboratory conditions. (a) Starfish showing a diurnal locomotory activity pattern when maintained in the laboratory under a 12h light and 12h dark regime. (b) The same starfish showing a free-running endogenously controlled activity patterns when placed in constant darkness; horizontal bars denote periods of constant light (▭) and dark (▬). (c) Periodogram analysis starfish subjected to 12h light and 12h dark, and (d) Starfish kept in constant darkness.


(a)
12
6
No. starfish active
(b)
12
6
No. starfish active
0
5
10
15
20
Time (h)
(c)
(d)
s-units
1.5
1.5
0
10
20
0
10
20
Time (h)

starfish were active throughout the dark period very little activity was recorded during the light period. When these experimental starfish were then kept in constant darkness they showed an endogenously controlled diurnal locomotory pattern of activity which remained free-running for approximately twenty-six hours before the pattern was lost (Figure 5.7b) suggesting, therefore, that the locomotory activity of starfish has the potential to become entrained to changes in illumination i.e. dawn and dusk. Figure 5.7c and d illustrate the periodogram analysis of the data in Figure 5.7a and b, which confirms an approximate twelve hour cycle in the locomotory activity of the starfish. In Red Wharf Bay, however, light does not penetrate down to the sea bed (Figure 5.8) suggesting that under natural conditions light may not be an important factor in controlling daily locomotory activity.

Figure 5.9a shows a significant (r=0.757, P<0.05) relationship between the size of the starfish and their activity; larger starfish are more active than smaller ones. Figure 5.9b, by contrast a negative relationship (r=-0.721, P<0.05) indicates that smaller starfish have more active periods than larger starfish. Thus although small starfish tend to have shorter periods when they are moving over the sediment surface, they have more of these periods per day than larger starfish. The activity of *A. irregularis* on the sediment surface, and the number of unsuccessful burrowing attempts to find prey, decreased once prey were introduced (Figure 5.10). It is suggested, that the reduced 'foraging' time was due to the time required by starfish to digest prey and so remain buried within the sediment, and the increase in the success of prey capture at this high prey density (~600m^{-2}). After prey were removed, however, the activity periods increased from a minimum of ~1.5h.d^{-1} to a maximum of ~6h.d^{-1}. In addition, the

Figure 5.8. The attenuation of visible light with changes in water depth (m) recorded in March 1996 at the main study site in Red Wharf Bay.

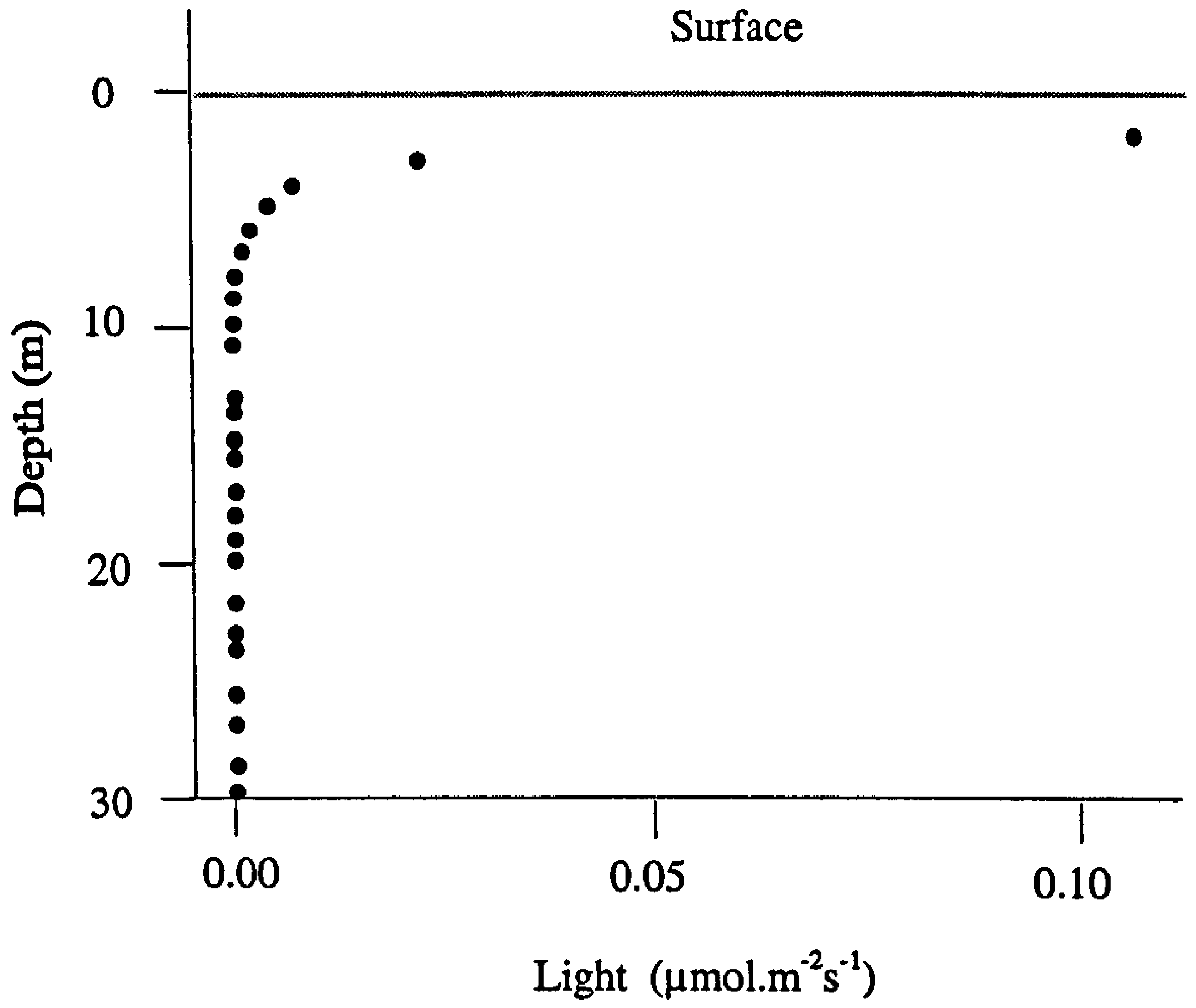

Surface
0
10
20
30
Depth (m)
0.00
0.05
0.10
Light (μmol.m-2s-1)

Figure 5.9. The relationship between: (a) arm length of *Astropecten irregularis* and their locomotory activity; and (b) Arm length of *A. irregularis* and the number of daily periods when starfish are moving across the sediment surface; *=$P<0.05$.

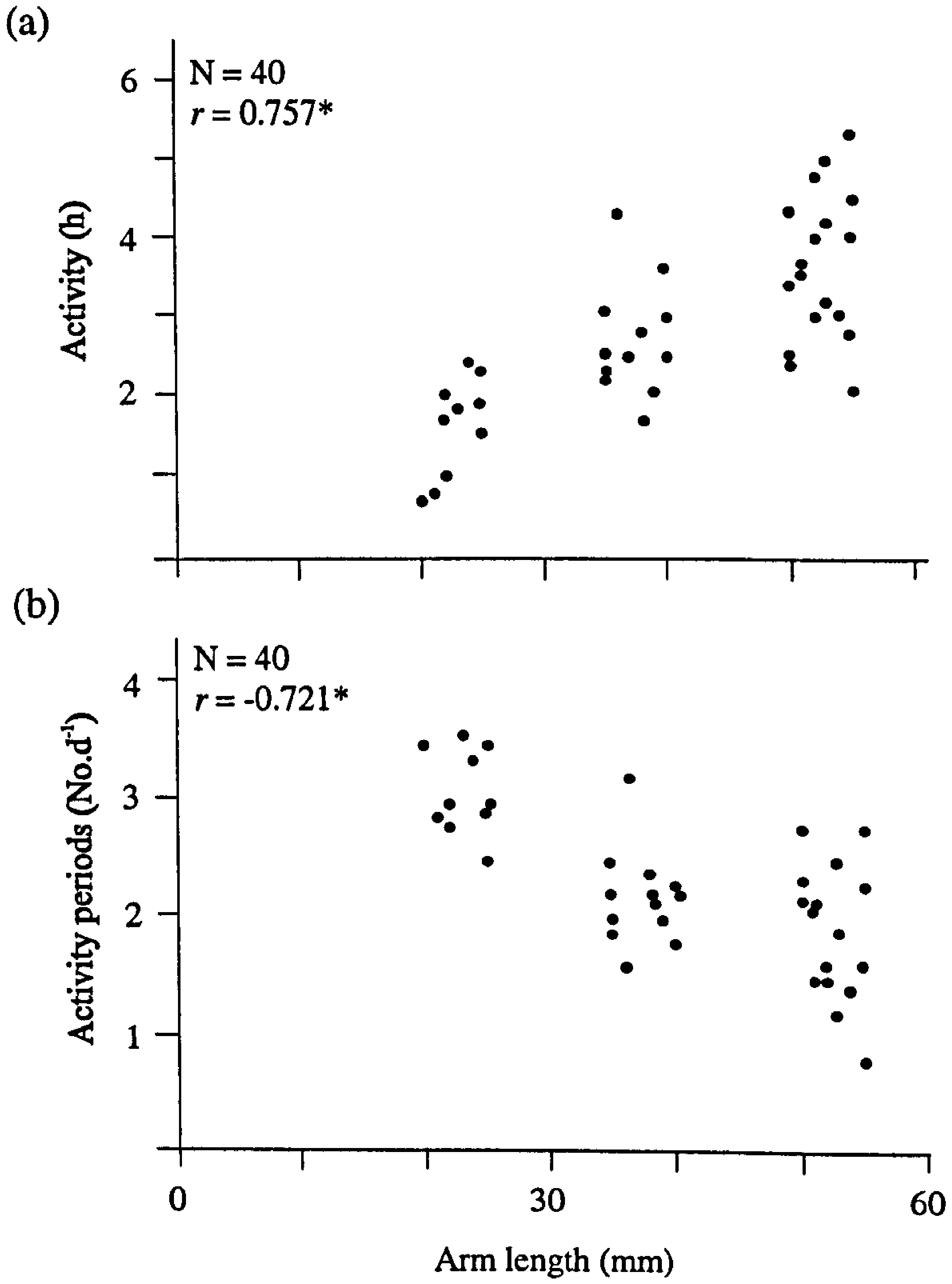
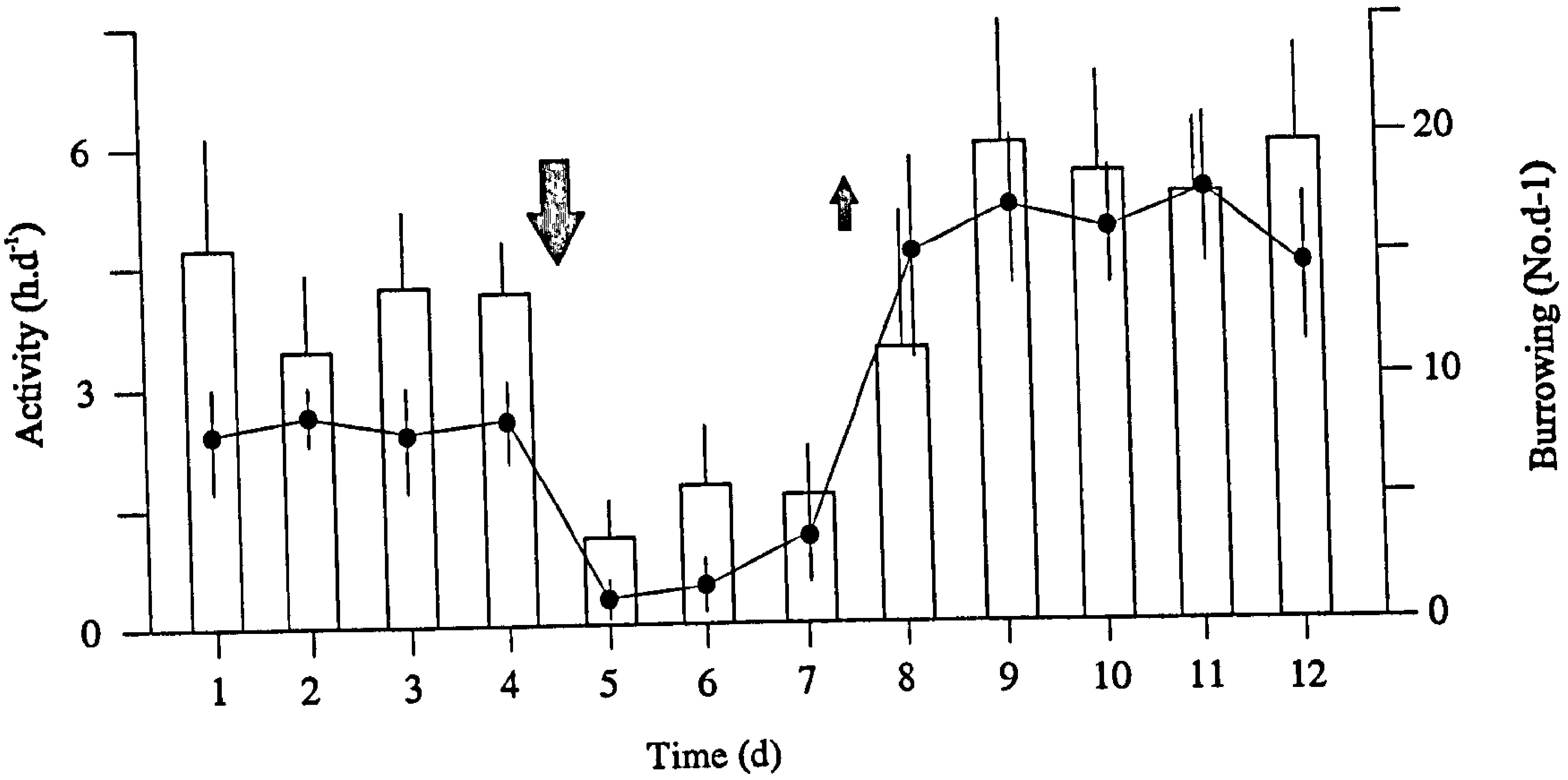

(a)
6
4
2
N = 40
r = 0.757*
Activity (h)
(b)
4
3
2
1
N = 40
r = -0.721*
Activity periods (No.d-1)
0
30
60
Arm length (mm)

Figure 5.10. The daily locomotory activity of *Astropecten irregularis* when starfish are moving over the sediment surface (□ +SD) and the number of unsuccessful burrowing attempts to find prey during these active periods (● ±SD); arrows denote periods when prey were introduced into the aquarium (large arrow) and when prey were removed (small arrow).


Activity (h.d-1)
6
3
0
1
2
3
4
5
6
7
8
9
10
11
12
Time (d)
Burrowing (No.d-1)
20
10
0

number of unsuccessful attempts to find prey, where starfish were engaged in 'ghost excavations' increased from a minimum of 2 to a maximum of ~15, suggesting that starfish retain some form of search image.

5.4. Discussion

Previously only the capture and ingestion of molluscan prey by several *Astropecten* spp. has been described, where prey items are excavated from the sediment and swallowed whole (Power, 1857; Mangold, 1908; Christensen, 1970). In this present study, laboratory observations have identified two methods used by *A. irregularis* to capture the bivalve, *Cerastroderma edule* and the gastropod, *Polinices polianus*. In addition, two other methods to capture the crustacean *Diastylis rugosa* and the echinoderm *Ophiura ophiura* have also been identified. The versatility of the techniques used to pursue and capture prey show that *A. irregularis* possesses considerable body flexibility, despite its rather rigid outward appearance. The techniques used by *A. irregularis* are clearly adapted to different prey species and appear to be, in part, dependent on the abundance, size and mobility of their prey. Body flexibility in asteroids is apparently not uncommon when capturing prey, the Antarctic species *Labidiaster annulatus*, for example, can catch small fish by wrapping its arm around the prey (Dearborn, 1977).

Under laboratory conditions when *C. edule* are provided in abundance, the close proximity of individual prey items, enables *A. irregularis* to gather several prey simultaneously using an 'arm curling' technique. Although this action involves the co-ordination of two or more arms, the excavation of buried prey and the transfer of these items towards the mouth by means of the tube feet is an important feature of this method. Christensen (1970) reported that even though *A. irregularis* has suckerless tube feet these do appear to have adhesive properties; this was clearly evident when molluscan prey items were picked up clear of the substratum and pushed into the stomach, and when starfish were observed climbing the walls of a glass aquarium. A different technique was used by *A. irregularis* when feeding on the gastropod *Polinices polianus* when following a short pursuit across the sediment surface, the starfish would quickly hunch over its prey thereby trapping it within a 'cage' created by the arms. This hunched position is a typical feeding position of other asteroids such as, *Asterias rubens* and *Pisaster ochraceus*, when consuming large mussels; in *Asterias* and *Pisaster*, however, the suckered tube feet attach to the shell of its prey allowing the values to be pulled open (Christensen, 1957). Other asteroid species use the entire body to envelop their prey, *Stegnaster inflatus* and *Anseropoda placenta*, for example, use a "pseudo-crevice" created by the arms to lure shrimp, which enter the crevice; these shrimp then become trapped once the starfish progressively reduces the crevice by sealing its margins against the substratum (Hunt, 1925; Martin, 1970).

Although the final ingestion phase of fast-moving prey such as *Ophiura ophiura* and *Diastylis rugosa* by *A. irregularis* is similar to that used for ingesting molluscan prey, different methods are used to pursue and capture these prey organisms. *O. ophiura* is initially pursued by the starfish using a 'scissor-like' action created by repeatedly opening and closing the leading pair of arms simultaneously. Usually the starfish catches the ophiuroid by pinning it down between its arms before starting the process of ingestion. Although the pursuit of ophiuroids by *Astropecten* has not previously been described, another intra-oral feeding asteroid *Luidia sarsi*, exhibits a characteristic leaping response whenever a brittlestar is encountered, and will even surface when buried to pursue a passing ophiuroid (Fenchel, 1965). In this present study the pursuit of the crustacean *D. rugosa* involved a 'swiping' action by one of the starfish arms, whereby any prey item touched became instantly attached to the tube feet. According to O'Brien (1976) and Anger *et al* (1977) relatively fast-moving animals like amphipods and isopods can be caught by *Leptasterias littoralis* and *A. rubens* owing to the suction force exerted by their tube feet. It is likely, therefore, that *A. irregularis* also uses a similar force to capture mobile prey.

In the laboratory, *O. ophiura* and *P. polianus* did not exhibit any apparent escape response until direct contact is made with *A. irregularis*, by which time it was usually too late for any effective escape to occur; starfish seem to be able to approach their prey undetected. Although there are several reviews on the response of animals to contact or to the near presence of starfish (Bullock, 1953; Kohn, 1961; Feder, 1972) most studies have focused mainly on molluscan prey. *P. catenus* (=*Natica catena*) for example, is able to draw a fold of tissue anteriorly from behind the shell to form a hood which then covers the shell thus preventing the starfish from adhering to the shell with its tube feet. However, on contact with the starfish *Pycnopodia*, a closely related species, *P. polianus*, reacts by rapidly withdrawing into its shell; this defensive response is not effective since this prey is usually swallowed whole (Feder, 1972). In the present study, *P. polianus* rarely showed this defensive response following contact with *A. irregularis*, attempting instead to burrow into the sediment once the starfish had surrounded the prey. No escape responses were observed in experiments using *C. edule* as prey, although Feder and Christensen (1966) noted that bivalves such as the cockle *Cardium echinatum* and the clam *Spisula subtruncata*, exhibited a leaping response in the presence of starfish. This suggest that *A. irregularis*, unlike other asteroids, may approach its prey undetected, such stealth presumably increasing the success rate of attacks.

Feder and Christensen (1966) noted that *Astropecten* spp. are amongst the fastest moving asteroids. However, generally, many other studies have reported speeds which usually represent the maximum speed of starfish once they have scented food or when they are avoiding immediate danger, i.e. predation from a predatory starfish. Romanes and Ewart (1881) for instance, reported that *A auranciacus* could move at speeds of 30-60 cm.min^{-1}, whereas Ferlin (1973) recorded an average velocity of 20cm.min^{-1} for this species, with instantaneous velocities ranging between 50 and 140cm.min^{-1}. Sigalas (1922) reported maximum speeds for *A. irregularis* of up to 60cm.min^{-1}. In this study medium-sized *A. irregularis* (arm length 35-40mm) moves at speeds which depended on whether the starfish was pursing fast-moving prey (up to 114cm.min^{-1}) cruising between patches of prey (51cm.min^{-1}) or 'creeping' over prey within a patch (24cm.min^{-1}).

Although ciliary-feeding using an everted stomach has been noted for many asteroid species e.g. the deep sea species *Thoracaster magnus* which feeds on surface detritus and micro-organisms (Madsen, 1956; Anderson, 1959; Mauzey *et al.*, 1968; Birkeland,1974; Dearborn, 1977; Scheibling, 1980b) these have been extra-orally feeding species. A few studies have also reported ciliary-feeding in intra-oral feeding starfish, including *A. irregularis* and *Luidia sarsi* (Gemmill, 1915; Gislen, 1924). Martin (1970) however, found no evidence for the ciliary ingestion of particulate material in *A. polyacanthus.* In this study, it is suggested that the increased frequency of *A. irregularis* in the 'inverted' position following prolonged periods of starvation is not associated with 'ciliary' feeding. During periods of starvation and when starfish are not in the 'inverted' position they are occasionally found on the sediment surface with their stomachs slightly everted, suggesting that they may also be feeding on detritus material present on or within the substrate. Hartman (1956) classifies *A. californicus* as a detritus feeder and Nojima (1989) noted that, although *A. latespinosus* feeds predominantly on bivalves, it can also feed on detrital material during the winter months.

Previously many studies have noted diurnal patterns in the locomotory activity of several *Astropecten* spp. (Power, 1857; Mori and Matutani, 1952; Burla *et al.*, 1972; Ferlin-Lubini and Ribi, 1978; Nojima, 1981). In the present study, however, freshly caught *A. irregularis,* maintained in the laboratory under still-water conditions and continuous darkness, demonstrated a quadri-diurnal pattern of locomotory activity with peaks of activity coinciding with expected times of slack water during periods of high and low tides in Red Wharf Bay. Thus, *A. irregularis* seems to have an endogenous pattern of locomotory activity entrained by changes in water velocity throughout the natural tidal cycle; this endogenous behaviour remained free-running for twenty-two hours. The disappearance of endogenous controlled tidal rhythmicity in many intertidal animals such as, *Carcinus maenas*, has been considered to be an advantage in habitats where tidal cycles may alter, since the modification of its behaviour to suit the new tidal regime will reduce the risk of being exposed to air at low tide and ensure 'foraging' takes-place at expected high tide (Naylor, 1958). Endogenously controlled tidal locomotory activity has been reported in several intertidal starfish, *Asterina minor*, a species which is confined to rock pools around the coast of Japan, (Soliman *et al.*, 1986) and *Pisaster ochraceus*, a North American species (Feder, 1959; Mauzey, 1966) where starfish were more active at high tide. Such rhythmic patterns, however, have not previously been documented in *A. irregularis*.

Flume experiments revealed that locomotory activity in *A. irregularis* is confined to periods of simulated slack water and reduced water velocity, and that with increased current flow starfish burrow into the sediment in order to avoid being dislodged. Maximum water velocity achieved in the flume experiment ($0.56 m.s^{-1}$) was less than that at spring ($1.5 m.s^{-1}$) and neap ($0.75 m.s^{-1}$) tides previously recorded in Red Wharf Bay by Morris (1986). If these experiments reflect what occurs in the field, then in Red Wharf Bay *A. irregularis* should remain buried during periods of elevated water current velocities. Ferlin-Lubini and Ribi (1978) noted the locomotory activity of *A. aranciacus* was generally influenced by heavy ground-swell forces, which when severe caused starfish to remain buried within the sediment. Morin *et al.*, (1985) similarly noted that the *A. verrilli* remained burrowed in the sediment during periods when high wave surges occur within the shallow coastal waters of California. In this study, high water current velocities within the flume caused *A. irregularis* to form subsurface aggregations in which the arms of individual starfish interlocked, although an arm tip or elevated part of the upper central body always maintained in contact with the sediment surface, presumably to sense the conditions prevailing in the overlying water. During strong tidal flow, *Ophiothrix fragilis*, also forms aggregations in which individual brittlestars interlock arms to prevent them from being dislodged (Warner, 1971).

Since light does not reach the sea bed in Red Wharf Bay during the winter period, it is perhaps (not surprising) that freshly caught *A. irregularis* did not exhibit an endogenously controlled diurnal locomotory activity pattern which coincided with expected times of dawn and dusk. In the laboratory, however, light has been shown to influence the locomotory activity of *A. irregularis*, where starfish were entrained to a twelve hour photo-period. Moreover, once starfish were placed under constant darkness they showed a free-running endogenously controlled diurnal locomotory activity pattern, which persisted for approximately twenty-six hours. Mori and Matutani (1956) similarly found that when *A. polyacanthus* were kept under constant darkness they showed an endogenously controlled diurnal locomotory activity pattern which persisted for twenty-four hours. Yamanouti (1939) found that in several species of tropical holothurians, endogenously controlled behaviour lasted up to seven days when animals were kept under constant darkness, and that exposure to light 'reset' this rhythm. Many previous studies have indicated that *Astropecten* spp. are most active on the sediment surface at dawn and dusk (Power, 1857; Mori and Matutani, 1952; Burla *et al.*, 1972; Ferlin-Lubini and Ribi, 1978; Nojima, 1981). However, these studies were generally conducted within shallow (<10m) inshore waters where light can easily penetrate to the sea bed. Mori and Matutani (1952) for instance, showed that *A. polyacanthus* exhibited a daily rhythmic behaviour governed by light and that peak feeding occurred around dawn and dusk. Ferlin and Ribi (1978) however, found that the activity periods of *A. aranciacus* change seasonally, with starfish having several peaks of activity during the summer months and only a single peak during winter. Naylor (1958) noted that peak activity in the shore crab, *Carcinus maenas*, could be either enhanced or suppressed depending on the relative position of the tide with respect to the time of day, suggesting, therefore, that activity may be governed by two or more superimposed factors. In the present study, it is suggested that light may not be an important factor in governing the daily locomotory activity of *A. irregularis* during winter, but could play a more prominent role during the summer months, especially when low spring tides coincide during the day light hours.

Burla *et al* (1972) reported a negative relationship between the size of *A. aranciacus* and the duration of daily locomotory activity, with larger specimens spreading their activity over a longer period of the day and smaller starfish tending to concentrate their activity into a more restricted period. In this study, a similar relationship was not only found between the size of *A. irregularis* and the duration of daily locomotory activity, but also between size and the number of active periods throughout the day. Smaller starfish had shorter 'foraging' times than larger starfish but had a greater number of 'foraging' episodes. In general, however, the average period of starfish activity was approximately two hours. Ribi and Jost (1978) reported that *A. aranciacus* remained active between two and five hours a day, whilst Nojima and Doi (1977) noted that *A. latespinosus* were active for two and three hours.

The number and duration of feeding excursions exhibited by *A. polyacanthus* and *A. aranciacus* are greatly reduced when prey are super-abundant, suggesting that the main activity of starfish is food gathering (Mori and Matutani, 1952; Ribi and Jost, 1978). Ribi and Jost (1978) proposed that the genus *Astropecten* has short periods of activity (~1-5h.d^{-1}) because intra-oral feeding requires more time to prepare prey for consumption than to actually kill it by depriving it of oxygen (also see Christensen, 1970). In this present study *A. irregularis* was also much less active when prey were abundant. Once prey were removed, however, the locomotory activity and the number of unsuccessful attempts to find prey by starfish also increased to a greater extent than that before prey had been introduced. This suggests that starfish retain some form of search image which presumably caused starfish to perform 'ghost excavations' for prey which were no longer present. The ability of asteroids to retain information about their prey has been described as 'ingestive conditioning'(Wood. 1968) and has been previously shown in many other invertebrate species.

CHAPTER 6

The Distribution and Occurrence of *Acholoë squamosa* a Commensal with the Burrowing Starfish *Astropecten irregularis*

6.1. Introduction

Acholoë squamosa (Chiaje) better known as its junior synonym *Acholoë astericola* (see Pettibone, 1996) belongs to the sub-family Acholoinae, scale worms which like other Polynoidae, are commonly found associated with molluscs, echinoderms and even with polychaetes (Pettibone, 1953, 1996). Polynoid-asteroid associations are poorly documented and previous studies have either focused on the chemical attractants released by the host, thus emphasizing the importance of such a partnership to the worm (Gerber and Stout, 1968; Dimock and Davenport, 1971) or have addressed the role of intra-specific aggression in determining the distribution of these upon their hosts (Dimock, 1970). Much of this work has been confined to the genus *Arctonoe* (Hickok & Davenport, 1957; Dimock and Dimock, 1969; Gibbs, 1969; Britaev and Smurov, 1985) which has been found in association with several different hosts. Fewer studies have investigated the association between *A. squamosa* and its principal host, the burrowing starfish *Astropecten irregularis.*

Davenport (1953) found that *A. squamosa* is unlike other polynoid symbionts, in that its chemical attraction towards its host, *A. irregularis,* was initiated only on physical contact. This suggested that adult worms were unable to search actively for their hosts and that host selection perhaps occurred at the time of larval settlement. Davenport (1954) described the early development in *A. squamosa,* but failed to rear larvae beyond the trochophore stage.

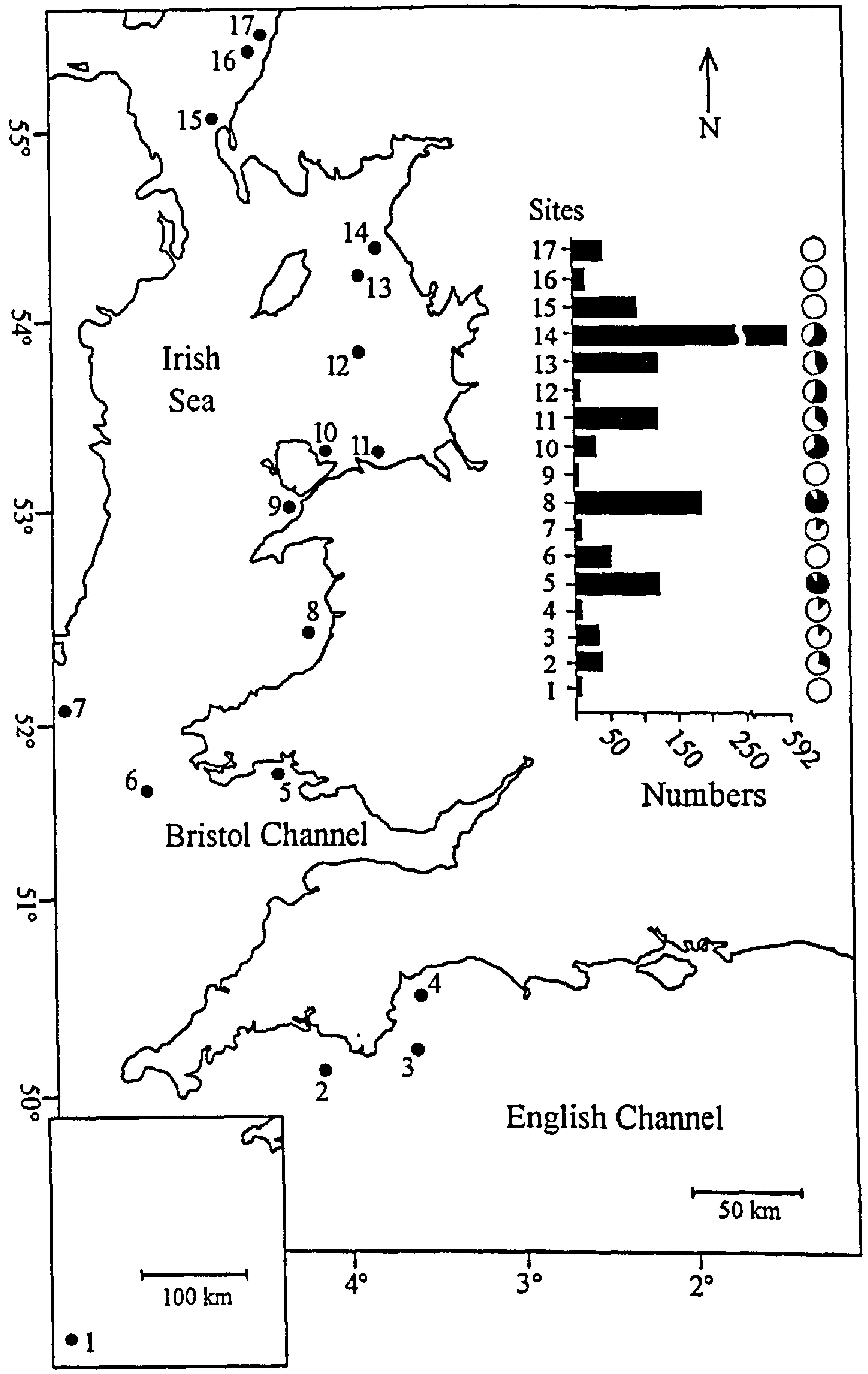
Adult *A. squamosa* are typically found as single individuals in the ambulacral grooves of *Astropecten,* although two or more worms of different size may sometimes co-occur (Davenport, 1953). In several Mediterranean species of *Astropecten,* where the adult worm occupies an ambulacral groove, juvenile worms are located between the spines of the marginal plates (Cuénot, 1912). Single infestations in other polynoid-asteroid associations, however, are rare and large numbers of worms may be found on a single host. Individual sea cucumbers, *Stichopus parvimensis,* for instance may accommodate 20 or more adult *Arctonoe pulchra* (Dimock, 1974).

In this study data is presented on the distribution and abundance of *A. squamosa* on *A. irregularis* from southern and western waters of the British Isles, and briefly examines the spatial distribution of this symbiont on its host.

6.2. Materials and methods

Samples of *Astropecten irregularis* were collected from seventeen sites off the southern and western coasts of the British Isles (Figure 6.1). Generally, the sea bed at the most southerly sites (sites 1-4) consisted of gravel and shell fragments, whilst that at the

Figure 6.1. The location of study sites off the southern and western coasts of the British Isles (●) and (inset) the abundance of *Astropecten irregularis* (No.ha-1) (■) and the percentage occurrence of *Acholoë squamosa* (○) at the corresponding sites. Site 1 is ca. 200km south-west of the Scilly Isles.


17
16
15
14
13
12
10
11
9
8
7
6
5
4
3
2
1
Irish Sea
Bristol Channel
English Channel
N
55°
54°
53°
52°
51°
50°
4°
3°
2°
50 km
100 km
Sites
17
16
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
50
150
250
592
Numbers

western sites (5-8 and 10-17) was predominantly sandy or muddy; at site 9, however, the sediment consisted of coarse shell gravel (Table 6.1). Water depth at sites 1-3, 6-7 and 15-17 ranged between 40m and 180m, whereas at sites 4-5 and 8-14, shallower water depths of 15-40m were recorded. During July 1995 and late October to November 1996, single samples of *A. irregularis* were collected from all the southern sites (1-4) using either a French dredge or beam trawl. At the main study location (site 10), an area approximately 1km^2, located in Red Wharf Bay, Anglesey, North Wales (53° 20' 50N 04° 06' 00W) where *Acholoë squamosa* has been reported associated with *A. irregularis* (pers. comm. E. I. S. Rees) regular collections were made between December 1995 and June 1997. During periods of neap tides *A. irregularis* samples were collected twice a month using a fine mesh 2m or 3m beam trawl. Each trawl was towed at a speed of 1.5 knots for a period of 8min and the coordinates recorded by Global Positioning Systems, to enable the same site to be relocated on subsequent visits. At the other western sites (sites 5-9 and 11-17) single collections of *A. irregularis* were taken by beam trawl during the period between March 1997 and August 1997. During the course of this investigation a total of 4,329 *A. irregularis* and 3,362 *A. squamosa* were examined.

Records included numbers of *A. irregularis* in each trawl, length of the longest arm of each starfish (measured from arm tip to centre of the mouth) and body length, colour and position on its host of each *A. squamosa*. All measurements, to the nearest 0.1mm, were made on board ship using vernier calipers. Most starfish and their commensals were individually preserved in 5% formalin in seawater although some were maintained in running seawater for subsequent observation in the laboratory.

Table 6.1. Main physical characteristics and features of the *Astropecten irregularis* populations at the study sites.

							Astropecten irregularis					
Site	Site	Co-ordinates		Water depth (m)		Sediment	No.	Density	No.	Length (mm)		%
No.	name	Latitude	Longitude	Mean	Range	type	examined	(No.ha^{-1})[1]	trawls	modal	range	infection
1	Little Sole Bank	48° 32.0'	08° 38.0'	135	(80-180)	shell/gravel	59	7 (2.5)	6	58	(24-88)	0
2	Western Channel	50° 16.2'	04° 23.3'	55	(50-60)	sand shell/ gravel	38	37 -	3	34	(20-76)	26
3	Western Channel	50° 20.5'	03° 25.0'	55	(50-60)	sand shell/ gravel	70	7 (5.3) -	11	48	(28-84)	17
4	Western Channel	50° 30.2'	03° 35.1'	35	(30-40)	sand	48	32 (49.6)	5	42	(28-84)	21
5	Carmarthen Bay	51° 39.9'	04° 30.5'	18	(17-20)	mud/sand	44	120 -	3	28	(20-44)	84
6	Celtic deep	51° 23.3'	05° 52.0'	89	(88-90)	mud/sand	38	60 -	3	40	(22-66)	0
7	Nymphe Bank	51° 59'.5	06° 45.3'	50	(49-51)	sand	24	10 -	2	42	(10-42)	29
8	Cardigan Bay	52° 20.7'	04° 18.5'	17	(15-20)	sand	214	186 -	3	26	(8-48)	88
9	Caernarfon Bay	53° 09.5'	04° 28.4'	20	(19-21)	shell/gravel	4	15 -	1	8	(18-46)	0
10	Red Wharf Bay	53° 20.5'	04° 06.5'	20	(18-20)	sand	81	30 (25.0)	13	34	(8-56)	70
11	Colwyn Bay	53° 21.0'	04° 43.0'	17	(15-20)	sand	191	122 (51.8)	4	26	(16-64)	33
12	Eastern Irish Sea	53° 45.3'	03° 40.7'	35	(32-40)	sand	105	9 (2.7)	4	26	(8-52)	56
13	Eastern Irish Sea	53° 56.7'	03° 48.5'	30	(28-34)	sand	546	123 (48.3)	8	26	(12-44)	40
14	Eastern Irish Sea	54° 06'.8	03° 25.0'	22	(20-25)	sand	453	592 (127.0)	4	22	(12-72)	58
15	Clyde Sea	55° 09.0'	05° 08.6'	40	(39-42)	mud/sand	58	47 -	2	38	(28-60)	0
16	Clyde Sea	55° 35.3'	04° 50.0'	63	(51-72)	mud/sand	50	14 -	2	45	(8-68)	0
17	Clyde Sea	55° 40.5'	04° 45.0'	40	(39-42)	mud/sand	72	96 -	3	40	(8-64)	0

[1] Values are mean (±SD) of *A. irregularis* No.ha^{-1} except for sites with <3 trawls (-)

Owing to the tendency for *A. squamosa* to fragment during collection it was occasionally difficult to measure body length accurately on board ship. To overcome this difficulty the maximum width (including parapodia) and length (anterior and posterior axis) of 25 intact preserved worms were measured under a low power dissecting microscope after gently squashing each worm beneath a coverslip. Britaev and Smurov (1985) previously demonstrated that, for *Arctonoe vittata,* body width provides a reliable estimate of overall length. Width of *A. squamosa* between the 10th-20th body segments similarly provides a reliable indicator of overall size. The length of fragmented worms, in those cases where the entire worm did not survive collection, was estimated using the relationship Length = 0.036 Width = 0.356 (r^2=0.979, P<0.05). Seawater temperature at the main study site was recorded at the times of sampling.

6.3. Results

The main physical characteristics and features of the starfish populations at the seventeen study sites are summarized in Table 6.1. Population densities of *Astropecten irregularis* and the percentage occurrence of *Acholoë squamosa* showed marked inter-site variations. The highest density of *A. irregularis*, 592ind.ha^{-1} was recorded in the eastern Irish Sea (site 14, April 1997) whilst the lowest density ~7ind.ha^{-1} occurred in the western Channel (sites 3-4 during October to November 1996) and south-west of the Scilly Isles (site 1 in July 1995). Elsewhere, starfish densities ranged between 9 and 186ind.ha^{-1}. In general, lower *A. irregularis* densities were associated with coarser sediments, whereas higher densities were typically associated with finer sediments ranging from sand to mud. At site 12 low starfish densities (9ind.ha^{-1}, 0.009m^{2}) were associated with finer sediments and many starfish in this population displayed damaged and/or regenerating arms, indicative of recent fishing disturbance. The percentage of starfish infested with *A. squamosa* ranged from 90% in Carmarthen Bay and Cardigan Bay (sites 5 and 8 respectively) to 0% south-west of the Scilly Isles (site 1) Celtic deep (site 6) Caernarfon Bay (site 9) and the three sites in south-west Scotland (sites 15-17) (see Table 6.1). Infestation was negatively correlated with modal arm size of the starfish indicating that the larger starfish had the lowest levels of infestation (Figure 6.2a). Since host size is in turn positively correlated with water depth (Figure 6.2b) water depth and % infestation are, not surprisingly, negatively correlated (Figure 6.2c). However, the level of infestation by *A. squamosa* was apparently independent of starfish density (Pearson r=0.318, P>0.05).

Of the 3,152 infested *A. irregularis* examined during this investigation 95% were single infestation with no multiple infestations involving adult *A. squamosa* (>15mm in length) being recorded. Where multiple infestations did occur these usually comprised a single adult worm and between 1-3 juvenile worms (i.e. <15mm in length). Adult worms generally occupied an ambulacral groove (95%) but occasionally some worms were observed with their head and up to half their body length extending into the cardiac stomach of the host (Figure 6.3). Table 6.2. shows the distribution and size of adult and juvenile *A. squamosa* on 1,093 infested starfish collected from three of the study sites. Although most juvenile worms (64%) also occupied the ambulacral grooves, large numbers (31%) were observed between the inferomarginal plates, a location where

Figure 6.2. The relationship between (a) The modal size of *Astropecten irregularis* and percentage colonization by *Acholoë squamosa*; (b) Water depth and modal size of *A. irregularis*; and (c) Water depth and the percentage colonization at the study sites; *=$P<0.05$. Data for site 9 are omitted only four starfish were collected at the site.

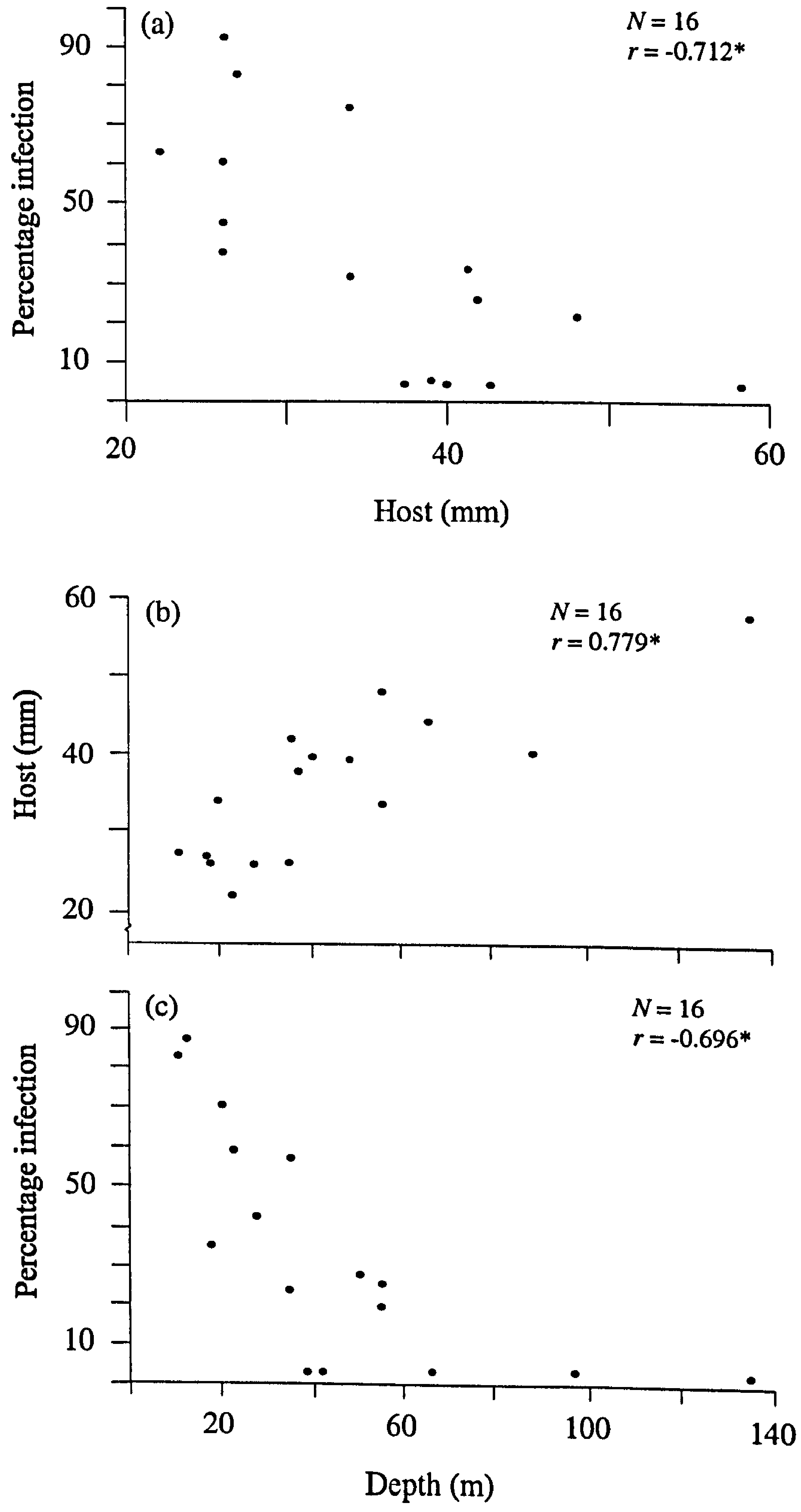

(a)
N = 16
r = -0.712*
Percentage infection
90
50
10
20
40
60
Host (mm)
(b)
N = 16
r = 0.779*
Host (mm)
60
40
20
(c)
N = 16
r = -0.696*
Percentage infection
90
50
10
20
60
100
140
Depth (m)

Figure 6.3. An adult female *Acholoë squamosa* situated across the arm and ambulacral grove of *Astropecten irregularis*; the head of the worm is located within the mouth of the starfish towards the left of the photograph. Scale bar = 5mm.

adult worms were never recorded. Both adult and juvenile worms were occasionally (<5%) found on the aboral surface of the host, but juveniles were never observed entering the stomach (Table 6.2). The largest worm recorded during this investigation, from the ambulacral groove of an *A. irregularis* with an arm length of 58mm, measured 48mm in overall length. The smallest worm, 1.5mm in length, occurred between the inferomarginal plates on a starfish with an arm length of 36mm. Whilst no significant differences between the size of adult worms occupying different locations on the host could be detected (Kruskal-Wallis H=5.74, *P*>0.05) juvenile worms located in ambulacral grooves were significantly larger than those occurring between the inferomarginal plates (H=103, *P*>0.05) (Table 6.2).

Table 6.2. The distribution and size of *Acholoë squamosa* on *Astropecten irregularis* collected from Cardigan Bay, Red Wharf Bay and Colwyn Bay (sites 8, 10 and 11) during April 1996 to April 1997 (n=1093).

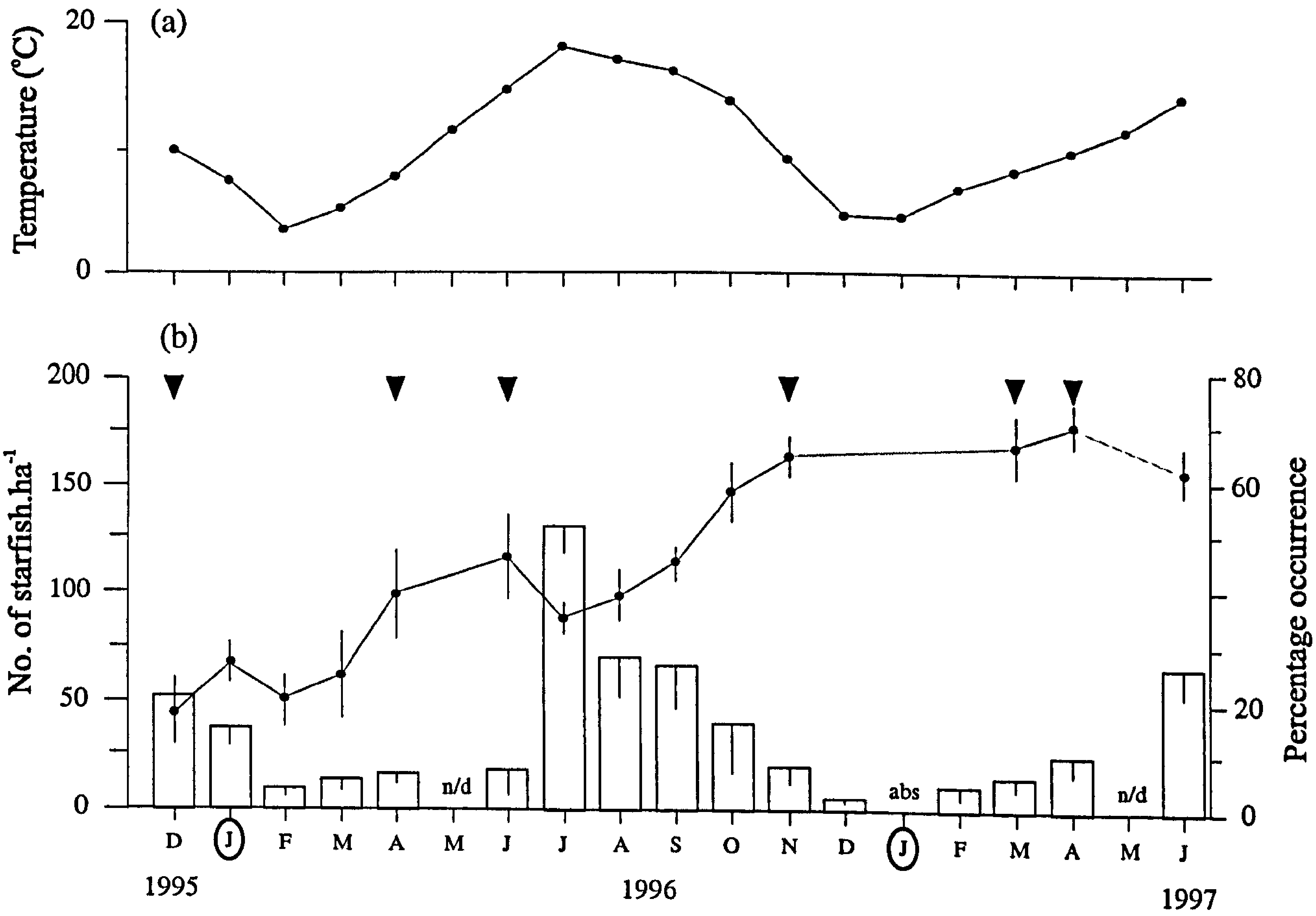
	Juveniles (<15mm)			Adults (>15mm)		
Location on host	n	%	mm[1]	n	%	mm[1]
Aboral surface	14	5.0	6.96 (2.61)	20	2.0	19.20 (4.03)
Inferomarginal plates	82	31.0	6.57 (1.69)	-	0.0	-
Ambulacral groove	172	64.0	9.93 (1.78)	778	95.0	20.72 (5.35)
Spines	-	0.0	-	4	0.0	18.75 (4.92)
Stomach[2]	-	0.0	-	23	3.0	19.13 (3.56)
Total	268	100.0		825	100.0	

[1] Length of *Acholoë squamosa* mean (± SD)

[2] Worms with head inside mouth of host

Seasonal variations in the population density of *A. irregularis* and the occurrence of *A. squamosa* in Red Wharf Bay are presented in Figure 6.4. *A. irregularis*

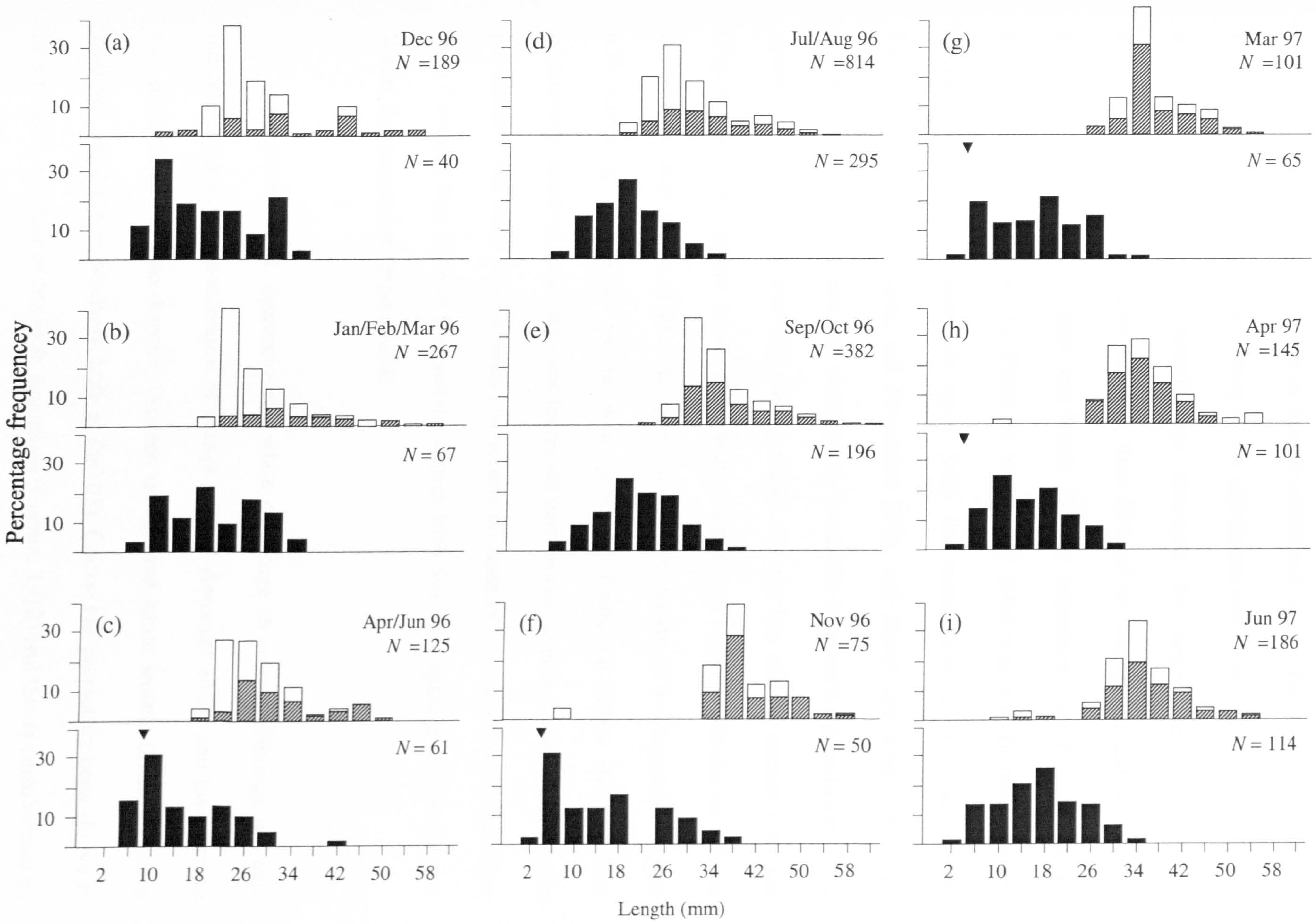
Figure 6.4. (a) Seasonal changes in seawater temperature in Red Wharf Bay; and (b) seasonal occurrence of *Astropecten irregularis* (□ -SE only) and percentage occurrence of *Acholoë squamosa* (— ±SE) in Red Wharf Bay; triangles denote periods of maximum occurrence of juvenile *A. squamosa* between the inferomarginal plates; n/d = no data; abs = *A. irregularis* absent.


(a)
Temperature (°C)
20
0
(b)
No. of starfish.ha-1
200
150
100
50
0
Percentage occurrence
80
60
20
0
n/d
abs
n/d
D
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
1995
1996
1997

showed marked seasonal trends in abundance, occurring at higher densities during summer and at much lower densities during the winter; occasionally during the colder months starfish were completely absent from the study area following migration offshore into deeper water (see Chapter 2). The maximum density of 130 starfish.ha^{-1} (0.013ind.m^{2}) was recorded during July 1996. The percentage of infested *A. irregularis* increased gradually over the study period from 18% in December 1995 to around 70% in the spring and early summer of 1997. No obvious seasonal trends could be discerned and infestation rates did not appear to be influenced by host population density. The appearance of small, apparently recently recruited worms between the inferomarginal plates, particularly during the autumn (November and December) (up to18% of the population) and during spring to early summer (March, April and June) (up to15%) suggested that two main periods of recruitment may occur each year. Samples collected during March and April 1997 in Cardigan Bay, Colwyn Bay and from the eastern Irish Sea also contained significant numbers (up to 13-16% in these populations) of small juveniles between the inferomarginal plates.

Over the study period *A. irregularis* arm length ranged between 5-58mm. Seasonal changes in the size frequency distribution of *A. squamosa* and *A. irregularis* at the main study site are presented in Figure 6.5. The modal arm length (22mm) of *A. irregularis* remained more or less constant (22mm) between December 1995 and March 1996 (Figure 6.5a and b). Between April and November 1996 modal arm length steadily increased to 34mm (Figure 6.5c to f). Following this period of apparent growth the structure of the starfish population remained relatively unchanged (Figure 6.5g to i)

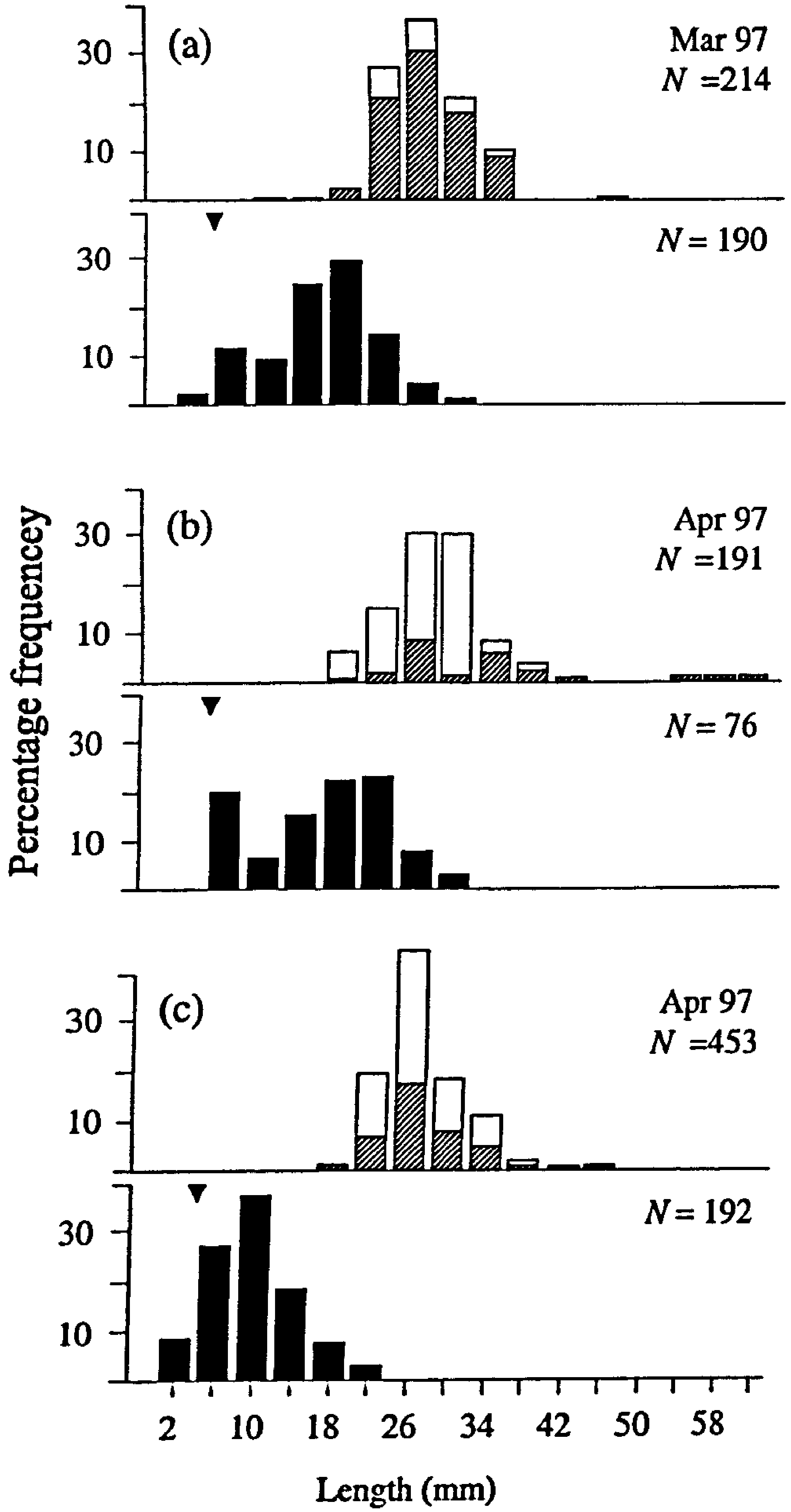
Figure 6.5. Seasonal changes in the size frequency of *Astropecten irregularis* (□) and *Acholoë squamosa* (■) in Red Wharf Bay. Cross-hatching within the open columns denotes the percentage of colonized starfish; triangles denotes periods of maximum occurrence of juvenile *A. squamosa* between the inferomarginal plates. Where successive monthly samples were similar the data were pooled.


(a)
Dec 96
N =189
N = 40
(d)
Jul/Aug 96
N =814
N = 295
(g)
Mar 97
N =101
N = 65
(b)
Jan/Feb/Mar 96
N =267
N = 67
(e)
Sep/Oct 96
N =382
N = 196
(h)
Apr 97
N =145
N = 101
(c)
Apr/Jun 96
N =125
N = 61
(f)
Nov 96
N =75
N = 50
(i)
Jun 97
N =186
N = 114
Percentage frequency
30
10
2
10
18
26
34
42
50
58
Length (mm)

albeit with an apparent recruitment of smaller individuals in October 1996 (Figure 6.5i). During 1997 there was little evidence of any significant recruitment of small starfish to this population. Although generally less abundant, the larger size classes of *A. irregularis* were more heavily infested, thus 60% of all starfish infestation with *A. squamosa* exceeded the median arm length for this population (see Figure 6.5). *A. squamosa* ranged from <2 to 42mm in length and there was no obvious seasonal changes in population structure, apart from the recruitment of juveniles during December 1995, April, June, and November 1996, and March and April 1997 (see Figures 6.4 and 6.5). Similar size distributions were also obtained for populations of *A. squamosa* and *A. irregularis* from Cardigan Bay, Colwyn Bay and the eastern Irish Sea (Figure 6.6i). Throughout most of the year a significant positive correlation existed between the body length of adult *A. squamosa* and arm length of *A. irregularis* (Figure 6.7) indicating that larger worms were generally found on larger starfish. This relationship, however, was lost when increased numbers of juveniles were present in the population since those worms tended to occupy all sizes of *A. irregularis*. Populations from Cardigan Bay, Colwyn Bay and the eastern Irish Sea were again similar to the Red Wharf Bay population (Figure 6.6ii).

Specimens of *A. squamosa* are white or orange in colour, although the data indicates a marked preponderance of orange worms. Amongst adults and juveniles no size differences could be detected between orange and white worms (Mann Whitney U=0.345 and 0.728 respectively, both at $P>0.05$). Colour has previously been shown to be a reliable indicator of sex in *A. squamosa* (Cuénot, 1912) and this is corroborated by

Figure 6.6. (i) Size frequency distribution of *Astropecten irregularis* (□) and *Acholoë squamosa* (■) in (a) Cardigan Bay; (b) Colwyn Bay; and (c) Eastern Irish Sea (site 3). Cross-hatching within the open columns denotes the percentage of colonized starfish; triangle denote periods of maximal occurrence of juvenile *A. squamosa* between the inferomarginal plates. (ii) The relationship between body length of *A. squamosa* and the arm length of *A. irregularis* collected from: (a) Cardigan Bay; (b) Colwyn Bay, and (c) Eastern Irish Sea (site 3); * = $P<0.005$; n.s. = $P>0.05$. (●) represents adult and (O) juvenile symbionts.


(a)
Mar 97
N =214
N = 190
(b)
Apr 97
N =191
N = 76
(c)
Apr 97
N =453
N = 192
Percentage frequencey
30
10
2
10
18
26
34
42
50
58
Length (mm)

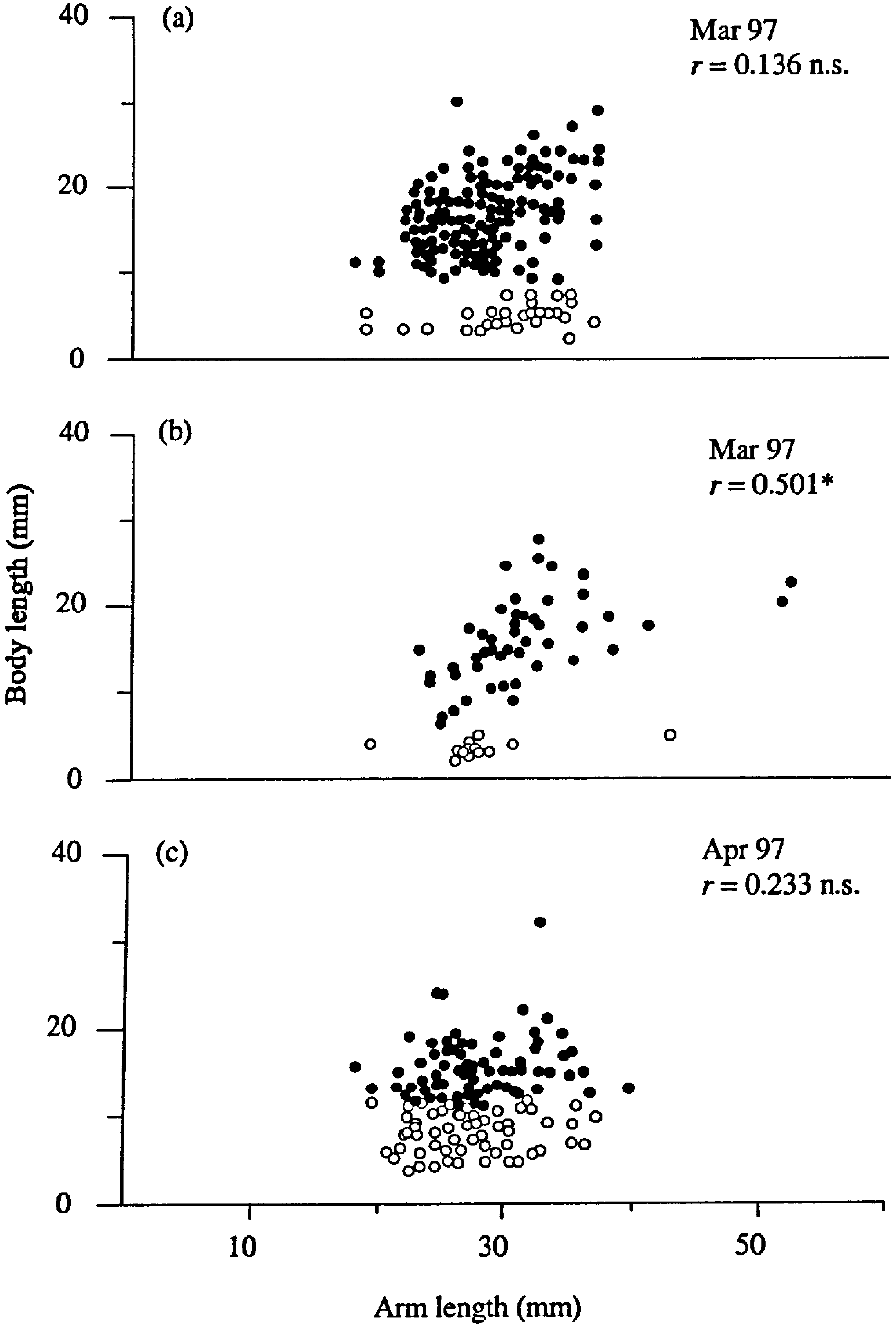
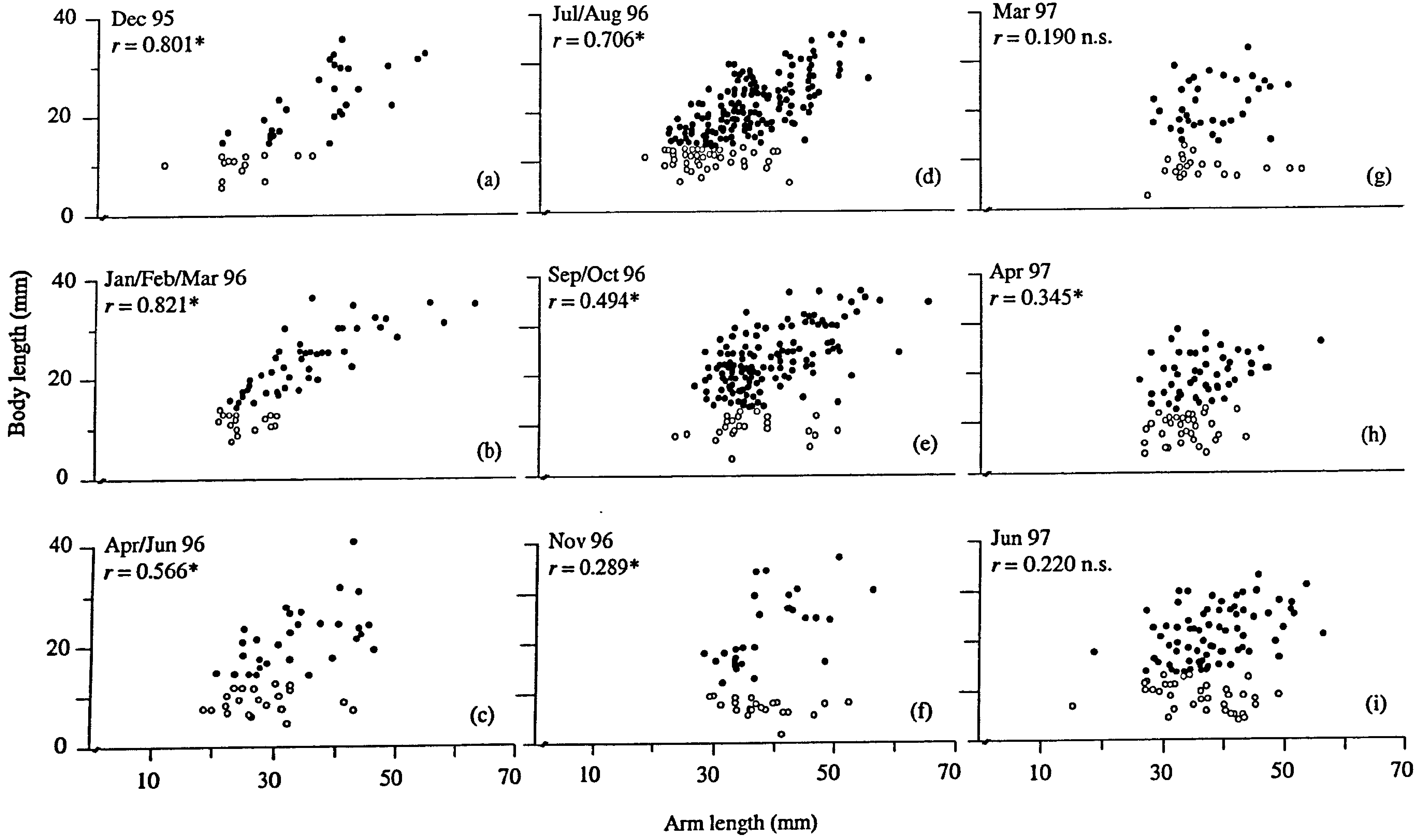

(a)
Mar 97
r = 0.136 n.s.
(b)
Mar 97
r = 0.501*
(c)
Apr 97
r = 0.233 n.s.
Body length (mm)
40
20
0
10
30
50
Arm length (mm)

Figure 6.7. The relationship between body length of *Acholoë squamosa* and *Astropecten irregularis* in Red Wharf Bay, between December 1995 and June 1997; 8 = $P<0.05$; n.s. = $P>0.05$.(●) represents adult and (O) juvenile symbionts. Where successive monthly samples were similar the data were pooled.


Dec 95
r = 0.801*
(a)
Jul/Aug 96
r = 0.706*
(d)
Mar 97
r = 0.190 n.s.
(g)
Jan/Feb/Mar 96
r = 0.821*
(b)
Sep/Oct 96
r = 0.494*
(e)
Apr 97
r = 0.345*
(h)
Apr/Jun 96
r = 0.566*
(c)
Nov 96
r = 0.289*
(f)
Jun 97
r = 0.220 n.s.
(i)
Body length (mm)
0
20
40
10
30
50
70
Arm length (mm)

our own observations of worms obtained during July in which white individuals contained only sperm and orange individuals contained only ripe eggs (average diameter 90.3 ± 9.6μm). There appears to be a substantial bias (20:1) towards female worms in the Red Wharf Bay population.

6.4. Discussion

Acholoë squamosa was first reported in British waters by Carrington (1865) at Southport Sands, eastern Irish sea, where it was associated with *Asterias aurantiaca* (= *Astropecten irregularis*). Published records of *A. squamosa* have been largely restricted to the English Channel (Claparède, 1870; Fauvel, 1923; Davenport, 1953) and Irish Sea (Mackie *et al.*, 1995). At the main study site in Re Wharf Bay unpublished archive records and E. I. S. Rees (pers. comm.) indicate that it has been found on *A. irregularis* regularly since 1935. On the west coast of Ireland it was reported from Galway Bay (McIntosh, 1876) and more recently by B. O'Connor (per. comm.).

In the present study *A. squamosa* occurred on *A. irregularis* from the English Channel in south-west England, northwards as far as the eastern Irish Sea. It was particularly abundant in our Cardigan Bay and Colwyn Bay samples and at all of the study sites in the eastern Irish Sea, but was absent from the deeper waters near the Little Sole Bank and from sites in the Clyde Sea (Figure 6.1). The population density of *A. irregularis* was usually higher at sites in which the sediment consisted of fine sand or mud and was generally lower in coarser sediments. Christensen (1970) similarly demonstrated that *A. irregularis* was not commonly found in coarse grain sediments, demonstrated that *A. irregularis* was not commonly found in coarse grain sediments, and comparison of Holme's (1966) plots shows how closely the abundance of *A. irregularis* depends on the presence of clean sand not far from the shore. Although there was no consistent relationship between population density of *A. irregularis* and incidence of *A. squamosa* in the present study, the latter was also generally associated with finer grained sediments. Since successful reproduction will depend on encounters between male and female worms, and as adult worms occur singly on individual starfish, and are not known to leave their host for purposes of reproduction, encounter rates at low starfish host densities could be substantially compromised.

In the Red Wharf Bay starfish population infestation by *A. squamosa* increased progressively from a relatively low level (18%) in 1995, when the average arm length of the recently established cohort of *A. irregularis* was 18mm, to 60-70% in the spring and early summer of 1997, when the average size of the host was 42mm. Similar levels of infestation (75%) have previously been reported by Davenport (1953) from the Eddystone ground *A. irregularis* population, although this was significantly higher than in the survey, conducted in this present study, in 1996 from the same general area, when only 26% of the population was infested. At the other sites infestations ranged from 0% to 88% (Figure 6.1). Such inter-site variability might perhaps be anticipated given that infestation rate is significantly correlated with host size and water depth, variables which are themselves strongly correlated (Figure 6.2). Why larger *A. irregularis* tend to occur in deeper water is unclear, although larger specimens of *A. arantiacus* have also been recorded from the deeper waters of the Mediterranean (Burla *et al.*, 1972). The

Irish Sea survey by Mackie *et al* (1995) who sampled mostly from depths >50m, only one *A. squamosa* (from fine sand at 25m). The absence of *A. squamosa* from site 1, south-west of the Scilly Isles and from site 6 in the Celtic deep may thus reflect either the generally large size of *A. irregularis* or increased water depth which in both sites is >90m.

In Caernarfon Bay the apparent absence of *A. squamosa* from a geographical area where it might be expected to occur in abundance, cannot be explained in terms of water depth and may simply reflect the small number of starfish obtained from this particular locality (Table 6.1). The absence of *A. squamosa* from our study sites in south-west Scotland, (sites 15-17) where sediment type would perhaps appear to be favourable, cannot be satisfactory attributed to either host size or water depth and suggests this region may be close to the northerly limit of *A. squamosa* in Britain. *A. irregularis* on the other hand has a geographical range from Lofoten in Norway to Morocco in Africa (Mortensen, 1927). It is interesting to note, therefore, that *A. squamosa* was not reported by Tebble and Chambers (1982) in their review of the Polynoidae of Scotland. In November 1996 two specimens of *A. squamosa* were found on another asteroid, *Luidia ciliaris,* from the Eddystone ground (site 2). In the same general area Davenport (1953) never recorded *A. squamosa* on *L. ciliaris*, despite the fact that this starfish occurred in the same trawls as infested *A. irregularis*, but he found that in his laboratory experiments, *A. squamosa* was unable to discriminate between *L. ciliaris* and *A. irregularis* and he noted that *L. ciliaris* is a common host for *A. squamosa* in the Mediterranean (see also McIntosh, 1876).

Although up to three juvenile *A. squamosa* could be found occupying the same individual host, adult worms always occurred singly. Experimental studies on two species of *Arctonoe,* associated with the holothurians *Stichopus parvimensis* and *Megathura crenulata,* have demonstrated that single infestations are strictly regulated through intra-specific aggression between the symbionts (Dimock, 1970; Britaev and Smurov, 1985). Single occupancy of a host suggests that these worms are strongly territorial, a behavioural response that would help to disperse the population (Britaev and Smurov, 1985). A strong positive correlation was found between the size of *A. squamosa* and the size of its host (Figure 6.5) indicating that once a suitable host has been located the worm remains faithful to that particular individual. However, during periods when juveniles are available for infestation, a wide size range of starfish are infested, and the correlation between size of worm and host may be temporarily lost. In the present study and that of Davenport (1953) *A. squamosa* has been recorded with its head and anterior body inside the mouth of *A. irregularis,* presumably in order to feed on the stomach contents of the host. Single adult occupancy, however achieved, would maintain an unchallenged access to the stomach contents. Another worm, the commensal hesionid, *Podarke pugettensis*, has also been observed to enter the stomach of its starfish host *Patiria minarta* (Davenport, 1966). In this study, laboratory observations indicate that *A. squamosa* makes regular excursions to the oral region of its host and when excised pieces of host body are presented to *A. squamosa* it is stomach tissue that elicits the strongest behavioural response (see also Davenport 1953).

Whilst both adult and juvenile *A. squamosa* were almost invariably located in the ambulacral grooves (95%) juvenile worms occurred both here (64%) and between the inferomarginal plates (31%) (Table 6.2) where the smaller, recently recruited and presumably more vulnerable individuals are protected from physical abrasion and interactions with any large adults by the over-arching ossicle spines. This refuge, however, can only be temporary, for as the worms increase in size they will be forced to leave the protection of the inferomarginal plates. In the case of multiple infestations intra-specific interactions will then force these larger juveniles to infest a different region of the host or, alternatively they may leave the starfish in order to locate another suitable host. Britaev and Smurov (1985) have shown that *Arctonoe vittata* become more aggressive as they increase in body size.

Increases in the overall infestation rate of *A. irregularis* in Red Wharf Bay were due to the recruitment of small juvenile *A. squamosa* between the inferomarginal plates in late autumn (November and December) and spring to early summer (April to June). In south-west England spawning in *A. squamosa* is believed to occur during late-summer to autumn (Davenport, 1954). Although we have no detailed data on the annual reproductive cycle of *A. squamosa* in Red Wharf Bay the presence of ripe gametes in the coelom could be detected during July. There is no documented information elsewhere on the reproductive cycle of *A. squamosa.* However, work by Strel'tsov (1966) on the free-living polynoid *Harmothoë imbricata*, reported two periods of larval settlement each year, one in March and the other in August. Whether there is any synchronization in the reproductive cycles of *A. squamosa* and *A. irregularis* is at present uncertain though such synchronization has previously been demonstrated in another polynoid-asteroid association (Britaev and Smurov 1985). Precisely how juvenile *A. squamosa* infest *A. irregularis* is not known but the requirement for physical contact with the host seems to be important (Davenport, 1953). In this present study laboratory observations have demonstrated that juvenile *A. squamosa,* dislodged from *A. irregularis,* make no obvious attempts to relocate a host but simply remain partially buried in the sediment, presumably awaiting an opportunity to infest a passing starfish. Isolated juvenile *A. squamosa* were also occasionally recorded in the sediment from grab samples at our main study site in Red Wharf Bay. Presumably the chances of such worms encountering a potential host will be significantly enhanced at higher population densities of the host e.g. *A. irregularis* and/or when the host is most active.

CHAPTER 7

General Discussion

Astropecten irregularis is an important predator of many subtidal communities around the coastal waters of the British Isles and is usually found inhabiting a wide variety of different substrates ranging from coarse gravel to find sand. In Red Wharf Bay the abundance of *A. irregularis* shows a seasonal trend with the highest densities typically occurring during the summer months and the lowest, or even a complete absence of starfish during the winter months. Seasonal changes in the population dynamics of *A. irregularis* and its prey exhibit complex interactions both with each other and with the physical environment, including such factors as substrate composition, seawater temperature, tidal cycle and water velocity. In general, *A. irregularis* has a seasonal preference for variety of different benthic fauna, including molluscs, crustaceans, polychaetes and echinoderms, although it has a particular preference for juvenile bivalves such as the clam, *Spisula subtruncata.*

It is suggested, that in Red Wharf Bay *A. irregularis* migrates offshore into deeper water during the winter months (Chapter 2). Although there is no direct evidence of migration by *A. irregularis*, it is clear that starfish are low in numbers or are completely absent from samples collected during the coldest winter months. During the absence of this predator from the study area the potential impact of predation on those prey species e.g. *S. subtruncata* inhabiting the area may be greatly reduced. Moreover, the settlement of several prey species such as *Corbula gibba*, to the study area occurs when starfish are absent so reducing the mortality of such species. Although the migration of starfish clearly provides a short-term benefit to many infaunal species, the reasons for this seasonal migration are much less clear. However, increases in heavy ground-swell forces which frequently occur in Red Wharf Bay during the winter months (Rees *et al*, 1975) and which generally disrupt the surface sediments by gradually transporting them inshore (Jago, pers. comm.) may be important contributing factors. The winter migration of *A. irregularis* to an offshore location and the mode of movement by starfish i.e. whether they crawl or use strong tidal currents to assist in their transport into deep water still requires further confirmation. During the summer months peak densities of *A. irregularis* may be associated with spawning rather than feeding assemblages, particularly since starfish reduce or cease feeding during this period. At such high densities the close proximity of sexually mature individuals will facilitate the successful reproduction of these broadcast spawners. In autumn 1997, however, high population densities of *A. irregularis* coincided with the settlement of several prey species such as *Gafrarium minimum* and *Fabulina fabula*, which are readily consumed by starfish and therefore, it is probable that these high starfish densities were indicative of feeding assemblages rather than spawning assemblages.

Although the diet of *A. irregularis* broadly reflects the seasonal availability of prey within the benthos, bivalve species e.g. *S. subtruncata*, *Chamelea gallina* and *Parvicardium ovule* are amongst the most common prey species consumed by starfish (Chapter 3). Moreover, similarities between the dietary characteristics of *A. irregularis* inhabiting different geographical locations throughout the southern and western coastal waters off the British Isles exist, reflecting the variability in the local abundance of different prey species. For example, at localities within the southern approaches to the English Channel, the diet of *A. irregularis* was dominated by the cockle, *Parvicardium* spp. whereas in the eastern Irish Sea the clam, *S. subtruncata*, was generally the most abundant. These findings support the dietary characteristics of *A. irregularis* found within Danish waters by Christensen (1970).

The use of cluster analysis (Bray-Curtis similarity) and multi-dimensional scaling (MDS) proved useful tools in the evaluation of seasonal changes in the diet of *A. irregularis* (Chapter 3). These multivariate techniques identified three significant seasonal groupings based on the composition of prey species found in the diet. During winter echinoderms such as *Ophiura ophiura* were a characteristic feature of the diet whilst in spring/summer the polychaete *L. koreni* and the bivalve *S. elliptica* were among the most dominant prey items, but in autumn the diet consisted almost exclusively of *S. subtruncata*. The numerical abundance of different prey species within the stomachs of *A. irregularis* provided a clearer picture of the seasonal trends in the diet than that estimated from biomass. Biomass, however, provided a clear insight into the overall contribution of individual species to the diet. The cumacean *Diastylis rugosa*, for example, was found to be a more important food source to *A. irregularis* than that estimated simply using its numerical abundance. Other seasonal trends were also detected, in particular, the diversity of species found within the diet of *A. irregularis* showed that this starfish is a relatively 'specialized' predator during the autumn months, when the preferred prey e.g. *S. subtruncata* is particularly numerically abundant, but functions more as a generalized feeder during the summer months when its preferred prey are less abundant. Diet breath, however, is related to starfish size.

Large starfish generally ingest a wider variety of different prey species than smaller starfish as a result of the restrictions imposed by the mouth diameter and greater efficiency at handling large prey such as *Echinocardium cordatum*, which are, therefore, not generally available to smaller starfish.

The availability of prey within the subtidal benthos is an important factor influencing prey selection by *A. irregularis* (Chapter 3). In March 1997, for example, *Chamelea gallina* was the most numerically abundant prey species in Cardigan Bay and was identified as the most preferred species using the Chesson's feeding index. Laboratory experiments confirmed the importance of prey density as a component in prey selection showing that *A. irregularis* exhibits a functional response to increases in prey density (Chapter 4). Furthermore, field evidence showed that *A. irregularis* is able to switch from one prey species to another depending on their availability, thus indicating the plasticity of its feeding preferences, a strategy ideally adapted to an environment where the availability of prey can often be highly unpredictable. However, the most abundant prey species in the benthos were not invariably the prey most preferred by *A. irregularis.* In Red Wharf Bay during March 1997, for example, *Corbula gibba*, was not preferred over *S. subtruncata*, even though the latter species was significantly less abundant, strongly suggesting that factors other than prey density are also important in prey selection.

The mechanism underlying the ability of *A. irregularis* to differentiate between different prey species is complex, involving a range of factors such as prey size, the retention time of prey within the stomach (which also varies with species and prey size) the palatability of prey, and changes in predator size (Chapter 4). Laboratory experiments have shown a strong relationship between the retention time of different prey species and their relative 'preference' ranking in the diet of *A. irregularis*. Moreover, the profitability of prey is directly related to their retention times, a factor which itself is negatively correlated to increases in both the size of the predator and prey. It is predicted, therefore, that *A. irregularis* should select those prey species which have short retention times e.g. *S. subtruncata*, and are also of a size which is most profitable e.g. large bivalve prey have a greater profitability than small prey (Chapter 4). Prey selection, however, is further complicated by the availability of prey within the benthos. For example, *A. irregularis* will tend to consume small prey, when they are numerically abundant in the benthos, thus maximizing the number of prey items packed into the stomach. However, *A. irregularis* will select larger prey items when prey are generally more uniformly distributed and so fewer prey items are encountered, since the ingestion of only a few large prey items will be more profitable. It is envisaged that a log-linear model will evaluate prey selection by *A. irregularis* based on the relationships between the profitability of prey, prey density, starfish size, and the maximum number of prey required to pack the starfish stomach. Such a model will identify the most important criteria influencing the 'decision' taken by starfish to either select or ignore prey during a foraging excursion. Some progress has already been made in this area but requires further work.

Christensen (1970) proposed that *A. irregularis* was a 'keystone' predator (*sensu* Paine, 1969) (Chapter 1). In this study *A. irregularis* does appear to satisfy the properties defining a 'keystone' predator, although one property which contributes to this concept that is not satisfied, is that a predator should consume prey which are dominant within the community and are competitively superior. In other soft-sediment benthic communities neither Peterson (1979) nor Wilson (1990) could not find a single dominant invertebrate predator capable of excluding a potentially dominant prey species, as occurs in the intertidal habitat, and that the concept of a 'keystone' predator may not be totally appropriate in this context.

The pursuit, capture and ingestion methods exhibited by *A. irregularis* when attacking different prey species involved a high degree of body flexible body (Chapter 5). These variable prey capture methods included 'arm-curling' to gather several prey (e.g. *Cerastoderma edule*) simultaneously, 'caging' to prevent burrowing prey (e.g. *Polinices polianus*) from escaping, 'scissoring' to pursue relatively fast-moving prey such as *Ophiura ophiura*, and 'swiping' for securing swimming prey such as *Diastylis rugosa*. No escape responses were elicited by prey until starfish had made physical contact, by which time it was generally too late and prey were quickly ingested. This suggests that *A. irregularis* possesses an ability to approach prey undetected, thus increasing its capture success.

The locomotory activity of freshly caught *A. irregularis* from Red Wharf Bay showed a quadri-diurnal pattern of rhythmicity, which coincided with times of slack water during expected high and low tide, and continued to remain free-running for approximately twenty-two hours (Chapter 5). Laboratory flume experiments showed that *A. irregularis* burrows rapidly in response to increases in water velocity and only move across the sediment surface during periods of simulated slack water.

Endogenously controlled locomotory activity in *A. irregularis* requires further examination in order to establish whether tidally dependent patterns are entrained by such exogenous factors. Information is also required to determine the plasticity of locomotory patterns in *A. irregularis* to changes in water velocity, particularly, since no previous information regarding this aspect of endogenously controlled behaviour in asteroids has been reported.

An interesting relationship between a commensal polychaete worm, *Acholoë squamosa*, and its principal host *A. irregularis* was investigated (Chapter 6). Whilst *A. squamosa* was recorded at sites along the southern and western coasts of the British Isles, it was apparently absent from Scottish waters. In Red Wharf Bay the percentage of *A. irregularis* colonized by these polynoid worms steadily increased from a low of <20% to a high of >90% during the course of the three year study period. Although, generally a single adult worm occupied the ambulacral groove of individual starfish, the seasonal occurrence of up to three juvenile worms were also recorded occupying the infra-marginal plates. There is little known about this *Astropecten-Acholoë* relationship and further work is needed to demonstrate the method used by adult worms to ensure contact with other sexually mature individuals in order to reproduce, especially since adults are 'effectively' isolated from each other by the single infestation of individual starfish.

A. irregularis is an important predator of may juvenile benthic species, ingesting considerably large numbers of these prey (up to 200-300 juveniles were found in the stomach of a single starfish) when they are available within the benthos. Moreover, since *A. irregularis* has a very cosmopolitan diet, its impact on infaunal species has the potential to affect a wide range of community assemblages. In addition, *A. irregularis* is an important controlling agent at several trophic levels since it feeds on the gastropod, *P. polianus*, a predator which also feeds on a similar range of molluscan prey, and consumes the prey species of commercially important flatfish such as Plaice, *Pleuronectes platessa* and Dab, *Limanda limanda.*

Preliminary stages in the design of a predictive model that evaluates the importance of *A. irregularis* as a controlling agent within a soft-sediment assemblage has already been initiated. However, this study is still in its infancy and further work is required to build and test the predictions of such a model. The model is a 'structured age-class' type and is driven by the size of *A. irregularis*, a component which integrates seasonal changes in growth and also the recruitment of starfish to the population. Moreover, starfish size is a factor that influences prey selection, prey mortality, diet breath, and the range and duration of foraging, it is, therefore, an important parameter underlying the mechanism of this particular model. Since the organization, structure and biodiversity of a community is of fundament importance in understanding how a system works, and has implications for the conservation of such systems, a model related to the *A. irregularis* community should provide considerable insight into the complex interactions between both the physical and biological components of such a community. In addition, it should enable predictions to be made on the effects on such a community by manipulating various parameters that are of ecological importance. Seawater temperature, on the other hand, a factor which is highly predictable, will form an important predictive factor with respect to the winter migration of starfish, summer spawning and feeding rates, events which themselves influence the overall impact of predation by *A. irregularis*. Furthermore, it is hoped that the findings described in this thesis will form valuable base-line data for further studies that examine the relationships between sediment dynamics and the ecology of *A. irregularis*.

PAGE

NUMBERING

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Appendix I

Table 1. Coordinates, number of *Astropecten irregularis* and seawater depth at all beam trawl sites collected between November 1995 and December 1997 in Red Wharf Bay; n/s denotes not sorted.

	Coordinates						
	Shot		Hauled				
Date	Latitude	Longitude	Latitude	Longitude	Ship	No. of starfish	Depth (m)
15/11/95	53 19 71	04 03 87	53 19 87	04 04 53	Prince Madog	n/s	11
	53 19 88	04 04 61	53 19 93	04 05 03	total	96	12
	53 19 95	04 05 16	53 20 02	04 05 56			11
	53 20 04	04 05 68	53 20 14	04 06 11			11
	53 20 17	04 06 21	53 20 30	04 06 78			13
	53 20 34	04 06 94	53 20 43	04 07 58			14
	53 20 47	04 07 76	53 20 64	04 08 32			14
	53 20 70	04 08 58	53 20 81	04 08 79			16
	53 20 92	04 09 23	53 20 86	04 08 55			17
	53 20 76	04 08 29	53 20 52	04 07 55			17
	53 20 37	04 07 15	53 20 21	04 06 51			15
	53 20 11	04 06 04	53 20 17	04 05 50			15
	53 20 18	04 05 27	53 20 25	04 04 32			16
	53 20 27	04 04 14	53 20 34	04 03 35			18
	53 20 35	04 03 19	53 20 34	04 02 33			18
	53 20 32	04 02 15	53 20 24	04 01 25			30
18/12/95	53 20 42	04 04 48	53 20 61	04 05 15	Prince Madog	13	18
	53 20 63	04 05 22	53 21 03	04 06 47		15	19
	53 21 11	04 06 87	53 20 21	04 08 01		11	16
	53 21 18	04 08 18	53 21 25	04 09 20		7	18
	53 20 89	04 09 28	53 20 88	04 08 45		4	15
	53 20 94	04 08 48	53 20 70	04 07 92		8	13
	53 20 77	04 08 11	53 20 52	04 07 57		2	12
	53 20 54	04 07 59	53 20 41	04 07 15		8	11
	53 20 41	04 07 00	53 20 20	04 06 65		44	10
	53 20 20	04 06 64	53 19 96	04 06 27		23	10
	53 20 08	04 06 30	53 19 96	04 05 84		17	9
15/01/96	53 20 18	04 04 93	53 20 35	04 05 33	Sandpebbler	4	11
	53 20 40	04 06 00	53 20 53	04 06 40		14	12
	53 20 53	04 06 59	53 20 54	04 07 07		22	11
	53 20 52	04 07 08	53 20 34	04 07 38		16	10
	53 20 33	04 07 34	53 20 88	04 08 45		13	11
	53 20 32	04 07 30	53 20 30	04 06 90		24	10
	53 20 56	04 06 52	53 20 59	04 06 03		14	11
	53 19 52	04 10 99	53 19 66	04 10 27		0	9
	53 19 ?	04 10 ?	53 20 ?	04 10 ?		5	10
	53 19 92	04 07 37	53 19 81	04 06 11		1	12
	53 17 94	04 02 43	53 17 65	04 02 69		0	12
15/02/96	53 20 25	04 06 20	53 20 43	04 06 54	Sandpebbler	1	12
	53 20 47	04 06 56	53 20 47	04 07 00		2	12
	53 20 58	04 07 00	53 20 71	04 07 39		5	12
	53 20 81	04 07 29	53 20 67	04 07 25		0	13
	53 19 91	04 06 43	53 19 90	04 06 11		0	11
26/02/96	53 21 16	04 03 65	53 21 15	04 04 27	Sandpebbler	0	23
	53 21 12	04 04 23	53 20 99	04 04 68		1	21
	53 20 99	04 05 05	53 20 99	04 05 18		0	15
	53 20 00	04 05 24	53 20 13	04 05 44		1	16
	53 20 16	04 06 00	53 20 22	04 06 17		0	11
	53 20 20	04 06 53	53 20 22	04 06 80		0	13
	53 20 18	04 06 60	53 20 11	04 06 14		3	13
	53 20 13	04 06 30	53 20 03	04 05 86		3	12

	53 20 12	04 05 90	53 20 06	04 05 57		4	12
28/02/96	53 20 17	04 06 20	53 20 38	04 06 72	Sandpebbler	5	12
	53 20 47	04 06 65	53 20 33	04 06 92		7	11
	53 20 34	04 06 62	53 20 34	04 06 69		0	11
	53 20 41	04 05 89	53 20 32	04 05 54		3	11
	53 20 83	04 04 93	53 20 78	04 04 53		0	17
	53 20 71	04 04 59	53 20 97	04 04 60		0	16
	53 21 51	04 04 48	53 21 52	04 05 02		0	21
	53 21 53	04 04 48	53 21 53	04 04 87		1	21
	53 21 23	04 05 17	53 21 22	04 05 49		2	18
	53 21 16	04 06 18	53 21 17	04 06 55		0	17
	53 21 21	04 07 79	53 21 27	04 08 21		2	16
	53 21 15	04 08 04	53 20 82	04 07 83		1	15
	53 20 53	04 07 50	53 20 34	04 06 92		7	12
06/03/96	53 20 45	04 08 12	53 20 61	04 08 70	Prince Madog	3	9
	53 20 65	04 08 82	53 20 84	04 09 63		1	9
	53 20 88	04 09 78	53 21 08	04 10 77		0	9
	53 21 11	04 10 94	53 21 05	04 10 20		0	9
	53 20 97	04 09 43	53 20 97	04 09 40		0	9
	53 20 95	04 09 39	53 20 73	04 07 26		0	10
	53 20 38	04 06 29	53 19 96	04 05 08		0	12
	53 19 86	04 04 78	53 19 80	04 03 85		0	12
	53 19 80	04 03 94	53 20 06	04 05 01		0	12
	53 20 12	04 05 18	53 20 57	04 06 40		14	13
	53 20 58	04 06 23	53 20 06	04 04 62		2	14
19/03/96	53 20 00	04 07 14	53 20 87	04 06 78	Prince Madog	0	13
	53 20 82	04 06 00	53 20 61	04 06 18		0	11
	53 20 56	04 06 80	53 20 34	04 06 58		4	10
	53 19 95	04 05 77	53 20 29	04 06 62		19	8
	53 20 35	04 06 78	53 20 80	04 07 66		22	9
	53 20 55	04 08 18	53 20 29	04 07 63		5	10
	53 20 16	04 07 30	53 19 99	04 06 88		5	10
20/03/96	53 19 82	04 05 99	53 20 05	04 07 17	Prince Madog	8	8
	53 20 12	04 07 39	53 20 52	04 08 30		1	8
	53 20 83	04 07 88	53 20 42	04 07 05		8	12
	53 20 36	04 06 92	53 20 01	04 06 05		1	12
	53 20 17	04 05 21	53 20 69	04 06 52		1	12
	53 20 73	04 06 62	53 20 99	04 07 39		0	12
17/04/96	53 20 20	04 05 56	53 20 45	04 06 03	Prince Madog	0	n/d
	53 20 49	04 06 11	53 20 70	04 06 68		7	
	53 20 81	04 06 82	53 20 97	04 07 24		2	
	53 20 80	04 07 26	53 20 40	04 06 44		1	
	53 20 38	04 06 39	53 20 05	04 05 63		1	
	53 19 94	04 06 00	53 20 22	04 06 54		9	
	53 20 28	04 06 73	53 20 58	04 07 42		10	
	53 20 40	04 07 40	53 20 10	04 06 79		4	
	53 20 00	04 06 60	53 19 73	04 06 07		5	
26/04/96	53 20 18	04 05 65	53 20 37	04 05 92	Sandpebbler	0	9
	53 20 41	04 05 96	53 20 60	04 06 14		2	11
	53 20 73	04 07 23	53 20 65	04 06 85		3	12
	53 20 49	04 06 74	53 20 39	04 06 34		5	12
	53 20 39	04 06 56	53 20 22	04 06 09		2	11
	53 20 27	04 06 02	53 20 19	04 05 59		4	10
	53 20 11	04 05 54	53 20 02	04 05 07		1	8
	53 20 12	04 05 43	53 20 27	04 05 72		0	9
	53 20 23	04 05 68	53 20 45	04 05 93		1	10
	53 20 59	04 06 84	53 20 30	04 06 38		2	12
	53 20 50	04 06 92	53 20 40	04 06 38		0	12

	53 20 70	04 06 10	53 20 63	04 06 50		0	15
	53 20 46	04 06 02	53 20 42	04 06 38		2	12
	53 20 09	04 08 35	53 20 26	04 08 83		3	9
	53 20 08	04 08 71	53 20 05	04 08 18		6	10
	53 19 95	04 08 44	53 19 78	04 07 91		2	12
	53 19 77	04 07 59	53 19 81	04 06 97		3	15
13/06/96	53 19 89	04 05 04	53 19 95	04 05 54	Sandpebbler	0	12
	53 19 92	04 05 82	53 20 02	04 06 40		1	13
	53 20 15	04 06 09	53 20 31	04 06 79		1	12
	53 20 28	04 06 95	53 20 36	04 07 49		4	12
	53 20 60	04 07 75	53 20 77	04 08 16		0	17
	53 20 69	04 08 28	?	?		3	14
	53 20 59	04 08 14	53 20 45	04 08 05		3	12
	53 20 51	04 08 10	53 20 36	04 08 08		1	12
	53 20 64	04 07 18	53 20 54	04 06 91		4	13
	53 20 52	04 07 13	53 20 34	04 06 89		5	12
	53 20 38	04 06 95	53 20 32	04 06 78		5	11
	53 20 29	04 06 56	53 20 34	04 06 31		6	11
	53 20 28	04 06 21	53 20 15	04 05 94		6	10
	53 20 12	04 06 96	53 20 02	04 06 12		0	11
	53 20 14	04 05 97	53 20 11	04 05 60		2	8
	53 20 09	04 05 62	53 20 08	04 05 35		1	9
	53 20 35	04 06 82	53 20 18	04 06 24		7	10
08/07/96	53 19 81	04 05 38	53 19 91	04 05 99	Prince Madog	11	11
(1500hrs)	53 19 93	04 06 06	53 20 01	04 06 44		16	12
	53 20 33	04 06 47	53 20 25	04 05 89		33	14
	53 20 34	04 05 30	53 20 28	04 05 84		22	16
	53 20 53	04 05 53	53 20 61	04 06 05		18	21
	53 20 65	04 06 17	53 20 67	04 06 43		63	18
(1900hrs)	53 19 81	04 05 38	53 19 91	04 05 99		18	11
	53 19 93	04 06 06	53 20 01	04 06 44		14	12
	53 20 33	04 06 47	53 20 25	04 05 89		27	14
	53 20 34	04 05 30	53 20 28	04 05 84		5	16
	53 20 53	04 05 53	53 20 61	04 06 05		21	21
	53 20 65	04 06 17	53 20 67	04 06 43		24	18
(2200hrs)	53 19 81	04 05 38	53 19 91	04 05 99		17	11
	53 19 93	04 06 06	53 20 01	04 06 44		20	12
	53 20 33	04 06 47	53 20 25	04 05 89		24	14
	53 20 34	04 05 30	53 20 28	04 05 84		34	16
	53 20 53	04 05 53	53 20 61	04 06 05		4	21
	53 20 65	04 06 17	53 20 67	04 06 43		23	18
(0400hrs)	53 19 81	04 05 38	53 19 91	04 05 99		13	11
	53 19 93	04 06 06	53 20 01	04 06 44		21	12
	53 20 33	04 06 47	53 20 25	04 05 89		18	14
	53 20 34	04 05 30	53 20 28	04 05 84		35	16
	53 20 53	04 05 53	53 20 61	04 06 05		14	21
	53 20 65	04 06 17	53 20 67	04 06 43		31	18
(0800hrs)	53 19 81	04 05 38	53 19 91	04 05 99		9	11
	53 19 93	04 06 06	53 20 01	04 06 44		28	12
	53 20 33	04 06 47	53 20 25	04 05 89		27	14
	53 20 34	04 05 30	53 20 28	04 05 84		12	16
	53 20 53	04 05 53	53 20 61	04 06 05		7	21
	53 20 65	04 06 17	53 20 67	04 06 43		8	18
(1100hrs)	53 19 81	04 05 38	53 19 91	04 05 99		14	11
	53 19 93	04 06 06	53 20 01	04 06 44		4	12
	53 20 33	04 06 47	53 20 25	04 05 89		26	14
	53 20 34	04 05 30	53 20 28	04 05 84		13	16
	53 20 53	04 05 53	53 20 61	04 06 05		16	21
	53 20 65	04 06 17	53 20 67	04 06 43		19	18
19/08/96	53 19 93	04 05 23	53 20 11	04 05 40	Sandpebbler	0	9
	53 19 91	04 05 50	53 20 02	04 05 96		0	9

	53 20 14	04 05 39	53 20 31	04 05 36		2	12
	53 20 68	04 05 36	53 20 90	04 05 49		0	19
	53 20 66	04 05 31	53 20 78	04 05 37		0	20
	53 20 55	04 06 03	53 20 65	04 06 15		2	19
	53 20 78	04 05 60	53 20 89	04 05 80		5	17
	53 20 79	04 06 48	53 20 83	04 06 75		5	17
	53 20 72	04 06 49	53 20 78	04 06 71		6	16
	53 20 64	04 06 51	53 20 79	04 06 91		3	16
	53 20 52	04 06 65	53 20 64	04 07 17		31	17
	53 20 41	04 06 51	53 20 58	04 07 08		25	14
	53 20 23	04 06 53	53 20 35	04 07 03		19	14
	53 20 07	04 06 55	53 20 21	04 07 25		15	15
	53 19 85	04 06 61	53 19 99	04 07 40		2	12
	53 19 99	04 07 60	53 20 12	04 08 04		1	13
	53 19 81	04 07 43	53 19 84	04 07 63		0	14
	53 20 71	04 07 35	53 20 80	04 07 64		0	15
17/09/96	53 20 24	04 06 90	53 20 30	04 07 42	Sandpebbler	5	14
	53 20 57	04 07 71	53 20 72	04 08 13		6	14
	53 20 65	04 08 24	53 20 42	04 08 10		5	14
	53 20 52	04 08 10	53 20 44	04 08 07		30	12
	53 20 50	04 08 12	53 20 39	04 08 10		34	11
	53 20 60	04 07 12	53 20 51	04 06 85		19	15
	53 20 50	04 07 09	53 20 35	04 06 90		13	14
	53 20 35	04 06 91	53 20 34	04 06 80		25	11
	53 20 23	04 06 50	53 20 37	04 06 38		30	10
	53 20 26	04 06 20	53 20 12	04 05 90		26	10
	53 19 98	04 06 20	53 19 92	04 05 82		25	12
21/10/96	53 19 99	04 05 99	53 20 19	04 06 54	Prince Madog	9	15
	53 20 22	04 06 61	53 20 34	04 07 38		3	14
	53 20 48	04 07 22	53 20 35	04 06 44		6	14
	53 20 32	04 06 30	53 20 13	04 05 63		0	14
	53 20 32	04 05 62	53 20 53	04 06 25		9	12
	53 20 57	04 06 37	53 20 79	04 07 11		16	12
	53 20 04	04 08 35	53 20 77	04 07 62		46	14
	53 20 12	04 05 63	53 19 92	04 04 95		22	10
22/10/96	53 20 42	04 07 18	53 20 37	04 06 45	Prince Madog	10	12
	53 20 30	04 06 33	53 20 17	04 05 60		26	11
	53 20 28	04 05 63	53 20 54	04 06 27		6	13
	53 20 55	04 06 36	53 20 86	04 07 17		4	11
	53 20 18	04 06 60	53 19 90	04 05 80		19	12
27/11/96	53 19 91	04 06 06	53 20 04	04 06 69	Prince Madog	3	16
	53 20 08	04 06 85	53 20 23	04 07 38		7	16
	53 20 34	04 07 33	53 20 16	04 06 84		6	17
	53 20 11	04 06 68	53 19 92	04 06 02		1	16
	53 20 08	04 05 97	53 20 18	04 06 61		14	16
	53 20 29	04 07 00	53 20 44	04 07 43		2	18
	53 20 55	04 07 31	53 20 45	04 06 75		12	18
	53 20 40	04 06 56	53 20 23	04 05 95		9	16
	53 20 36	04 06 05	53 20 66	04 06 89		2	23
	53 20 78	04 06 90	53 20 52	04 06 39		10	18
	53 20 54	04 06 25	53 20 37	04 05 63		0	17
	53 20 57	04 05 59	53 20 89	04 06 79		0	13
	53 20 89	04 07 18	53 20 44	04 07 62		4	14
	53 20 11	04 07 47	53 19 87	04 06 77		3	15
	53 19 80	04 06 58	53 19 74	04 06 28		2	18
12/12/96	53 20 42	04 04 48	53 20 61	04 05 15	Sandpebbler	0	12
	53 20 63	04 05 22	53 21 03	04 06 47		0	13
	53 20 21	04 06 87	53 21 15	04 07 01		0	16
	53 20 89	04 07 28	53 20 88	04 06 45		0	12

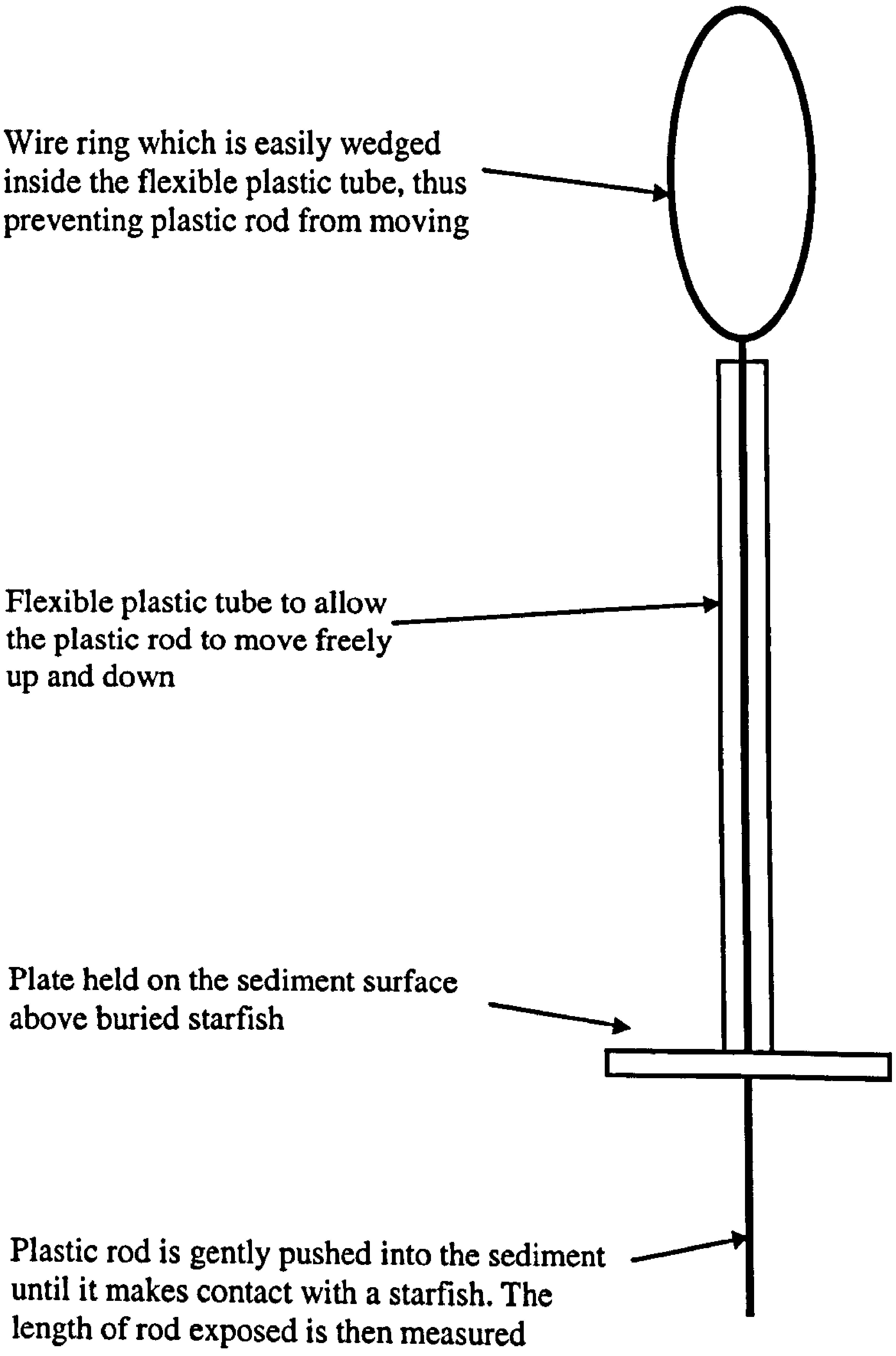
	53 20 94	04 07 48	53 20 70	04 06 92		1	12
	53 20 77	04 07 11	53 20 52	04 06 57		0	11
	53 20 54	04 06 59	53 20 41	04 07 15		0	11
	53 20 18	04 07 18	53 20 25	04 06 20		2	16
	53 20 10	04 05 85	53 20 01	04 05 00		0	15
	53 19 80	04 06 25	53 19 98	04 06 58		0	18
05/01/97	53 20 17	04 05 63	53 20 30	04 05 94	Sandpebbler	0	10
	53 20 43	04 05 92	53 20 61	04 06 12		0	12
	53 20 70	04 07 25	53 20 62	04 06 81		0	10
	53 20 50	04 06 80	53 20 33	04 06 34		0	11
	53 20 35	04 06 52	53 20 23	04 06 10		0	12
	53 20 30	04 06 03	53 20 21	04 05 55		0	10
20/02/97	53 19 86	04 06 24	53 20 00	04 06 69	Sandpebbler	3	16
	53 20 05	04 06 93	53 20 23	04 07 45		2	16
	53 20 19	04 06 19	53 20 37	04 06 67		8	17
	53 20 22	04 06 70	53 20 41	04 07 26		4	16
	53 20 36	04 05 71	53 20 68	04 06 64		2	17
05/03/97	53 20 63	04 06 79	53 20 58	04 06 47	Prince Madog	2	10
	53 20 58	04 06 40	53 20 52	04 06 21		2	10
	53 20 24	04 06 17	53 20 38	04 06 42		0	10
	53 20 44	04 06 52	53 20 59	04 06 79		8	10
	53 20 34	04 07 04	53 20 18	04 06 71		2	10
	53 20 13	04 06 59	53 20 04	04 06 19		0	9
	53 20 40	04 05 99	53 20 53	04 06 23		4	8
	53 20 57	04 06 33	53 20 62	04 06 71		3	9
	53 20 44	04 06 84	53 20 32	04 06 47		2	9
	53 20 29	04 06 35	53 20 18	04 06 01		7	10
	53 20 01	04 06 04	53 20 08	04 06 38		3	12
	53 20 12	04 06 54	53 20 22	04 07 00		4	8
06/03/97	53 19 98	04 06 17	53 20 11	04 06 62	Prince Madog	6	14
	53 20 16	04 06 92	53 20 25	04 07 30		2	14
	53 20 44	04 07 36	53 20 30	04 07 10		5	16
	53 20 25	04 06 97	53 20 10	04 06 54		3	15
	53 20 34	04 06 19	53 20 53	04 06 82		0	16
	53 20 46	04 07 01	53 20 35	04 06 55		5	14
	53 20 38	04 06 94	53 20 26	04 06 59		7	13
	53 20 23	04 06 50	53 20 13	04 06 20		3	13
	53 20 26	04 06 17	53 20 46	04 06 79		10	14
	53 20 67	04 06 83	53 20 61	04 06 65		0	14
	53 20 56	04 06 52	53 20 44	04 06 17		1	15
	53 20 53	04 06 09	53 20 71	04 06 63		3	15
10/04/97	53 20 01	04 05 99	53 20 15	04 06 29	Prince Madog	4	14
	53 20 22	04 06 43	53 20 40	04 06 88		18	16
	53 20 20	04 07 02	53 19 95	04 06 35		2	15
	53 20 09	04 05 88	53 20 27	04 06 23		11	16
	53 20 31	04 06 31	53 20 44	04 06 60		8	18
	53 20 57	04 06 69	53 20 33	04 06 00		1	20
	53 20 41	04 05 87	53 20 62	04 06 40		2	19
	53 20 70	04 06 59	53 20 87	04 07 01		30	20
	53 20 86	04 07 10	53 20 62	04 06 58		3	17
	53 20 54	04 06 43	53 20 34	04 06 01		0	18
	53 20 26	04 06 05	53 20 43	04 06 75		27	17
	53 20 38	04 07 03	53 20 18	04 06 67		15	18
	53 20 13	04 06 56	53 19 97	04 06 13		11	18
	53 20 44	04 06 05	53 20 10	04 05 53		10	17
16/05/97	53 19 76	04 06 14	53 10 00	04 05 59	Sandpebbler	5	12
	53 20 00	04 06 91	53 20 20	04 07 41		6	12
	53 20 14	04 06 17	53 20 27	04 06 57		1	10

	53 20 25	04 06 73	53 20 40	04 07 22		3	12
	53 20 31	04 05 85	53 20 70	04 06 69		1	10
	53 20 10	04 06 23	53 20 06	04 05 82		2	14
06/06/97	53 20 29	04 05 42	53 20 53	04 05 85	Prince Madog	0	17
	53 20 64	04 06 11	53 20 85	04 06 69		60	22
	53 20 71	04 06 82	53 20 55	04 06 41		20	18
	53 20 45	04 06 15	53 20 29	04 05 74		20	17
	53 20 23	04 05 77	53 20 31	04 06 33		24	13
	53 20 39	04 06 55	53 20 56	04 06 91		24	13
	53 20 49	04 06 99	53 20 32	04 06 70		21	19
	53 20 28	04 06 55	53 20 17	04 06 24		15	17
12/07/97	53 20 53	04 06 49	53 20 50	04 06 18	Sandpebbler	12	14
	53 20 28	04 06 12	53 20 34	04 06 45		8	12
	53 20 42	04 06 50	53 20 53	04 06 89		5	12
	53 20 38	04 07 08	53 20 10	04 06 74		6	10
	53 20 08	04 06 64	53 20 02	04 06 24		8	12
	53 20 43	04 05 87	53 20 59	04 06 20		13	13
	53 20 54	04 06 34	53 20 61	04 06 75		10	10
	53 20 47	04 06 85	53 20 34	04 06 43		5	10
	53 20 30	04 06 34	53 20 23	04 06 08		11	10
	53 20 04	04 06 08	53 20 06	04 06 32		6	9
28/08/97	53 20 00	04 05 78	53 20 11	04 06 23	Sandpebbler	0	10
	53 20 24	04 06 45	53 20 49	04 06 68		0	11
	53 20 23	04 07 12	53 19 90	04 06 45		5	11
	53 20 08	04 05 83	53 20 23	04 06 24		1	10
	53 20 39	04 06 35	53 20 47	04 06 64		0	9
	53 20 47	04 06 79	53 20 32	04 06 08		1	14
	53 20 45	04 05 83	53 20 67	04 06 44		1	12
	53 20 73	04 06 60	53 20 81	04 07 04		0	10
	53 20 87	04 07 11	53 20 65	04 06 57		1	10
	53 20 55	04 06 40	53 20 34	04 06 03		0	12
	53 20 20	04 06 15	53 20 33	04 06 73		0	13
	53 20 32	04 07 05	53 20 12	04 06 60		1	15
	53 20 14	04 06 53	53 19 86	04 06 18		0	15
	53 20 48	04 06 10	53 20 14	04 05 51		3	18
	53 20 01	04 05 90	53 20 18	04 06 27		2	14
	53 20 23	04 06 47	53 20 38	04 06 85		1	14
	53 20 25	04 07 06	53 19 94	04 06 37		0	12
	53 20 30	04 06 39	53 20 48	04 06 62		1	15
	53 20 56	04 06 72	53 20 32	04 06 01		4	16
	53 20 87	04 07 12	53 20 65	04 06 52		4	11
	53 20 57	04 06 43	53 20 30	04 06 03		7	12
	53 20 10	04 06 59	53 19 92	04 06 14		3	14
	53 20 45	04 06 04	53 20 11	04 05 51		1	14
11/09/97	53 20 45	04 07 07	53 20 60	04 06 23	Sandpebbler	0	10
	53 20 14	04 06 12	53 20 30	04 06 40		2	10
	53 20 47	04 06 49	53 20 49	04 06 72		3	15
	53 20 34	04 07 06	53 20 15	04 06 75		0	12
	53 20 12	04 06 59	53 20 04	04 06 17		0	10
	53 20 49	04 05 95	53 20 51	04 06 27		5	11
	53 20 54	04 06 35	53 20 60	04 06 72		0	10
	53 20 45	04 06 80	53 20 35	04 06 46		0	14
	53 20 20	04 06 36	53 20 21	04 06 05		2	13
	53 20 03	04 06 05	53 20 05	04 06 37		0	12
	53 20 57	04 06 43	53 20 50	04 06 20		4	12
	53 20 22	04 06 21	53 20 39	04 07 45		3	10
	53 20 46	04 06 56	53 20 52	04 06 76		0	11
	53 20 31	04 07 05	53 20 12	04 06 70		3	10
	53 20 15	04 06 51	53 20 01	04 06 15		0	9
	53 20 47	04 05 93	53 20 50	04 07 03		2	10

	53 20 57	04 06 33	53 20 62	04 06 71		5	10
	53 20 44	04 06 84	53 20 32	04 06 47		0	13
	53 20 29	04 06 35	53 20 18	04 06 01		0	10
	53 20 01	04 06 04	53 20 08	04 06 38		1	10
07/10/97	53 20 42	04 05 62	53 20 60	04 05 97	Prince Madog	12	18
	53 20 66	04 06 13	53 20 77	04 06 47		17	18
	53 20 51	04 06 36	53 20 28	04 05 67		8	14
	53 20 18	04 05 74	53 20 30	04 06 05		5	13
	53 20 33	04 06 14	53 20 46	04 06 62		10	15
	53 20 25	04 06 74	53 19 99	04 05 91		11	14
	53 20 14	04 05 72	53 20 20	04 06 17		9	12
	53 20 22	04 06 30	53 20 28	04 06 70		17	15
13/11/97	53 20 72	04 06 89	53 20 49	04 06 36	Prince Madog	4	19
	53 20 44	04 06 13	53 20 32	04 05 65		14	16
	53 20 40	04 05 65	53 20 62	04 06 18		21	18
	53 20 70	04 06 41	53 20 89	04 07 00		25	19
	53 20 71	04 07 19	53 20 56	04 06 80		17	18
	53 20 51	04 06 69	53 20 37	04 06 33		24	17
	53 20 46	04 07 06	53 20 32	04 06 66		17	15
	53 20 28	04 06 54	53 20 04	04 05 93		23	15
	53 19 93	04 06 06	53 20 07	04 06 73		21	12
1512/97	53 20 34	04 06 46	53 20 62	04 06 24	Sandpebbler	0	15
	53 20 28	04 06 10	53 20 30	04 06 40		0	14
	53 20 42	04 06 52	53 20 52	04 06 67		2	12
	53 20 36	04 07 08	53 20 17	04 06 70		1	11
	53 20 10	04 06 58	53 20 05	04 06 12		2	12
	53 20 49	04 06 01	53 20 48	04 06 29		3	12
	53 20 56	04 06 32	53 20 60	04 06 75		0	10

Appendix II

Figure 1. Diagrammatic representation of the specially adapted gauge used to determine the depth burrowed by *Astropecten irregularis.*



Appendix III

Table 1. Seasonal abundance (%) of difference prey species within the stomachs of *Astropecten irregularis* collected from Red Wharf Bay: (a) Bivalve prey species; and (b) Gastropod, Crustacean, Echinoderm, Polychaete and Foraminiferan prey species; only those species which contribute to >0.1% are presented.

(a)		1995								1996												1997					
Species	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D
Bivalves:																											
Spisula subtruncata	92.7	87.0	90.8	86.1	65.0	65.7	37.7		40.2	20.9	13.8	22.4	83.6	53.0	25.0		10.5	27.1	38.6	14.5	12.9	9.8	35.2	43.9	77.0	68.4	47.4
Nucula nitidosa	0.4	0.1		1.7		3.7	4.5		5.5	0.3	1.8	2.7	0.6	2.6	12.5		1.8	6.3	2.7	3.0	2.3	6.4	0.2	0.2	0.4	0.5	4.5
Gari fervensis		0.1	1.1	2.7		2.0	5.2		8.0	27.7	36.0	7.0	0.6	5.2	12.5			15.6	3.2	3.0	3.4	1.6	1.2	1.1	0.9	1.3	1.5
Mysella bidentata	0.1	0.3	1.3	1.3	4.8	3.9	4.5		8.0	3.27	0.5	2.8	0.7	2.6	25.0		70.2		6.5	4.5	1.8	9.7	0.4	2.8		0.2	6.8
Circumphalus casina																											
Chamelea gallina	1.1	0.1		1.0	4.8	9.6	9.7		4.8	3.0	7.3	7.4	0.6	5.2			5.3	6.3	6.5	5.6	3.4	1.6	4.8	6.5	0.8	1.5	2.3
Venerupis senegalensos	0.3	4.6	3.5	3.9		2.9	2.7		4.0	2.3	1.5	0.5	0.6					3.1	4.0	3.2	0.5		0.4			0.7	2.3
Parvicardium ovale	0.7	0.1							1.1	1.2	0.5	0.8	0.1	5.2					1.3	1.5	0.3		2.8	2.7	0.7	1.5	8.8
Gafrarium minimum	0.5						2.3		7.6	2.4	0.2	0.6	0.8				1.8	15.6	6.5	2.7	1.0		1.6	0.5	0.2	0.4	
Dosinia lupinus	0.6						5.3		4.0	2.0	0.5								5.3	3.7	0.1	1.7	3.5				
Corbula gibba			1.2						3.8	6.4	16.4	7.0	0.2	2.6	13.0		3.5		2.7	2.1	1.8	1.1	0.4	2.0		0.2	
Thracia phasoelina	0.2	0.3				2.9	1.9		2.5	1.5	1.1	3.0	0.8					3.1	1.3	2.0	1.6	6.4	1.6	0.5	0.8	0.2	0.3
Spisula elliptica	1.0								1.3		7.0	0.7	0.1						3.2	22.8	52.3	43.6	1.6	0.4	0.2	0.4	
Ensis spp.		0.1								0.3		1.0	0.3							0.2	1.8			0.7			0.8
Fabulina fabula											0.3	5.0							2.7	1.2		3.2	2.3	8.3	6.0	3.2	18.8
Astarte trianglaris							0.1		0.1	0.2	0.2	0.1	0.1						0.2	0.5	0.1						
Morella pygmaea												0.9	1.3							0.8	0.1			0.2	0.1		0.1
Donax vittatas	1.0	0.9	0.4	1.7			1.9				1.5		1.3	2.8													
Mactra stultorum																											
Modiolus modiolus																											
Timoclea ovata																											
Chlamys varia																											
Abra nitida																											
Morella donacina												0.9	1.3							0.8	0.1			0.2	0.1		0.1
Astarte elliptica																											
Mya truncata																											
Laevicardium spp.																				0.7	0.2	0.3					

(b)

	1995			1996												1997											
Species	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D
Gastropods																											
Polinices polianus	0.2	0.1	0.2	0.7			1.7		2.5	1.3	0.7	3.3	1.2	5.2	12.0			3.1	4.6	1.4	0.8		2.8	2.6	2.0	1.9	
Obstusella intersecta		4.7	2.4	1.5			0.9		3.0	2.0										0.5	2.1		1.8	0.2		3.7	
Scaphander lignarius																											
Skenea serpuloides																											
Coriandria fulgida																											
Acteon tornatilis																											
Turritella communis																											
Crustaceans:																											
Diastylis rugosa	1.0	1.6	2.7	2.8	3.2	3.6	2.2		5.5	4.2	6.9	22.8	5.2	2.6			3.5	9.4	2.7	3.5	3.6	4.8	28.9	18.0	9.9	13.3	3.6
Amphipod			0.9	0.3		2.9	2.7		1.9	1.5		0.6							1.3	2.8	1.6	3.2	0.8	0.5			
Corystes cassivelaunus	0.1						1.7		1.9	3.7	2.0	0.3								3.7	5.1		0.8	0.5		0.2	
Pagurus sp.																											
Gammaridea																											
Crangonidae																											
Majidae																											
Echinodermata:																											
Ophiura ophiura	0.2		1.4	3.0	22.2	8.6	5.6		1.9	1.9	0.5	2.8	0.2	10.4			3.4	8.4	1.3	0.7	0.5	3.2	3.9	0.2	0.2	1.6	1.5
Echinocardium cordatum				0.7		2.9	1.5				0.1	0.3	0.1	2.6					0.	0.5			6.3	5.6			
Polychaetes:																											
Lagis koreni			0.3						2.1	22.9	0.4	0.2						2.0	1.3	1.8	2.1	3.2	0.2			0.3	
Lanice conchilega																											
Foraminiferans:																											
Quinqueloculina dimidata																											
Quinqueloculina seminulum																											
Cibicides lobutulus																											
Other groups:																											
Bryozoans																											
Aranean (spider)																											
Hydroid																											
Sipuncata																											
Nemertae																											
Fish																											

Appendix IV

Table 1. Seasonal abundance (%) of difference prey species within benthic grab samples collected from Red Wharf Bay: (a) Bivalve prey species; and (b) Gastropod, Crustacean, Echinoderm, Polychaete and Foraminiferan prey species; only those species which contributed to >0.1% are presented

(a)

	1995			1996											1997											
Species	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D
Bivalves:																											
Spisula subtruncata		50.5		44.3		34.0				9.3		13.5	46.3		33.0			21.2			14.4		21.8		53.7	20.0	
Nucula nitidosa		3.0		4.1		1.0				1.4		1.9	6.6		0.7			1.8			4.1		13.1		1.7	2.0	
Gari fervensis		0.8		2.0		2.0				14.6		0.3	1.9		0.5			3.3			8.2		7.3		0.7	0.6	
Mysella bidentata		1.1		2.0		14.0				3.6		1.5	6.2		9.2			5.5			0.5		4.3		1.0	3.4	
Circumphalus casina																											
Chamelea gallina		6.1		10.0						8.9		16.4	8.2		2.0			0.6			1.5		5.1			2.7	
Venerupis senegalensis		1.4		0.1		15.3							4.3		1.9			1.0			0.4		0.7		0.4	0.9	
Parvicardium ovale		1.9		0.2		4.0				0.5		1.0	0.4		0.7			0.2			0.5		2.9			1.3	
Gafrarium minimum		7.2		0.2		1.0				0.7			2.9		5.2			7.9			0.3				0.6	1.0	
Dosinia lupinus		0.3		1.0		2.0				0.2		0.2	0.4		1.3			0.4			0.3				0.6	1.0	
Corbula gibba		0.1		1.5		1.0				1.9		10.4	1.5		5.2			38.8			1.0				1.3	2.0	
Thracia phasoelina		12.1		3.6		1.0				4.2		29.0	7.3		13.7			1.8			0.5		2.9		4.3	11.5	
Spisula elliptica				1.0								0.5	0.3		1.0						50.0		6.5		1.4	6.1	
Ensis spp.		1.2		3.6						3.1		0.4	1.4								1.0					3.2	
Fabulina fabula		0.3		02.0		0.5				0.1		3.0	0.3		2.6			0.3			0.5		2.9		25.1	8.1	
Astarte trianglaris		0.3		2.0									2.9		0.1												
Morella pygmaea		4.6		0.3		4.0																					
Donax vittatas				0.1						1.4					0.3			3.7			0.5		2.2		0.4	0.4	
Mactra stultorum												0.3															
Modiolus modiolus																											
Timoclea ovata																											
Chlamys varia																											
Abra nitida		2.3		0.5		4.0				4.2		2.3	1.9		1.3						0.3		1.1		2.2		
Morella donacina										3.7			5.3		0.3			1.9			1.5		0.6		2.9	2.0	
Astarte elliptica																		1.0			2.6				0.4	2.4	
Mya truncata		1.3		2.0		2.0				2.7			0.2		5.9			1.0			0.5				2.5	8.7	
Laevicardium spp.		0.8		0.1		2.0						0.4			0.7			0.8			6.7		4.4				

(b)

			1995							1996													1997				
Species	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D
Gastropods																											
Polinices polianus		0.1		0.5		2.0				0.5		0.2	1.0		5.2			0.2			0.5		0.7		0.7	1.2	
Obstusella intersecta		3.8		1.0		0.7				0.2					0.7			0.5								1.2	
Scaphander lignarius																											
Skenea serpuloides																											
Coriandria fulgida																											
Acteon tornatilis																											
Turritella communis																											
Crustaceans:																											
Diastylis rugosa		0.4		0.3		3.0				0.9		0.2	0.5		0.3			1.9			2.1		15.3		0.4	3.4	
Amphipod										0.2		0.4						1.0			0.3		1.5			2.0	
Corystes cassivelaunus										1.4								0.5								1.2	
Pagurus sp.																											
Gammaridea																											
Crangonidae																											
Majidae																											
Echinodermata:																											
Ophiura ophiura		0.4		0.3		6.0				0.3		7.3	0.2		6.5			3.7			0.5		0.2			6.7	
Echinocardium cordatum				17.3		0.5						0.4			1.3						6.1		61.5			2.0	
Polychaetes:																											
Lagis koreni										37.7		10.4						2.1			2.1		0.2			0.3	
Lanice conchilega																											
Foraminiferans:																											
Quinqueloculina dimidata																											
Quinqueloculina seminulum																											
Cibicides lobutulus																											
Other groups:																											
Bryozoans																											
Aranean (spider)																											
Hydroid																											
Sipuncata																											
Nemertae																											
Fish																											

Appendix V

Table 1. Seasonal occurrence of difference prey species/taxa within the stomach contents of *Astropecten irregularis* collected from Red Wharf Bay: (a) Bivalve prey species; and (b) Gastropod, Crustacean, Echinoderm, Polychaete, Foraminiferan prey species/taxa and other types of prey.

(a)

															Months											
		1995							1996												1997					
Species	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D
Bivalves:																abs											
Spisula subtruncata	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●		●	●	●	●	●	●	●	●	●	●	●
Nucula nitidosa	●	●				●	●	●	●	●	●	●	●	●	●		●	●	●	●	●	●	●	●	●	●	●
Gari fervensis	●	●	●	●			●	●	●	●	●	●	●	●	●			●	●	●	●	●	●	●	●	●	●
Mysella bidentata	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●		●		●	●	●	●	●		●	●	
Circumphalus casina	●				●		●	●	●	●	●	●	●	●			●	●	●	●	●	●	●	●	●	●	●
Chamelea gallina								●	●	●	●	●	●	●				●	●	●	●	●	●	●	●	●	●
Venerupis senegalensis	●	●	●	●		●	●	●	●	●	●	●	●					●	●	●	●	●	●	●	●	●	
Parvicardium ovale	●	●						●	●	●	●	●	●	●					●	●	●	●	●	●	●	●	●
Gafrarium minimum	●						●	●	●	●	●	●	●				●	●	●	●	●	●	●	●	●	●	
Dosinia lupinus	●						●	●	●	●	●	●							●	●	●	●	●	●	●	●	●
Corbula gibba									●	●	●	●	●	●	●		●		●	●	●	●	●			●	
Thracia phasoelina	●	●				●			●	●	●	●	●					●	●		●	●	●	●	●	●	●
Spisula elliptica									●	●	●	●	●							●	●	●	●	●	●	●	
Ensis spp.		●								●	●	●	●								●	●		●	●	●	●
Fabulina fabula																			●	●	●	●	●	●	●	●	●
Astarte trianglaris							●	●		●	●	●	●						●						●	●	
Morella pygmaea												●	●								●	●	●	●	●	●	
Donax vittatas	●	●	●										●	●	●												
Mactra stultorum							●	●				●	●										●				
Modiolus modiolus													●					●					●			●	
Timoclea ovata										●	●										●						
Chlamys varia		●	●												●												
Abra nitida												●															
Morella donacina												●															
Astarte elliptica							●																				
Total No. of prey types	11	10	6	4	3	5	11	12	13	17	17	20	19	9	7	abs	6	9	14	13	17	17	18	15	17	19	11
No. of *Astropecten* examined	56	73	59	50	59	48	52	50	51	55	54	62	59	33	8		20	44	59	58	59	51	58	60	50	52	40

(b)

Species			1995							1996						Months							1997				
	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D
Gastropods																ab											
Polinices polianus	•	•	•				•	•	•	•	•	•	•	•	•			•	•	•	•	•	•	•	•	•	•
Obstusella intersecta		•	•	•				•	•	•	•										•	•	•	•	•	•	
Scaphander lignarius			•	•				•	•	•	•	•									•	•					
Skenea serpuloides							•				•													•	•		
Coriandria fulgida																				•							
Acteon tornatilis																		•									
Turritella communis							•																				
Crustaceans:																											
Diastylis rugosa	•	•	•	•	•	•	•	•	•	•	•	•	•	•			•	•	•	•	•	•	•	•	•	•	•
Amphipod			•	•		•	•	•	•	•	•	•							•	•	•	•	•	•	•	•	
Corystes cassivelaunus	•									•	•	•								•	•	•	•	•	•	•	
Pagurus sp.	•								*											•	•		•				
Gammaridea		•	•					•	•																		
Crangonidae			•	•								•															
Majidae				•																							
Echinodermata:																											
Ophiura ophiura	•	•	•	•	•	•	•	•	•	•	•	•	•	•			•	•	•	•	•	•	•	•	•	•	•
Echinocardium cordatum				•		•	•			•		•	•	•					•	•			•	•	•	•	
Polychaetes:																											
Lagis koreni			•					•	•	•	•	•							•	•	•	•	•	•	•	•	
Lanice conchilega			•				•			•	•		•								•		•			•	
Foraminiferans:																											
Quinqueloculina dimidata					•		•	•	•			•	•					•	•	•	•	•	•	•			
Quinqueloculina seminulum					•		•											•					•				
Cibicides lobutulus																			•				•				
Other groups:																											
Bryozoans																			•							•	
Aranean (spider)																										•	
Hydroid																											
Sipuncata																											
Nemertae																											
Fish																										•	
Total No. of prey types	5	5	10	8	4	4	10	9	10	10	10	10	6	4	1		2	7	9	10	11	9	13	10	9	12	3

Table 2. The occurrence of different prey species within the stomach contents of *Astropecten irregularis* collected from various locations off the southern and western coasts of the British Isles. Samples from Red Wharf Bay are pooled data between October 1995 and May 1998; Cardigan Bay and Colwyn Bay samples were collected during March 1997; The CEFAS research vessel the Corystes collected starfish specimens from the Little Sole Bank and the Western Channel during 1995 and 1996 (see Chapter 6; Table 6.1).

	Locations				
Species	Red Wharf Bay	Cardigan Bay	Colwyn Bay	Little sole Bank	Western Channel
Bivalves:					
Abra nitida	*				
Astarte elliptica					
Astarte trianglaris	*				
Chamelea gallina	*	*			
Chlamys varia	*				
Chlamys sp.				*	
Circumphalus casina					*
Corbula gibba	*				
Donax vittatas	*		*	*	*
Dosinia lupinus	*				
Ensis sp.	*	*	*		
Fabulina fabula	*		*		
Gari fervensis	*		*		
Gafrarium minimum	*		*		
Laevicardium crassum	*		*		
Mactra stultorum	*				
Modiolus modiolus	*	*	*		
Morella donacina	*				
Morella pygmaea	*				
Mya arenaria		*		*	*
Mya truncata	*		*		
Mysella bidentata	*		*		
Nucula nitidosa	*	*			
Nucula nucleus					*
Parvicardium ovale	*				
Parvicardium scabrum				*	*
Pecten maximus	*				*
Spisula elliptica	*				
Spisula subtruncata	*	*	*		*
Thracia phasoelina	*				
Timoclea ovata	*				
Venerupis senegalensis	*				
Gastropods:					
Acteon tornatilis	*				
Coriandria fulgida	*				
Cytharella sp.		*			
Erato voluta					*

Hinia pygmaea				*	*
Jujubnus striatus				*	*
Mangelia rebula				*	*
Nebaliccea sp.				*	*
Obstusella intersecta	*				
Odostomia unidentata				*	*
Oenopota turricula				*	*
Palliolum tigerinum				*	*
Polinices catenus					
Polinices polianus	*	*	*	*	*
Rhaphitoma lineavis				*	*
Retusa truncata	*	*	*		
Rissoella sp.				*	
Scaphander lignarius	*			*	*
Skenea serpuloides	*				
Turritella communis	*				
Crustaceans:					
Amphipod	*	*			
Corystes cassivelaunus	*				
Crangonidae	*				
Diastylis rugosa	*	*	*	*	
Gammaridea	*				
Majidae	*			*	
Pagurus spp.	*			*	
Echinodermata:					
Echinocardium cordatum	*			*	*
Ophiura ophiura	*			*	*
Polychaetes:					
Tube worm				*	
Lanice conchilega	*			*	
Lagis koreni	*		*		
Pomatoceros sp.		*			
Foraminiferans:					
Caecum imperforatum				*	
Cibicides lobatulus				*	*
Cornuspira selseyensis	*		*		
Quinqueloculina dimidata	*		*	*	
Quinqueloculina seminulum	*				
Others groups:					
Aranean	*				
Bryozoan	*			*	
Fish bones			*		
Hydroid	*			*	
Nemertea	*				
Sipuncata	*				

Appendix VI

X-ray radiography protocol

A: Film preparation

In a darkroom inset a CURIX RP1 x-ray film (18x24cm) into a film cassette, protected from moisture.

B: Processing liquids

In order to develop x-ray film a number of processing liquids are prepared in separate tanks. Tank 1: AGFA G150 developer (1 in 5 dilution e.g. 200ml developer and 800ml water). Tank 2: Stop bath, using 2% glacial acetic acid or Kodak MaxStop (1 in 4 dilution). Tank 3: AGFA 0350 fixer (1 in 4 dilution).

C: Taking an x-ray

Place a single x-ray film cassette, protected against moisture, beneath the aquarium. Position the x-ray machine (Chirana KOM 5) directly over the aquarium at a vertical distance of 30cm. Each film exposure should be taken at a shutter speed of 0.4sec. Film is then developed in a darkroom following the protocol outlined below.

D: Processing film

In a darkroom (under a red light) immerse film in AGFA G150 developer for 15min. Transfer film into stop bath for 15sec and then transfer film into the AGFA 0350 fixer and soak for 1min. In normal light leave film for 15min in fixer before washing film under a running tap; hand film to dry for approximately 3h.

Appendix VII

Table 3. The mean calorific value of different molluscan prey species ($J.mg^{-1}$).

Species	Calorific value ($J.mg^{-1}$) Mean (±SD)	Range	N
P. polianus	25.88 (1.17)	24.42-27.23	6
S. subtruncata	23.71 (0.17)	23.60-23.93	6
C. edule	23.65 (0.43)	23.10-24.42	6
C. gallina	23.31 (0.58)	21.45-23.10	6
N. nitidosa	18.79 (0.53)	18.18-19.47	6