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OUTBREAK DYNAMICS OF THE GREEN SEA URCHIN *STRONGYLOCENTROTUS DROEBACHIENSIS* O.F. MÜLLER

by

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

ABSTRACT

Outbreak initiation, the formation of destructive feeding aggregations, was studied by quantifying the green sea urchins' patterns of feeding, aggregation, and microhabitat utilization in laboratory tanks. Maximum levels of aggregation, exposure and feeding were observed in treatments with a high density of starved, large urchins in the absence of refuges and predators. The formation of exposed feeding aggregations was inhibited by the presence of Atlantic wolffish, *Anarhichas lupus*, and to a lesser extent by increased spatial heterogeneity, a prehistory of plentiful food supply, winter conditions, and the presence of decapod predators, *Homarus americanus* and *Cancer irroratus*.

Wolffish and decapods demonstrated functional predator responses, *i.e.* increased consumption of urchins, when prey density was experimentally inflated. The two kinds of predators had similar diurnal consumption rates of small urchins, but wolffish excelled at exploiting large urchins.

Effects of predation, recruitment, and urchin behaviour on the outbreak dynamics of *S. droebachiensis* were explored in a simulation model. The model suggests that seasonally migratory visual predators (*e.g.* wolffish), which presumably are incapable of exploiting cryptic prey, have little effect on the urchins overall capacity to destroy seaweed and maintain barren grounds, whereas perpetually present predators (*e.g.* decapods) have a theoretical potential to prevent or terminate outbreaks, irrespective of their ability to exploit cryptic prey. However, the effects of a given level of predation could always be nullified by increasing the recruitment density of the urchins.

LIST OF TERMS AND SYMBOLS

m_2	mean aggregation size
$\overset{*}{m}_2$	index of mean crowding within aggregations
$\frac{\overset{*}{m}_2}{m_2}$	index of patchiness
M	mean final urchin density
N	final observed number of urchins on a particular tankday
Tankday	single observation of a particular treatment
Treatment	specified combination of factor levels
φ	hypothetical outbreak initiation threshold: the minimum adult sea urchin level of crowding required for the formation of destructive feeding aggregations
$\Sigma\#$	cumulative occurrence of sea urchins: the total number of sea urchins recorded at a specific tank map location for all tankdays of a particular treatment
ξ	hypothetical outbreak termination threshold: the minimum sea urchin density required to prevent kelp recolonization in an overgrazed area

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CHAPTER 1 GENERAL INTRODUCTION

Outbreak populations of the green sea urchin, *Strongylocentrotus droebachiensis*, are capable of widespread destruction of macrophyte beds and indefinite prevention of vegetation recovery, whereas interoutbreak populations of the same sea urchin may function as passive detritivores with apparent negligible ecological impact. Sea urchin-mediated alternations between the kelp-dominated interoutbreak state and the urchin-dominated outbreak state are correlated with sudden fluctuations in sea urchin density and behaviour. The mechanisms which initiate and terminate outbreaks, however, are still not completely understood (Lawrence 1975; Hagen 1983, 1987; Harrold & Pearse 1987).

The first description of a sea urchin outbreak was published almost 150 years ago by von Düben (1847). His investigation was triggered by complaints from fishermen that local kelp bed resources on the southwest coast of Norway were being destroyed by masses of green sea urchins. Initial skepticism was replaced by support for the fishermen's hypothesis after von Düben dissected a number of *S. droebachiensis* and found their guts packed with kelp fragments.

Half a century later, Scott (1902), reported a similar case from southeastern Canada when fishermen expressed

concern over seaweed destruction by *S. droebachiensis* (Breen 1980).

Scott's (1902) observation was not an isolated case. Several other papers refer to anecdotal evidence of past outbreaks (*e.g.* "Maine Lobstermen have observed … several-year cycles in kelp beds where heavy kelp growth and few sea urchins occur some years, whereas coralline bottoms are virtually bare and urchins abundant in other years." quoted from Adey & MacIntyre 1973; Stephens 1972; Breen 1980; Wharton & Mann 1981; Pringle *et al.* 1982; Miller 1985a), or mention high densities of *S. droebachiensis* in the shallow subtidal of southeastern Canada and New England (Stimpson 1854; Verrill 1866; Ganong 1885; Dexter 1944; Swan 1966).

More recently Mann (1972) observed the first aggregations of *S. droebachiensis* in patches of barren substratum inside the otherwise extensive kelp beds of St. Margaret's Bay, Nova Scotia. Following this initial observation the sea urchins proceeded to overgraze most of the kelp beds along the entire Atlantic coast of Nova Scotia (Wharton & Mann 1981), and maintain a barren state for more than a decade before being killed by epizootic disease in the early 1980's (Miller & Colodey 1983; Scheibling & Stephenson 1984). Now the kelp beds have returned (Miller 1985b; Novaczek & McLachlan 1986; Scheibling 1986; Johnson & Mann 1988), and the cause of the disease has been identified as a previously undescribed amoeba, *Paramoeba invadens* Jones (1985).

Almost simultaneously the first large-scale overgrazing event to be noted in Norwegian waters since von Düben's (1847) observation was occurring on the other side of the North Atlantic Ocean (Hagen 1983, 1987 Sivertsen 1984). The Norwegian outbreak populations of *S. droebachiensis* were heavily infested by another previously undescribed epizootic disease, the nematode *Echinomermella matsi* Jones & Hagen (1987), yet barren areas continue to persist (Hagen 1983, 1987).

Barren bottoms dominated by *S. droebachiensis* also have a widespread distribution elsewhere in the northernmost North Atlantic (Propp 1977; Hooper 1980; Gulliksen *et al.* 1980; Himmelman *et al.* 1983). It is not known whether these bottoms supported kelp beds in the past, but experimental removal of *S. droebachiensis* in areas with no record of past kelp beds (Keats *et al.* 1982; Himmelman *et al.* 1983), in areas with partial kelp cover (Harris 1982, Witman 1987), and in recently overgrazed areas (Breen & Mann 1976a) have consistently been followed by kelp colonization.

The recent large-scale outbreaks of *S. droebachiensis* off Canada's southeastern coast, and off Norway's west coast, have stirred controversy about the possible causes of outbreaks. Successful recruitment of sea urchin larvae from the plankton is an obvious prerequisite for outbreak initiation, and it has therefore been suggested that outbreaks may be triggered by recruitment of strong year

classes of sea urchins in response to favourable hydrographic conditions (Foreman 1977; Hagen 1983, fig. 7; Pringle 1986; Hart & Scheibling 1988). Conversely, insufficient recruitment may be responsible for outbreak termination as suggested by Foreman (1977).

Although planktonic processes may be of ultimate importance in the final analysis of the outbreak dynamics of *S. droebachiensis*, recruitment effects are difficult to distinguish from the effects of subsequent variations in the survivorship of juvenile benthic stages (Ebert 1983; Harrold & Pearse 1987), and any inferred relationship between recruitment pattern and adult population density is tentative at present.

Another hypothesis in the outbreak debate emphasizes the role of predators in preventing outbreaks, as they reduce urchin numbers and modify urchin behaviour. In its present form this predator hypothesis is concerned only with outbreak initiation but does not consider outbreak termination.

The predator hypothesis and associated speculations have two major components, one numerical and the other behavioural. The numerical component is of ultimate importance and has understandably received considerable attention (Mann & Breen 1972; Breen & Mann 1976b; Pringle *et al.* 1982). The implication is that some "natural", undisturbed, unfished, presumably high population density of

predators can effectively maintain a low population density of *S. droebachiensis,* and that sea urchin outbreaks are initiated by release from predation pressure. This view is opposed by those who believe the evidence in support of the predator hypothesis is inconclusive (Pringle *et al.* 1982; Miller 1985a; Elner & Campbell 1987).

The behavioural aspect of the predator hypothesis is based on Mann's (1977) observation that "... sea urchins consumed only a few percent of the production of the kelp in a healthy kelp bed, yet within a few years they had destroyed the beds. The explanation is that local concentrations of urchins, by destroying a whole kelp plant, not only consume the biomass of that plant but prevent it from completing its annual cycle of production. Since the ratio of production to biomass is high, a modest consumption of biomass can remove a large amount of potential production.". The kelp beds could presumably have supported much higher sea urchin densities had the urchins been randomly or uniformly distributed rather than concentrated in aggregations capable of quickly destroying entire kelp plants. Thus, the proximate cause of kelp bed destruction would appear to be the formation of such destructive feeding aggregations.

K.H. Mann, B.B. Bernstein & coworkers at Dalhousie University have proposed that the formation of exposed aggregations of grazing urchins, characteristic of the early stages of kelp bed destruction, is governed by the

behavioural responses of individual sea urchins exposed to a combination of stimuli from other urchins, potential food plants and predators (Bernstein *et al.* 1981, 1983; Bernstein & Mann 1982; Mann 1985).

The alleged role of predators in inducing sea urchin aggregations has been challenged by R.L. Vadas, R.W. Elner & associates who claim that the formation of urchin aggregations is independent of the presence of predators and depends solely on the presence of food plants (Vadas *et al.* 1986).

In this thesis I use experimental and theoretical approaches to study the outbreak dynamics of *S. droebachiensis*. First I examine the formation of destructive feeding aggregations by quantifying the aggregating behaviour (Chapter 3), microhabitat utilization (Chapter 4), and feeding behaviour (Chapter 5) of *S. droebachiensis* under controlled laboratory conditions. This is an attempt to resolve the Bernstein-Mann vs. Vadas-Elner controversy by shedding new light on the mechanisms of outbreak initiation.

Second, I analyse sea urchin mortality during the laboratory experiment and arrive at new estimates of diurnal predation rates. These estimates are interpreted as Holling (1959) type functional responses and compared with other recent estimates of predation rates on green sea urchins. Disease-related morbidity during the laboratory experiment is

considered in relation to the critical temperature hypothesis of Scheibling & Stephenson (1984).

Third, I incorporate both behavioural effects and predation data into a simulation model. The model is used to assess the numerical impact of predation on pre- and post-overgrazing sea urchin populations. I critically examine the notion of predator control, and discuss my findings in the context of the numerical component of the predator hypothesis.

In the last chapter I attempt to synthesize the outbreak dynamics of *S. droebachiensis* in the North Atlantic by comparing the results of this study with those of other investigations.

CHAPTER 2 GENERAL METHODS

2.1 Experimental design and execution

To investigate the behavioural responses governing the formation of destructive feeding aggregations, I designed a multifactorial experiment including the seven factors: season, urchin size, prefeeding, urchin density, food, refuges, and predators (Tables 2.1, 2.2). This experiment was designed to facilitate testing of hypotheses suggested by previous authors (Garnick 1978; Bernstein *et al.* 1981, 1983; Vadas *et al.* 1986), and to facilitate the formulation of simple hypotheses suitable for independent retesting under field conditions.

Garnick (1978) found that field populations of *S. droebachiensis* exhibited dynamic patterns of aggregation with temporary feeding aggregations in exposed microhabitats, and more persistent non-feeding aggregations in cryptic microhabitats. He interpreted the observed patterns as the active behavioural response of individual urchins exposed to chemical stimuli from food and other urchins.

Bernstein *et al.* (1981, 1983) suggest that the aggregating and cryptic behaviour of *S. droebachiensis* fluctuates seasonally, and is influenced by the urchins' size, nutritional history and density, and by the presence of predators, refuges and food. The effects of fish predators on the aggregating behaviour of *S. droebachiensis* was inferred

from field-observations, but not investigated experimentally (Bernstein *et al.* 1981).

Bernstein *et al.* (1983) also postulate the existence of interaction terms, *i.e.* that the effects of predators on urchins differ with different urchin sizes and densities. The possibility of interaction effects necessitates the use of a factorial experimental design (Underwood 1981; Winer 1971).

Vadas *et al.* (1986) carried out experiments using sea urchins, invertebrate predators and food algae, but ignored the effects of season, refuges, nutritional history, and interactions documented in the studies of Bernstein *et al.* (1981, 1983). These authors de-emphasize the effect of decapod predators, and claim that the presence of food is the main cause of aggregating behaviour in the sea urchin *S. droebachiensis*.

I have included all these factors in my experimental design in an attempt to resolve the conflicting views of the aforementioned authors. My factor levels are not equivalent to those employed in earlier studies, and my experiment also differs by being exclusively laboratory based. However, my approach permits a higher level of replication, which in turn allows for a more powerful statistical analysis.

The chosen factor levels, five 2-level and two 3-level, made $2^5 \cdot 3^2 = 288$ distinct treatment combinations. All

treatments were replicated at least 5 times for a grand total of 1511 observations or tankdays.

Table 2.1 Design of the multifactorial experiment. Factors and factor levels are tabulated.

Season	Size	Prefeeding	Density	Food	Refuges	Predators
summer	small	starved	low	no kelp	absent	no predators
winter	large	well fed	medium	kelp	present	crab & lobster
			high			wolffish

The factor, sea urchin density, had three levels: low (5 animals/tank), medium (15 animals/tank), and high (30 animals/tank; Table 2.2) However, as these initial densities were frequently reduced due to predation and disease, each initial density level generally consisted of a range of final densities (Fig. 2.1; Table 2.2). Quantitative statements about final densities are thus expressed in terms of the mean final density, **M**, as defined by the arithmetic average of the observed final densities in a given treatment:

$$\mathbf{M} = \frac{1}{\mathbf{r}} \sum_{i=1}^{\mathbf{r}} \mathbf{N}_i,$$

where **r** is the number of tankdays in the treatment, and $\mathbf{N}_i$ is the final number of sea urchins in tankday number i.

Table 2.2 Definition of experimental factor levels.

Factor	Definition
SEASON	
summer	May 14 to September 15, 1986
winter	October 16, 1985 to February 14, 1986; and October 22 to December 4, 1986
SIZE	
small	Test diameter 5 - 20 mm
large	Test diameter > 20 mm
PREFEEDING	
starved	Collected from barren grounds, maintained without feeding
well fed	Collected from barren grounds, fed *ad libitum* on *Laminaria longicruris* or *L. digitata* for at least two weeks
DENSITY	
low	Initial density: 5 sea urchins/tank Final density: 3-5 sea urchins/tank
medium	Initial density: 15 sea urchins/tank Final density: 8-15 sea urchins/tank
high	Initial density: 30 sea urchins/tank Final density: 19-30 sea urchins/tank
FOOD	
kelp	1 plant or large fragment of *Laminaria longicruris* or *L. digitata*
REFUGES	
present	4 clay pipes - 25 cm long, 9 cm internal diameter, hexagonal perimeter
PREDATORS	
crab & lobster	1 each of *Cancer irroratus* and *Homarus americanus*
wolffish	1 *Anarhichas lupus*

The predator factor had three levels: a control with no predators, a decapod treatment with the simultaneous presence of one crab and one lobster, and a treatment with one

Atlantic wolffish (Table 2.2). Although in earlier studies of the effects of decapod predators on sea urchins, crabs and lobsters have traditionally been separated (Breen 1976; Evans & Mann 1977; Elner 1980; Bernstein *et al.* 1981, 1983; Vadas *et al.* 1986), it was assumed that a higher degree of realism could be achieved by combining the two decapods. These predators do frequently occur together in nature, and there is no *a priori* reason to assume that their combined effect is equal to the sum of their separate effects. The combined predatory impact of the two decapods on urchins was actually expected to be less severe, because crabs are a more highly preferred lobster food than sea urchins, thereby yielding a conservative estimate (Evans & Mann 1977; Elner 1980).

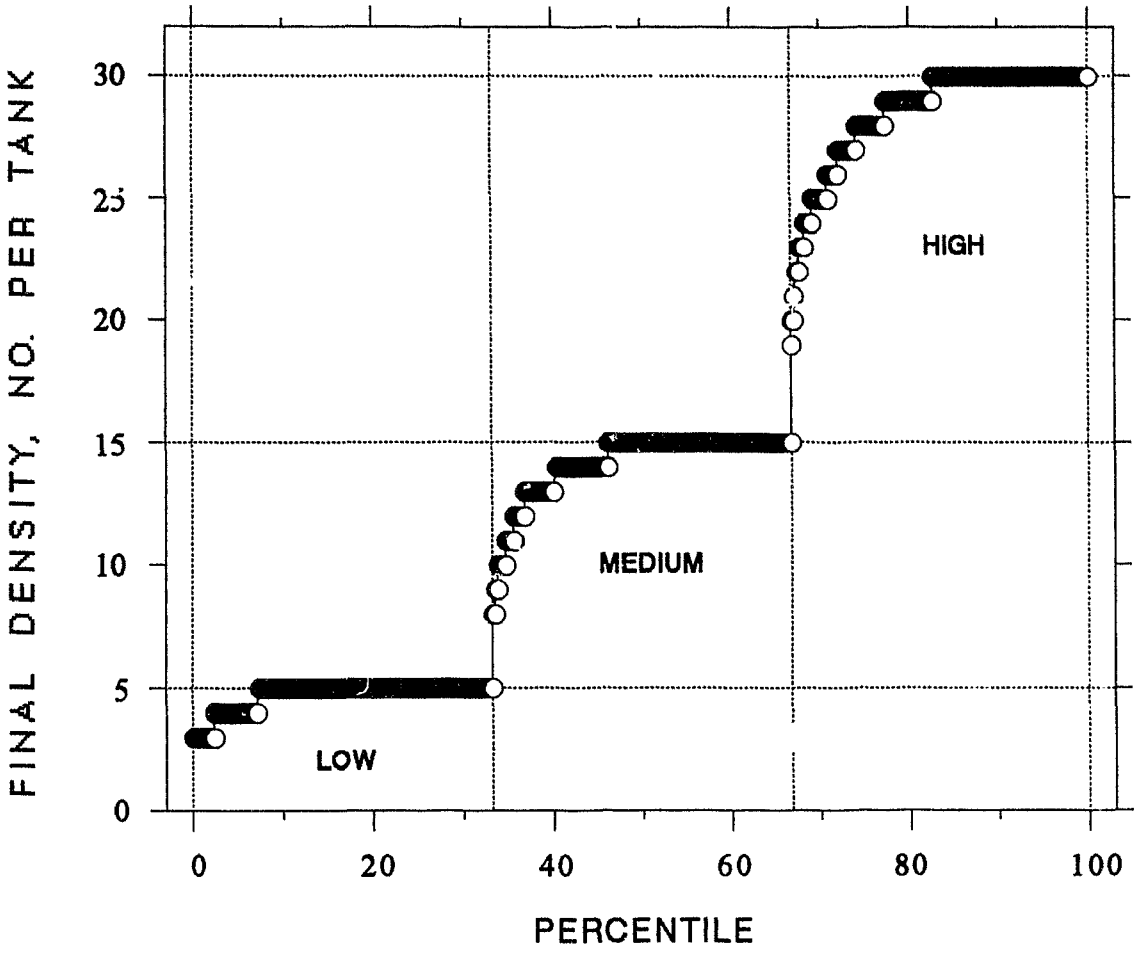

Fig. 2.1 PERCENTILE PLOT OF FINAL SEA URCHIN DENSITIES. The plotted percentiles represent final sea urchin densities in the behavioural dataset. Initial sea urchin densities used in the multifactorial experiment were "low" (5 animals/tank), "medium" (15 animals/tank), and "high" (30 animals/tank), but final densities were frequently reduced by predation and disease-related mortality as indicated in the plot. **n** = 1439 tankdays.

The experiment was carried out in eight 60 × 90 cm laboratory tanks with rounded edges and a water depth of 35 cm (Fig. 2.2). The water level in the tanks was determined by a vertical standpipe drain. The interior of the tanks was

smooth with the exception of three vertical grooves in the tank walls. Excluding the standpipe and the grooves, the wetted interior surface of each tank was equal to [0.9 × 0.6 + 2 × 0.35 × 0.6 + 2 × 0.35 × 0.9] m^2 = 1.59 m^2. Assuming that a single large urchin occupied an area of approximately 5 × 5 cm^2 = 0.0025 m^2, the total tank area occupied by large sea urchins at high density was ≈ 30 × 0.0025 m^2 = 0.075 m^2, or less than 5 % of the available space.

These particular experimental tanks were selected for their convenient size and shape, which appears to have permitted a satisfactory execution of the chosen experimental design, while allowing for an acceptable level of replication. It is possible that different results would have been obtained in larger tanks or field enclosures, but the use of such structures would have imposed severe logistic constraints and is therefore best reserved for less complex experimental designs.

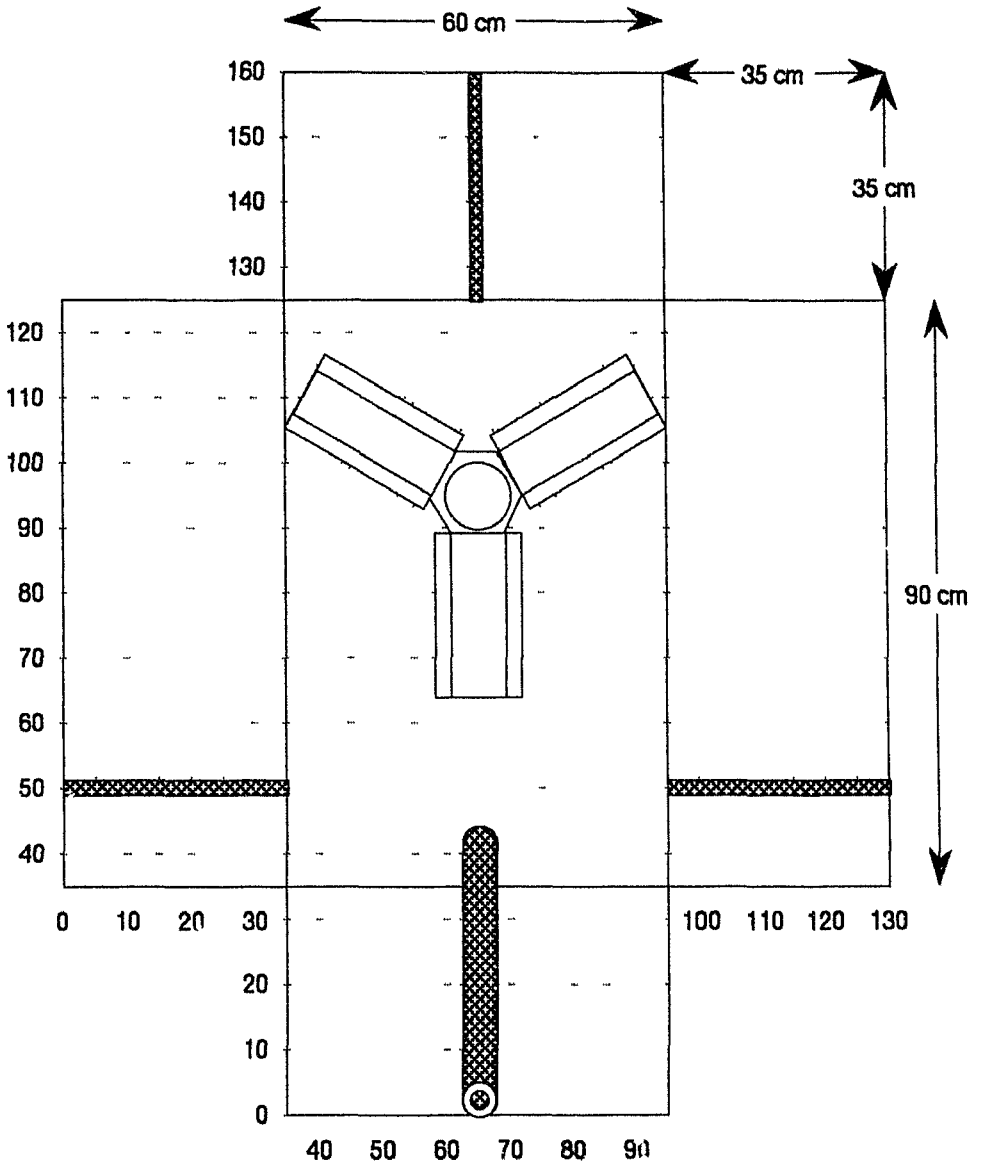

Fig. 2.2 REDUCED VERSION OF THE TWO-DIMENSIONAL TANK MAP USED TO RECORD DATA FROM THE MULTIFACTORIAL EXPERIMENT. The map is subdivided into a 5 x 5 cm coordinate grid (dotted lines). The wide, dark-shaded column at the bottom represents the standpipe water drain. The three narrower, dark-shaded areas indicate vertical indentations (grooves) in the tank walls. The refuge in the central portion of the tank consisted of 4 hexagonal claypipes.

The experimental tanks, which were located in a fourth floor laboratory with large windows, were covered with fish-net screens to prevent wolffish from escaping. Water hoses were suspended over the screens to facilitate aeration, and the tanks were drained and rinsed on a daily basis prior to setting up new treatments. Running seawater was supplied from Dalhousie University's aquatron facility.

Sea urchins were collected in a typical barren ground environment at Half Island Cove, Chedabucto Bay, Nova Scotia, and kept in separate holding tanks prior to experimentation. Lobsters (approximately 0.5 kg), kelp, rock crabs, and wolffish were also stored temporarily in holding tanks. The holding tanks, which were not used for experimental purposes, were located in a basement room beneath the laboratory.

To randomize their selection, sea urchins were taken haphazardly from the holding tanks and transferred to the experimental tanks containing the assigned combination of stimuli. Only individuals with a healthy appearance were used. The choice of experimental tank used on any given day, for any given treatment, was designated on a strictly arbitrary basis. The duration of each treatment was approximately 24 hours.

At the termination of every tankday I recorded on a tank map the position of each individual sea urchin and indicated whether it was cryptic or feeding (Fig. 2.2). Small sea

urchins were recorded as cryptic when found hiding in the vertical tank grooves (Fig. 2.2), underneath kelp, or when found under or inside the clay pipe refuges (Table 2.2). Large sea urchins had outgrown the vertical grooves but were recorded as cryptic when found hiding behind the water drain, underneath kelp, or when found under or inside the clay pipe refuges (Table 2.2). All observations were made during daylight hours.

Seawater temperature in the tanks was monitored on a daily basis when the experiment was in progress. Sea-water temperatures varied from 3 to 17°C over the 14 month duration of the experiment (Fig. 2.3).

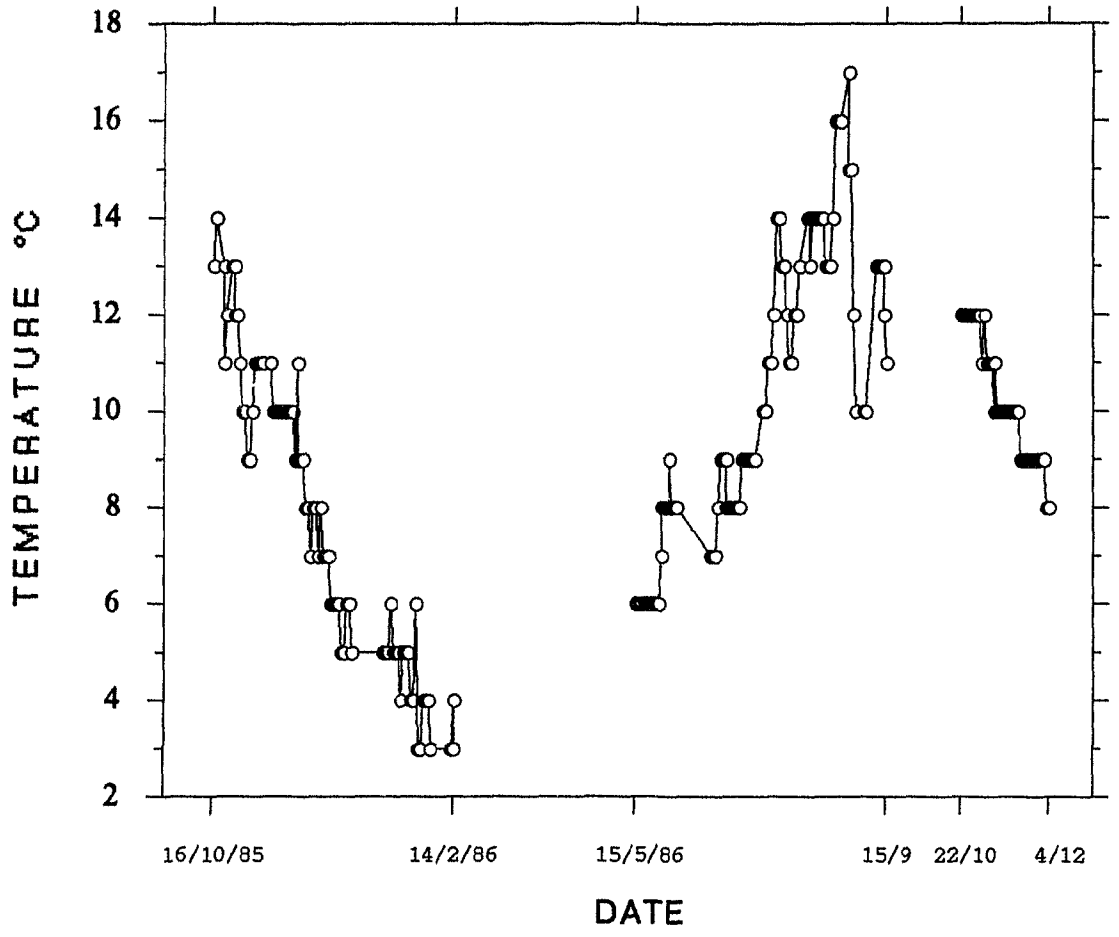

Fig. 2.3 FLUCTUATIONS IN SEAWATER TEMPERATURE DURING THE MULTIFACTORIAL EXPERIMENT.

2.2 Data analysis

Three different indices of aggregation (see Section 3.2.1), as well as the percentage of cryptic sea urchins, were obtained for all 1439 tankdays in the behavioural dataset. The percentage of feeding sea urchins was obtained for the 719 tankdays where kelp was present. These quantitative measures of urchin behaviour were then analysed using standard analysis of variance (ANOVA) techniques supplemented with graphs displaying treatment effects. Assumptions of the ANOVA's were tested using the graphical methods outlined by Draper & Smith (1981) and Neter *et al.* (1985). There was no evidence of dependence among the residuals (Appendix 1). Homoscedasticity and normality of error terms were achieved by logarithmic transformation of indices of aggregation, and angular transformation of % cryptic sea urchins (Appendix 1).

The family level of significance in the multifactorial ANOVA's was controlled at $\alpha \leq 0.05$ by using the Bonferroni inequality (Neter & al. 1985). Thus, a complete 7-way ANOVA consisted of 127 individual tests, each of which was evaluated with individual level of significance, $\alpha_i = \frac{0.05}{127} = 0.0004$.

The entire dataset was used in analyses of predation and disease-related mortality. In the analyses of sea urchin behaviour, however, replicates where more than 50 % of the experimental population was lost to predators or disease were

discarded. All discarded replicates but one (summer season; large, well fed urchins; low density; refuges present; kelp; wolffish) were repeated. Thus, the behavioural data consisted of [(288 · 5) - 1] = 1439 tankdays when the experiment was terminated. A balanced behavioural dataset was obtained by substituting the single missing observation by the mean of the remaining 4 replicates of that particular treatment. This substitution simplified computational procedures in statistical analyses, but necessitated minor corrections prior to evaluation of final test statistics due to the introduction of one spurious degree of freedom.

The raw data from the experiment were transferred to a database of my own design, programmed in MacForth Plus from Creative Solutions Inc.. Relevant information was extracted from the database and analysed using SYSTAT, Microsoft Excel, and StatView II (Abacus Inc.) software on an Apple Macintosh II computer.

The percentile comparison graphs in this thesis were constructed using the StatView II program (Feldman *et al.* 1987). This program compares 19 corresponding percentiles of two variables. The percentiles compared are: 1, 2, 3, 4, 5, 10, 20, 30, 40, 50, 60, 70, 80, 90, 95, 96, 97, 98, and 99. See Cleveland (1985) or Chambers *et al.* (1983) for technical discussions of percentile comparison graphs.

PART I

OUTBREAK INITIATION: THE FORMATION OF DESTRUCTIVE FEEDING AGGREGATIONS

Experimental manipulations in the field have become firmly established as the methodological norm in benthic marine ecology since publication of the classic intertidal field experiments by Connell (1961) and Paine (1966). However, field experiments are superior to laboratory experiments only if adequately controlled and replicated (Connell 1974; Dayton & Oliver 1980). Unfortunately, recent reviews have uncovered a disturbingly high incidence of serious shortcomings in experimental design and data analysis in experimental field ecology (Hurlbert 1984; Underwood 1981, 1986; Underwood & Denley 1984). It would therefore seem that part of the price for the apparent success of field experimentation has been a loss of some of the scientific rigor usually associated with laboratory experiments.

In this section I attempt to reassess a number of hypotheses derived from earlier observations and field experiments, by using new data from a complex multifactorial laboratory experiment. I address the main question of what factors control the formation of destructive feeding aggregations by quantifying the aggregating behaviour (Chapter 3), microhabitat utilization (Chapter 4), and feeding behaviour (Chapter 5) of *S. droebachiensis* in

response to controlled manipulations of: urchin size, nutritional history and density; in the presence or absence of predators, refuges, and food; under both summer and winter conditions.

CHAPTER 3 PATTERNS OF AGGREGATION

3.1 Introduction

Whether sea urchins will coexist with kelp, or decimate it, is to a certain degree determined by the urchins' pattern of aggregation. Aggregated populations of sea urchins destroy large kelp beds because localized aggregations eliminate entire kelp plants, whereas randomly dispersed urchin populations of a similar density presumably would consume only a minute fraction of the kelp beds annual productivity (Mann 1977).

The mechanisms giving rise to aggregation in sea urchin populations are not completely understood and much debated. The null hypothesis of a random spatial pattern was tested by Russo (1979) who found that Californian populations of the sea urchin *S. franciscanus* had a random pattern in an area with little kelp, but were highly aggregated in another area where kelp was abundant. The New Zealand sea urchin *Evechinus chloroticus*, however, was significantly aggregated in habitats dominated by either kelp or crustose coralline algae, although the urchins were more densely aggregated in the kelp habitat (Andrew & Stocker 1986).

Bernstein *et al.* (1981, 1983) proposed a complex model consisting of several interacting causal factors including: urchin density, size and nutritional status; season; predators; and refuge availability. These factors purportedly

accounted for observed patterns of aggregation in North Atlantic populations of *S. droebachiensis*. However, the validity of this model was questioned by Vadas *et al.* (1986) who claimed that sea urchins aggregate only in the presence of food. These authors (Bernstein *et al.* 1981, 1983; Vadas *et al.* 1986) did not consider the null hypothesis of a random pattern of aggregation.

In this chapter I describe the results from a multifactorial laboratory experiment designed to investigate the effects of causal factors suggested by previous authors. I quantify the aggregation behaviour of *S. droebachiensis* under laboratory conditions using three different indices of aggregation. The null hypothesis of a random spatial pattern is tested prior to analyses of treatment effects.

3.2 Material and methods

3.2.1 Measurements of aggregation

There is no consensus on how to define the degree of aggregation in a given population. To arrive at a definition involves choosing among several possible indices of aggregation, with different mathematical properties, which measure different aspects of a population's spatial characteristics (Pielou 1977).

A "good" index, in the present context of sea urchin outbreak dynamics, should emphasize aggregation size, because outbreak initiation occurs when the number of sea urchins in an aggregation is large enough to cause severe damage to kelp plants (Mann 1977; Bernstein *et al.* 1981).

Earlier attempts to quantify the aggregating behaviour of *Strongylocentrotus droebachiensis* utilized the mean number of sea urchins per aggregation as a measure of aggregation (Bernstein *et al.* 1983; Vadas *et al.* 1986). This approach excludes information on solitary urchins which then has to be provided in a separate measure, such as the percentage of non-aggregated animals. Direct comparison of previously published figures on mean aggregation sizes is further complicated by lack of consensus on the definition of the unit of aggregation (Table 3.1).

Table 3.1 Some definitions of *Strongylocentrotus droebachiensis* aggregations.

Term	Definition	Source
Aggregation	solitary urchins or groupings with ≥ 2 urchins in close proximity	This study
Aggregation	> 2 urchins in physical contact	Bernstein *et al.* (1981)
Aggregation	≥ 3 urchins in cohesive three dimensional grouping	Vadas *et al.* (1986)
Association	≥ 2 urchins in two dimensional or surficial grouping	Vadas *et al.* (1986)
Feeding aggregation	≥ 3 exposed urchins in close proximity feeding on kelp	Garnick (1978)
Destructive feeding aggregation	> 10 (80+) exposed urchins in close proximity feeding on and destroying whole kelp plants	Bernstein *et al.* (1981, 1983)
Non-feeding aggregation	≥ 3 urchins hiding in dark sheltered locations (refuges) with their spines closely interlocked	Garnick (1978)

Some of these definitional difficulties can be overcome simply by considering solitary individuals as aggregations of size one, and any group of sea urchins in close proximity to one another as an aggregation, irrespective of the feeding activity of the urchins (Table 3.1). By this definition the mean aggregation size, m_2, equals the total number of sea urchins in the experimental unit, N, divided by the total number of aggregations, n (including solitary urchins as aggregations of size one):

$$m_2 = \frac{N}{n} .$$

The mean aggregation size is an adequate measure of aggregation in populations where the number of individuals per aggregation is randomly distributed. However, as noted by Bernstein *et al.* (1983), m_2 gives a deflated impression of extreme aggregation sizes in populations where the number of individuals per aggregation is non-randomly distributed. It is therefore preferable to introduce a slightly more sophisticated measure of aggregation such as $\overset{*}{m}_2$, the index of mean crowding. This index is a measure of the mean number of aggregation cohabitants per urchin, and is defined as the mean aggregation size plus the amount by which the variance:mean ratio of the aggregation sizes differs from unity (Table 3.2; Pielou 1977; Lloyd 1967)

$$\overset{*}{m}_2 = m_2 + \left(\frac{v_2}{m_2} - 1\right),$$

where m_2 is the mean aggregation size, as defined above, and v_2 is the variance of the aggregation sizes.

The index of mean crowding, $\overset{*}{m}_2$, is calculated as follows:

$$\overset{*}{m}_2 = \frac{\sum_{j=1}^{n} x_j (x_j - 1)}{\sum_{j=1}^{n} x_j},$$

where x_j denotes the number of individuals in the jth aggregation in the experimental unit; $\sum_{j=1}^{n} x_j$ is equal to N, the total number of individuals in the experimental unit; and n

is the total number of aggregations, including solitary urchins as aggregations of size one. Accordingly, $\overset{*}{m}_2$ must equal zero in a population of solitary sea urchins, indicating that the individual urchins experience no crowding.

Table 3.2 Summary of terminology and measurements of aggregation.

Term	Symbolic expression	Description
Aggregation		One solitary urchin, or a group of two or more urchins in close proximity.
Number of aggregations	n	Total number of aggregations in experimental unit.
Aggregation size	x_j	Number of urchins in jth aggregation, $j = 1, 2, \ldots, n$.
Number of urchins	$N = \sum_{j=1}^{n} x_j$	Total number of urchins in experimental unit.
Mean aggregation size	$m_2 = \frac{N}{n}$	
Mean crowding	$\overset{*}{m}_2 = m_2 + \left(\frac{v_2}{m_2} - 1\right)$	Theoretical definition of mean crowding.
	$\overset{*}{m}_2 = \frac{\sum_{j=1}^{n} x_j (x_j - 1)}{\sum_{j=1}^{n} x_j}$	Computational formula for mean crowding expressed as the mean number of aggregation cohabitants per urchin.
Patchiness	$\frac{\overset{*}{m}_2}{m_2}$	The ratio of mean crowding to mean aggregation size.

The defining property of a random discrete distribution is that its variance:mean ratio equals unity (Pielou 1977). Therefore, $\overset{*}{m}_2$ is smaller than, equal to, or larger than, the mean aggregation size m_2 in non-crowded, random (Poisson), or crowded distributions, respectively (Table 3.3). For clarity I have adopted Pielou's (1977, p. 117) recommendation of referring to the distribution of a statistical variable, and the pattern of a collection of organisms.

Table 3.3 Patterns of aggregation expressed as mean aggregation size, m_2; the index of mean crowding of individual sea urchins within aggregations, $\overset{*}{m}_2$; and the index of patchiness, $\frac{\overset{*}{m}_2}{m_2}$.

Mean crowding	Patchiness	Description of pattern
$\overset{*}{m}_2 = 0$	$\frac{\overset{*}{m}_2}{m_2} = 0$	uniform pattern of aggregation; all urchins solitary
$\overset{*}{m}_2 < m_2$	$\frac{\overset{*}{m}_2}{m_2} < 1$	non-crowded pattern of aggregation
$\overset{*}{m}_2 = m_2$	$\frac{\overset{*}{m}_2}{m_2} = 1$	random pattern of aggregation
$\overset{*}{m}_2 > m_2$	$\frac{\overset{*}{m}_2}{m_2} > 1$	crowded pattern of aggregation

The ratio of mean crowding to mean aggregation size, $\frac{\overset{*}{m}_2}{m_2}$, is known as the index of patchiness (Table 3.2; Pielou 1977; Lloyd 1967). It is smaller than, equal to, or larger than unity, in non-crowded, random (Poisson), or crowded distributions, respectively (Table 3.3).

As the index of patchiness is unaltered by random fluctuations in population density (Pielou 1977), it is recommended as an alternative to Morisita's index when a detailed analysis of the pattern of aggregation in field populations is required (Elliott 1977). In the present laboratory study $\frac{\overset{*}{m}_2}{m_2}$ is useful as a direct indicator of departures from randomness.

It is important to note that calculations of treatment means for all three indices of aggregation are based on individual tankday values because, according to a rule known as "the fallacy of averages", the treatment means for $\frac{\overset{*}{m}_2}{m_2}$ are generally not equal to the quotient of the corresponding treatment means for m_2 and $\overset{*}{m}_2$ (Welsh *et al.* 1988). This is so because both m_2 and $\overset{*}{m}_2$ are calculated from data that were obtained from the same experimental units, and are therefore not statistically independent. As an example consider the values of the three indices for the small sea urchin treatment (Fig. 3.1):

the mean aggregation size for small urchins is

$$m_{2,small} = \frac{1}{n_{small}} \sum_{j=1}^{n_{small}} m_{2,j} = 2.1579,$$

the index of mean crowding for small urchins is

$$\overset{*}{m}_{2,small} = \frac{1}{n_{small}} \sum_{j=1}^{n_{small}} \overset{*}{m}_{2,j} = 2.2394,$$

and the correct estimate of the index of patchiness for small urchins is

$$\left(\frac{\overset{*}{m}_2}{m_2}\right)_{small} = \frac{1}{n_{small}} \sum_{j=1}^{n_{small}} \left(\frac{\overset{*}{m}_2}{m_2}\right)_j = 0.8599,$$

which is not the same as the estimate obtained from the quotient of the mean crowding and the mean aggregation size for small sea urchins, that is

$$\frac{\overset{*}{m}_{2,small}}{m_{2,small}} = \frac{2.2394}{2.1579} = 1.0378,$$

thus illustrating the fallacy of averages (Fig. 3.1).

The present scheme of three different indices of aggregation permits unequivocal distinction of crowded, random, and non-crowded patterns of aggregation in sea urchin populations (Table 3.3), either by testing for equality of the estimated values of m_2 or $\overset{*}{m}_2$, or equivalently by testing $\frac{\overset{*}{m}_2}{m_2}$ for departures from unity. The degree of aggregation in

different population samples can be assessed by comparing either index (Fig. 3.1). In the present context $\hat{m}^*_2$ is a "better" indicator than m_2, because $\hat{m}^*_2$ provides a more accurate measure of the size of the largest aggregations, which is the critical parameter of outbreak initiation.

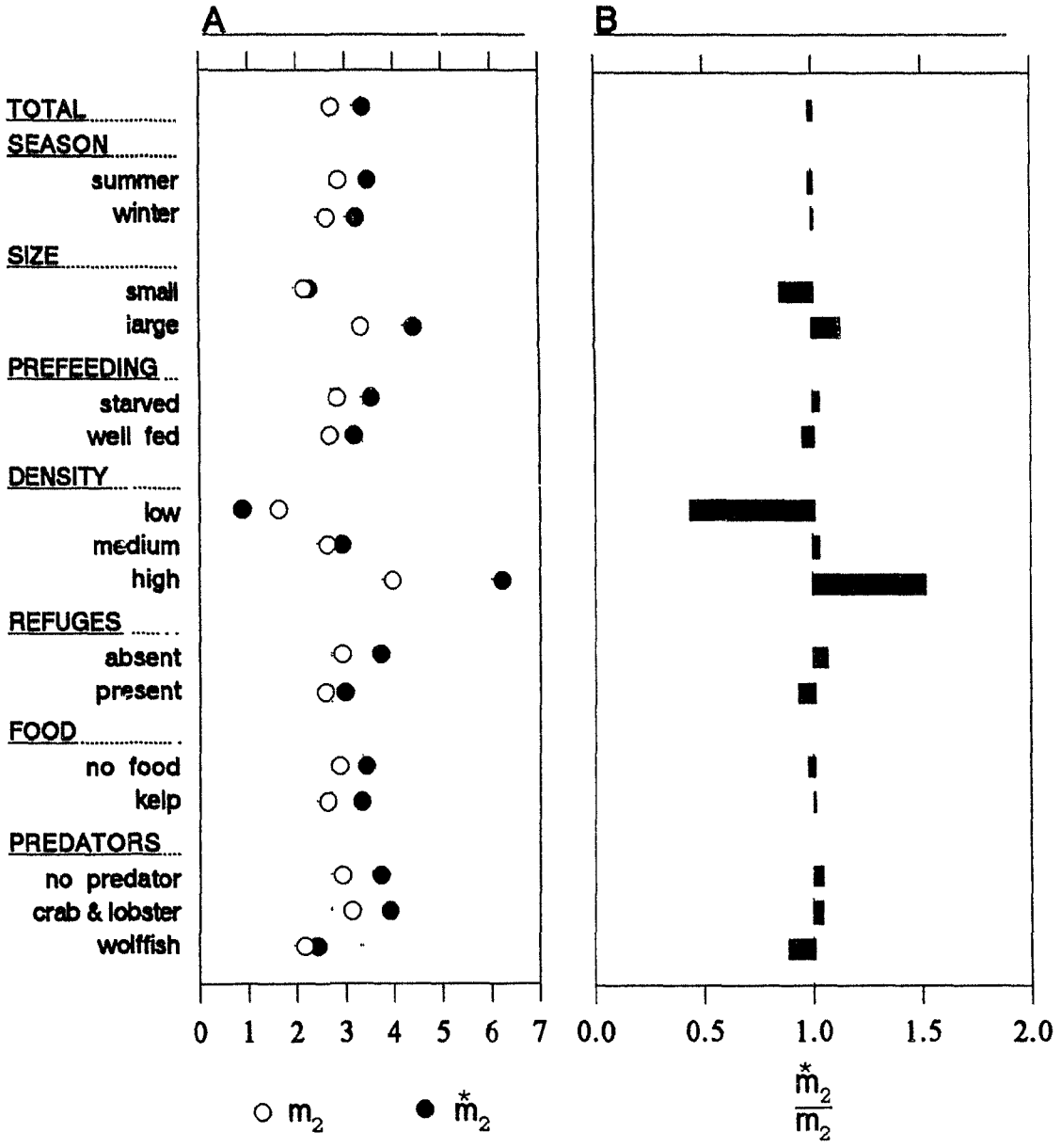

Fig. 3.1 THREE MEASURES OF AGGREGATION. A. Mean aggregation size, m_2, and the index of mean crowding, $\overset{*}{m}_2$, are graphed for the main treatments of the multifactorial experiment. The two vertical dotted lines indicate the location of the two indices for the grand total of the dataset. These two indices have identical values in randomly aggregated populations. B. The index of patchiness, $\frac{\overset{*}{m}_2}{m_2}$, equals unity in randomly aggregated populations, and is therefore graphed with reference to a vertical base line through the unit point of the horizontal axis.

3.3 Results

3.3.1 Patterns of aggregation

The null hypothesis of a random pattern of aggregation was formulated as H_0: $m_2 = \overset{*}{m}_2$, and tested in a repeated measures ANOVA (Table 3.4). The test for the repeated measure factor is significant, hence the null hypothesis is rejected. Five significant main factor tests and two significant two-factor interaction tests indicate treatment-specific variability in the sea urchins' pattern of aggregation. This variability is analysed further in separate ANOVA's for m_2, $\overset{*}{m}_2$, and $\frac{\overset{*}{m}_2}{m_2}$ (Table 3.5).

The main factor effects for sea urchin density and size have the largest F-values for all three indices of aggregation (Table 3.5). Predators and refuges also have significant main factor effects for all three indices of aggregation. Season and food have the smallest main factor F-values, and these are significant for only one index of aggregation. Prefeeding has no significant main factor effects, but is involved in a significant two-factor interaction with refuges, and a significant three-factor interaction with refuges and density. Density, food and predators are involved in significant two-factor interactions with size. This means that all main factor effects except season interacted significantly with other factors. These

interaction effects and the main factor effect for season are analysed in the next six subsections.

Table 3.4 Testing for departures from a random pattern of aggregation. Repeated measures ANOVA testing the null hypothesis H_0: $m_2 = m^*_2$. Degrees of freedom (df), mean squares (MS), F-values, and p-values for main effects and significant interactions. Prior to analysis the data were transformed using the logarithmic transformations: $\log_{10}(1 + m_2)$ and $\log_{10}(1 + m^*_2)$. The Bonferroni family level of significance for the repeated measure ANOVA is $\alpha \leq 0.05$, with $\alpha_i = 0.0004$ for each individual test. $n = 1439$ tankdays.

Source of variation	df	MS	F	p
Repeated measure (RM)	1	363.74	143582.62	0.0001
Season × RM	1	0.13	16.05	0.0001
Size × RM	1	0.84	100.28	0.0001
Prefeeding × RM	1	0.00	0.00	0.9541
Density × RM	2	0.05	5.92	0.0028
Refuges × RM	1	0.12	14.32	0.0002
Food × RM	1	0.16	18.81	0.0001
Predators × RM	2	0.35	42.34	0.0001
Size × Density × RM	2	0.13	16.0	0.0001
Density × Predators × RM	4	0,06	7.1	0.0001
Error	1151	0.01		

Table 3.5 ANOVA table for the analysis of aggregation behaviour. Degrees of freedom (df) and F-values for significant main effects and interactions are tabulated for separate analyses of three indices of aggregation: mean aggregation size (m_2), mean crowding ($\overset{*}{m}_2$), and patchiness $\left(\frac{\overset{*}{m}_2}{m_2}\right)$. Error mean squares are included for each analysis. Prior to analysis the data were transformed using logarithmic transformations: $\log_{10}(m_2)$, $\log_{10}(1 + \overset{*}{m}_2)$, and $\log_{10}\left(1 + \frac{\overset{*}{m}_2}{m_2}\right)$. The Bonferroni family level of significance for the entire ANOVA is $\alpha \leq 0.05$, with $\alpha_i = 0.0004$ for each individual test. The number in brackets is approaching significance. $n = 1439$ tankdays.

Source of variation	df	m_2	$\overset{*}{m}_2$	$\frac{\overset{*}{m}_2}{m_2}$
Season	1	14.74		
Size	1	378.401	394.469	175.924
Density	2	793.631	1315.704	1205.71
Refuges	1	78.237	81.249	47.589
Food	1	17.649		
Predators	2	111.981	94.949	37.273
Size × Density	2	15.255	16.206	
Size × Food	2		15.533	22.19
Size × Predators	2	8.006	(7.632)	
Prefeeding × Refuges	1	14.657		
Prefeeding × Density × Refuges	2	7.885		
Error mean square	1151	0.02	0.029	0.006

3.3.1.1 The size × density interaction

The size × density interaction is significant for both the mean aggregation size, m_2, and the mean crowding $\overset{*}{m}_2$ (Table 3.5). Although both large and small urchins tended to aggregate more at high densities, the large sea urchins were still significantly more aggregated than the small urchins (Fig. 3.2, Appendix 3).

The main factor effects for urchin size and density are significant for $\frac{\overset{*}{m}_2}{m_2}$, however, the interaction effect is not significant for this index (Table 3.5). Urchins had a non-crowded pattern of aggregation at low densities, a nearly random pattern at medium density, and a crowded pattern at high density (Fig. 3.1, Table 3.3). Averaged over all densities small urchins had non-crowded, and large urchins had crowded, patterns of aggregation (Fig. 3.1, Table 3.3).

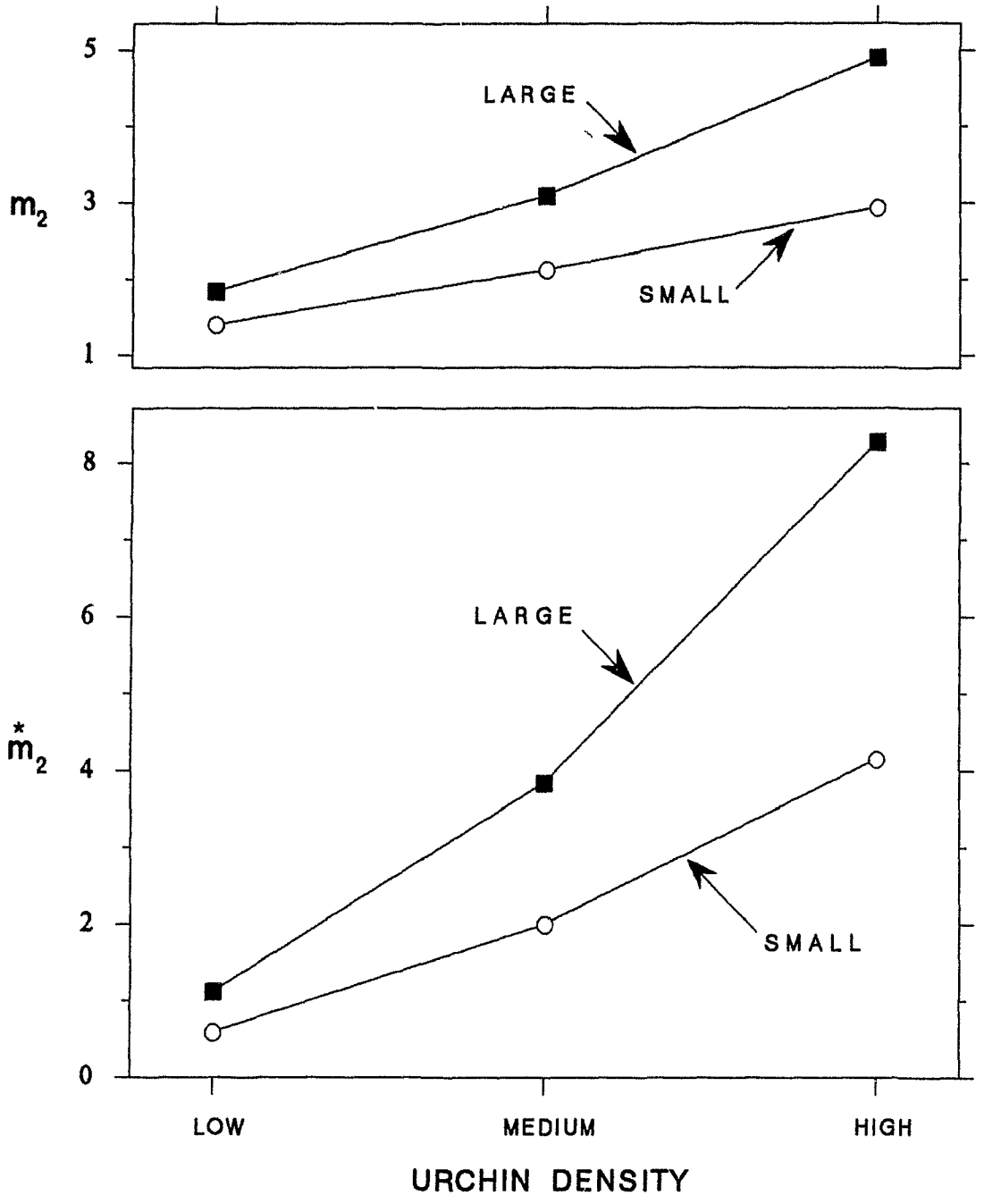

Fig. 3.2 SIZE × DENSITY INTERACTION PLOT. In the top panel m_2 values for small and large sea urchins are plotted separately for each density level. In the bottom panel the corresponding $\overset{*}{m}_2$ values are plotted. n = 240 tankdays per datapoint.

3.3.1.2 The size × predators interaction

The size × predators interaction is significant for the mean aggregation size, m_2, and approaches significance for mean crowding, $\overset{*}{m}_2$ (Table 3.5). Decapod predators and wolffish had opposite effects on the aggregation pattern of *S. droebachiensis*. The sea urchins were more aggregated in the presence of decapod predators, but less aggregated when a wolffish was present. The wolffish had the greatest effect on large sea urchins (Fig. 3.3, Appendix 3).

Due to acts of predation the mean final sea urchin d ɹsities are lower in the predator treatments than in the control treatments without predators (Table 3.7). The general effect of lowering sea urchin density is to make the sea urchins less aggregated (Figs 3.1, 3.2; Appendix 3). An attempt to quantify this effect is made in Tables 3.6 and 3.7, where linear regressions of final sea urchin densities are used to predict m_2 and $\overset{*}{m}_2$ for small and large sea urchins.

The differences between observed and predicted values of m_2 and $\overset{*}{m}_2$ are graphed in Fig. 3.4. The magnitude of the differences between observed and predicted values are larger for the predator treatments than for the control treatments. This would suggest that the observed treatment effects are a result of sea urchin behavioural responses to the presence of predators, rather than a passive result of the predators numerical impact, but the suggestion is tentative due to the

poor fit of the regression lines ($r^2 \leq 0.5$; Table 3.6). The predicted values for the control treatments, however, are reasonably close to the observed values, particularly for the small sea urchins. Hence, the local fit of the regression lines might be somewhat better than the low r^2-values would suggest.

Only the main factor effect for predators is significant for the index of patchiness, $\frac{\overset{*}{m}_2}{m_2}$ (Table 3.5). Sea urchins had a non-crowded pattern of aggregation in the presence of wolffish, but were slightly crowded in the presence of decapod predators and in the control treatments without predators (Fig. 3.1, Table 3.3). This result agrees with the preceding suggestion that decreased aggregation in the presence of wolffish is partly due to behavioural responses from the urchins, and is not merely a result of predatory density reduction, because the numerical value of $\frac{\overset{*}{m}_2}{m_2}$ is unaltered by random density fluctuations (Pielou 1977).

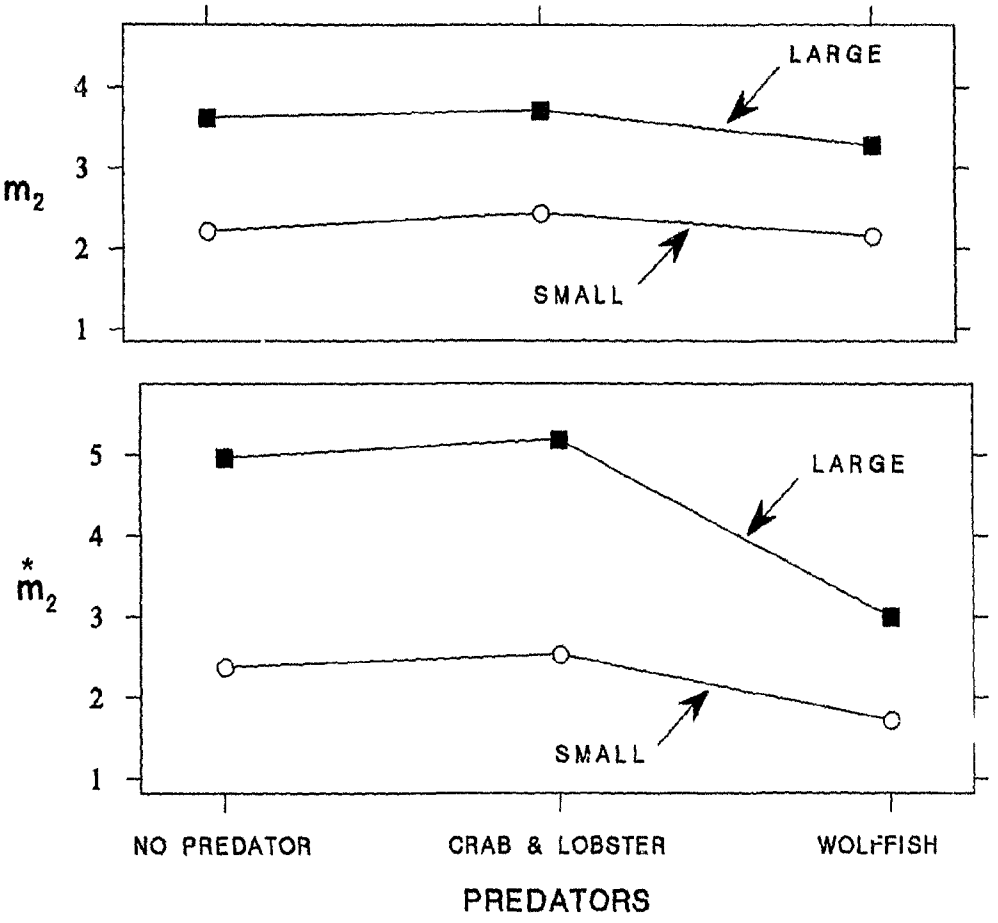

Fig. 3.3 SIZE × PREDATORS INTERACTION PLOT. In the top panel m_2 values for small and large sea urchins are plotted. In the bottom panel the corresponding $\overset{*}{m}_2$ values are plotted. n = 240 tankdays per datapoint.

Table 3.6 Relationship between final sea urchin density, x, mean aggregation size, m_2, and mean crowding, $\overset{*}{m}_2$, for small and large *S. droebachiensis*.

	Small		Large	
	m_2	$\overset{*}{m}_2$	m_2	$\overset{*}{m}_2$
Regression line	0.06x + 1.15	0.15x - 0.14	0.14x + 1.12	0.32x - 0.56
r^2	0.37	0.47	0.34	0.5

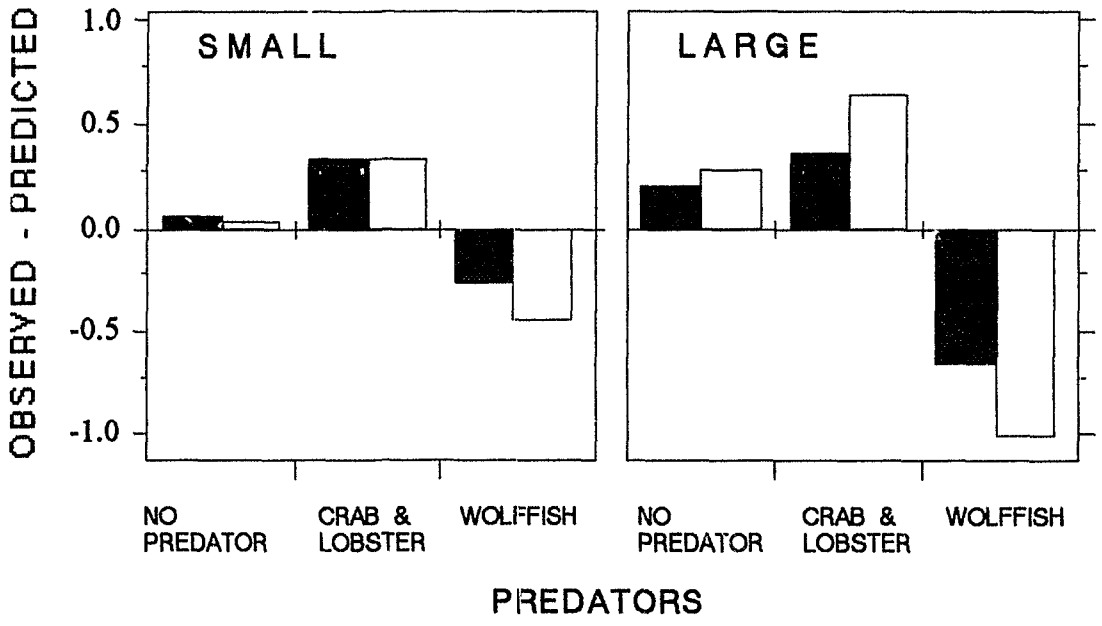

Fig. 3.4 NUMERICAL VERSUS BEHAVIOURAL IMPACT OF PREDATORS. The difference between observed and predicted values of m_2 and $\overset{*}{m}_2$ are plotted separately for small and large sea urchins. The predicted values are estimates based on linear regressions of observed final sea urchin densities. Key to symbols: ■ m_2, □ $\overset{*}{m}_2$.

Table 3.7 Estimated numerical impact of predators on the aggregation pattern of *S. droebachiensis*. The predicted values of mean aggregation size, m_2, and mean crowding, $\overset{*}{m}_2$, are estimates based on linear regressions of observed final sea urchin densities.

	Small		Large	
	Observed	Predicted	Observed	Predicted
NO PREDATOR				
Final density	16.58		16.47	
m_2	2.21	2.15	3.64	3.43
$\overset{*}{m}_2$	2.39	3.35	5.00	4.71
CRAB & LOBSTER				
Final density	15.79		16.02	
m_2	2.44	2.1	3.73	3.36
$\overset{*}{m}_2$	2.57	2.23	5.23	4.56
WOLFFISH				
Final density	15.56		14.39	
m_2	1.83	2.1	2.48	3.14
$\overset{*}{m}_2$	1.75	2.19	3.03	4.05

3.3.1.3 The size × food interaction

The main effect of food is significant only for the mean aggregation size, m_2, which was slightly lower when kelp was present than in the control treatments without food (Table 3.5; Fig. 3.1). However, the size × food interaction is significant for both the mean crowding m^*_2, and the patchiness $\frac{m^*_2}{m_2}$ (Table 3.5). As measured by these two indices the presence of food had opposite effects on the aggregation behaviour of small and large sea urchins. Small urchins were less aggregated, while large urchins were more aggregated when kelp was present (Fig. 3.5, Appendix 3).

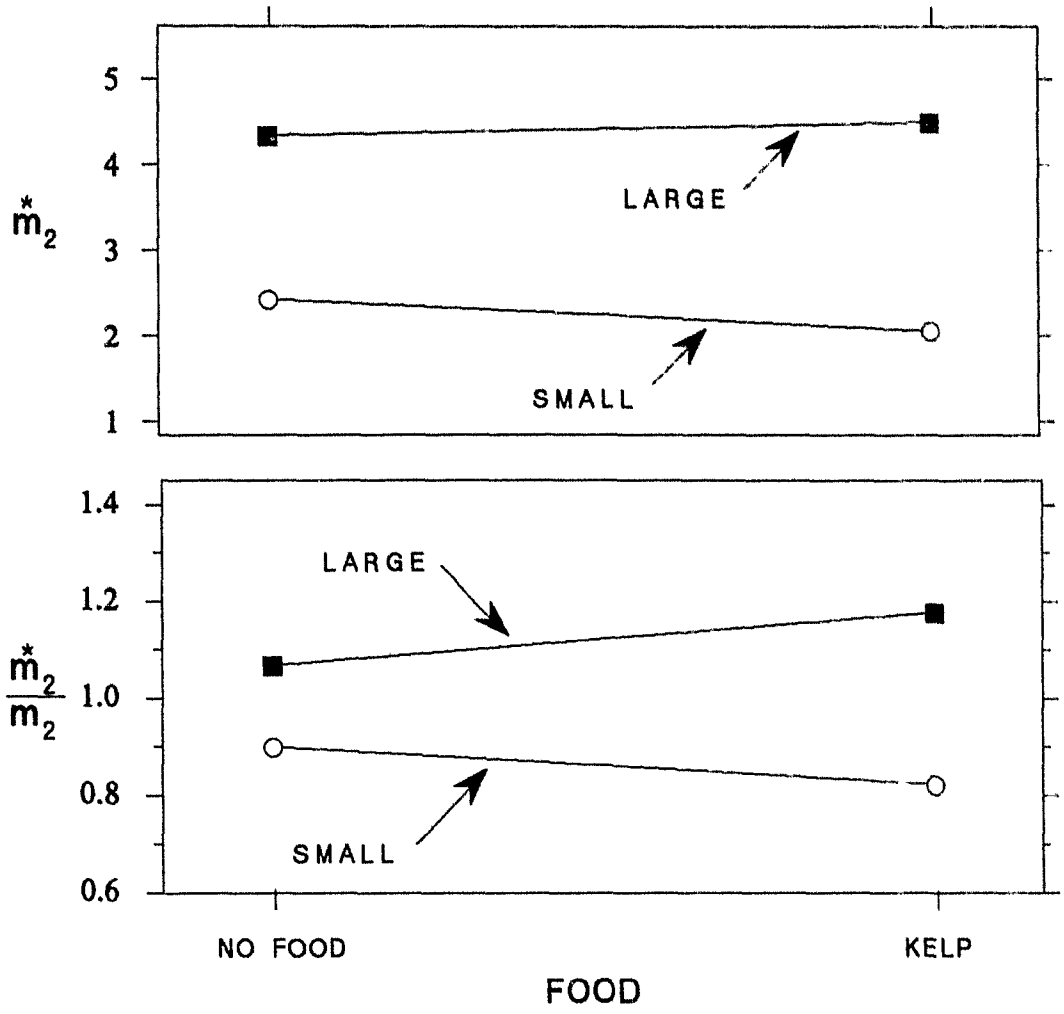

Fig. 3.5 SIZE × FOOD INTERACTION PLOT. In the top panel $\dot{m}_2$ values for small and large sea urchins are plotted separately for treatments with and without kelp. In the bottom panel the corresponding values for $\frac{\dot{m}_2}{m_2}$ are plotted. The dotted horizontal line through $\frac{\dot{m}_2}{m_2}$ = 1.0 indicates the threshold value for a random pattern of aggregation. n = 360 tankdays per datapoint.

3.3.1.4 The prefeeding × density × refuges interaction

The main effect for refuges was significant for all three indices of aggregation (Table 3.5). Both $\overset{*}{m}_2$ and $\frac{\overset{*}{m}_2}{m_2}$ were lower in the presence of refuges than in the control treatments without refuges, indicating that the sea urchins were less aggregated in the presence of refuges (Fig. 3.1). The mean aggregation size, m_2, was also lower in the presence of refuges, although the effect of refuges as measured by this index interacted significantly with prefeeding, and prefeeding × density (Table 3.5).

Prefeeding had no significant main effect, but interacted significantly with refuges and density (Table 3.5). The effects of prefeeding were detected only by the mean aggregation size, m_2 (Table 3.5). Well fed sea urchins had highest mean aggregation sizes when refuges were absent irrespective of urchin density (Fig. 3.6). Starved urchins had higher mean aggregation sizes in the absence of refuges only at low and medium densities. At high density the starved urchins had lower mean aggregation sizes when refuges were absent (Fig. 3.6).

At low density the starved sea urchins had higher mean aggregation sizes than the well fed urchins when refuges were absent, and lower mean aggregation sizes than the well fed urchins when refuges were present (Fig. 3.6). This pattern is reversed at medium and high densities, where starved urchins

had lower mean aggregation sizes than well fed urchins in the absence of refuges, and higher mean aggregation sizes than well fed urchins in the presence of refuges. Thus the effect of refuges on the aggregation behaviour of *S. droebachiensis* as measured by the mean aggregation size, m_2, depends on both the prefeeding status and the population density of the sea urchins.

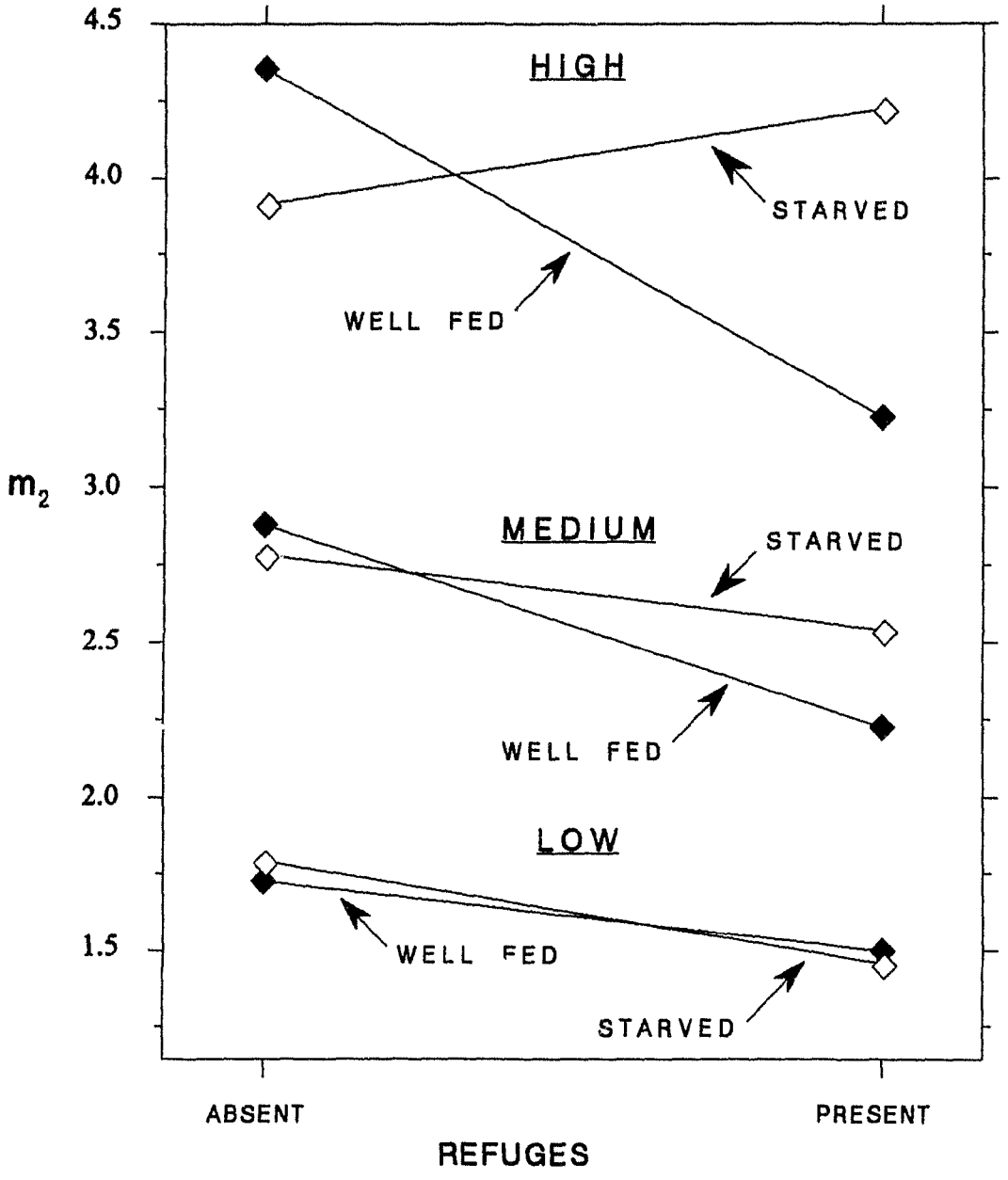

Fig. 3.6 PREFEEDING × DENSITY × REFUGES INTERACTION PLOT. Mean aggregation size, m_2, is plotted separately for starved and well fed sea urchins, at different densities in treatments with and without refuges. n = 120 tankdays per datapoint. (*NB* Vertical scale differs from other interaction plots in this chapter.)

3.3.1.5 Season

Season had significant effects only on the mean aggregation size, m_2 (Table 3.5), which was higher in the summer treatments (Fig. 3.1).

3.4 Discussion

3.4.1 Effects of urchin size, urchin density, and wolffish

The aggregating behaviour of *S. droebachiensis* in laboratory tanks was to a large extent determined by the population density and body size of the sea urchins. Sea urchins had a non-crowded pattern of aggregation at low density, a nearly random pattern at medium density, and a crowded pattern at high density. As noted in Section 2.1, even large urchins at high density occupied less than 5 % of the available tank surface area, thus eliminating the possibility that the urchins were simply "crowded" for lack of space. Averaged over all densities small sea urchins had a non-crowded pattern of aggregation, and large urchins had a crowded pattern. Similar results were obtained by Bernstein *et al.* (1981, 1983).

The basic tendency for large sea urchins to aggregate, particularly at high population density, was reversed in the presence of Atlantic wolffish. My results suggest that wolffish reduced the size of aggregations both by decreasing the population density, and by eliciting behavioural responses from the sea urchins.

3.4.2 Effects of decapod predators

Indices of mean aggregation size and mean crowding within aggregations were slightly higher when decapod predators were present than in the control treatments without predators. Predictions based on the numerical impact of decapod predators would suggest the reverse effect since both the aforementioned indices of aggregation decrease when urchin density decreases. It is therefore tentatively suggested that the presence of decapod predators elicits behavioural responses, whose end result is an increase in the size of sea urchin aggregations.

Bernstein *et al.* (1981, 1983) reached similar conclusions, particularly regarding the role of crabs. Unfortunately, their conclusions were based on uncorrected individual significance levels, $\alpha = 0.05$, in a 5-way analysis of variance consisting of 31 separate significance-tests. If the family level of significance in this analysis were kept at $\alpha \leq 0.05$, then the critical significance level for individual tests would be controlled at $\alpha_i \leq \frac{0.05}{31} \approx 0.0016$, according to the Bonferroni inequality (Neter *et al.* 1985; Wilkinson 1986). Bernstein *et al.*'s (1983) results for decapod predators were not significant at this level, and should therefore be interpreted with caution.

The purported effects of decapod predators on the size of sea urchin aggregations is a central theme in the Bernstein-Mann versus Vadas-Elner controversy. Vadas *et al.* (1986)

argue that the presence of decapod predators does not elicit formation of sea urchin aggregations. They base their argument on results from several single factor experiments aimed at investigating the aggregation behaviour of *S. droebachiensis* in response to the presence of decapod predators. However, there appear to be certain problems with the execution and interpretation in Vadas *et al.*'s (1986) experiments, and their approach precludes assessment of interaction effects (Bernstein *et al.* 1983). One of these experiments is considered below.

My modified sketch of the experimental frame used in this experiment is shown in Fig. 3.7. The frame, which had 0.15 m legs, was positioned on the sea bottom "... over a randomly selected, natural patch of urchins" (Vadas *et al.* 1986). Neither the random selection procedure nor the concept of a "natural patch of urchins" are specified beyond the single sentence in which they are introduced. The experiment consisted of three treatments, lobster, crab, and control. It was repeated three times for a total of 9 observations.

Data from this experiment were recorded as the initial and final (after 24 hours) number of urchins within each of the twentyfive 0.2 × 0.2 m^2 subdivisions of the experimental frame (Fig. 3.7). Initial and final numbers of sea urchins within the perimeter (16 subdivisions) and within the center (9 subdivisions) were separately compared for each of the 9 experimental observations using t-tests based on a sampling

of subdivisions within unreplicated experimental units (Vadas *et al.* 1986, table 2). This is an example of an invalid statistical practice known as pseudoreplication, and any conclusions based on such tests are inconclusive (Hurlbert 1984).

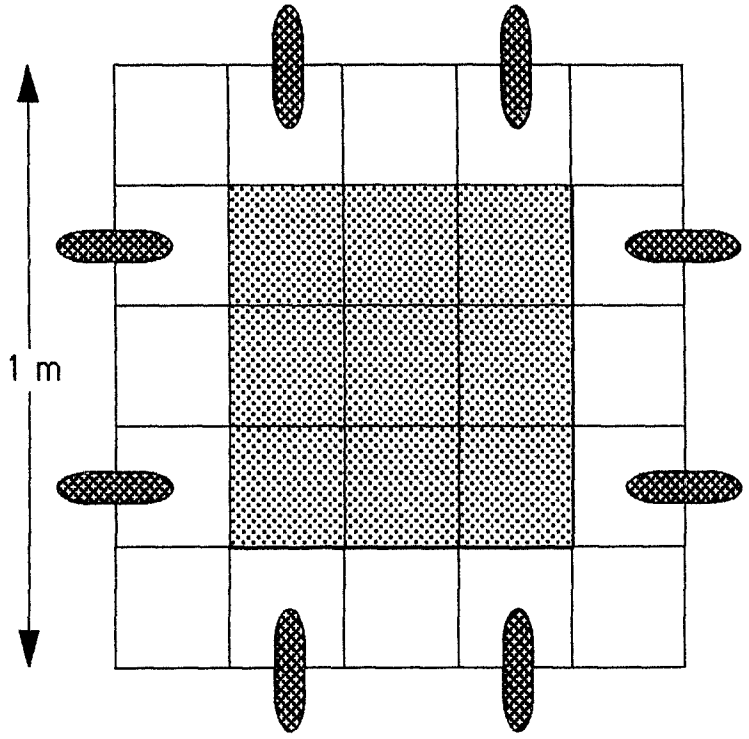

Fig. 3.7 MODIFIED SKETCH OF THE EXPERIMENTAL FRAME USED IN VADAS *ET AL.*'S (1986) TETHERED PREDATOR EXPERIMENT. Eight predators (rock crabs or lobsters) were restrained in individual plastic stretch mesh bags and tied to the the periphery of the frame, presumably as indicated. The nine interior subdivisions (shaded) were referred to as the "center" and the sixteen outer subdivisions were referred to as the "perimeter".

It would appear therefore that the Bernstein-Mann versus Vadas-Elner controversy is based on non-significant and inconclusive evidence. However, as my laboratory results are also equivocal, independent retesting (*sensu* Connell 1974) of the null hypothesis that decapod predators have no effect on the aggregation behaviour of sea urchins in the field is recommended.

3.4.3 Effects of refuges and prefeeding

The main effect for refuges was significant for all three indices of aggregation. Sea urchins were less aggregated when refuges were present than in the control treatments without refuges. However, the effect of refuges, as measured by mean aggregation size, interacted significantly with prefeeding and density, giving starved sea urchins at high density the largest mean aggregation size when refuges were present. This was the only detectable effect of prefeeding.

3.4.4 Effects of urchin size and food

The size × food interaction was significant for both the mean crowding and the index of patchiness, although the main effect of food was non-significant for these two indices. The presence of food (kelp) had small opposite effects on the two sizegroups of sea urchins. Large urchins were slightly more aggregated, while small urchins were slightly less aggregated in the presence of kelp.

Although the mean aggregation size was only slightly, but significantly, lower in the presence of kelp, this index was not involved in any significant interactions. Thus, the three indices agree that small sea urchins were less aggregated when kelp was present.

Large sea urchins had lower mean aggregation size and higher mean crowding when kelp was present. This is an indication of a pattern with more solitary urchins and larger aggregations. Such a pattern would decrease the mean aggregation size while increasing the mean crowding. The net result is a slightly more aggregated pattern as indicated by the index of patchiness.

Several authors have observed that starved *S. droebachiensis* in barren areas tend to aggregate on introduced seaweeds (Himmelman & Steele 1971; Fletcher *et al.* 1974; Garnick 1978; Bernstein *et al.* 1981; Vadas *et al.* 1986). This appears to be primarily a feeding response

(Chapter 5), since both prefeeding and food had little effect on the overall aggregation behaviour of *S. droebachiensis*.

3.4.5 Effects of season

Sea urchins in the experimental tanks had a significantly higher mean aggregation size during the summer season. No significant effects of seasonal changes were detected by the other two indices of aggregation.

Bernstein *et al.* (1981) found a lower degree of aggregation during the summer season in field populations of *S. droebachiensis*. They attributed this observation to the seasonal inshore appearance of Atlantic wolffish. My results are in agreement with this suggestion. All three indices of aggregation were significantly lower when wolffish were present (Section 3.4.1).

CHAPTER 4 MICROHABITAT UTILIZATION

4.1 Introduction

Strongylocentrotid sea urchins occur in a variety of microhabitats ranging from cryptic cracks and crevices to unprotected, exposed surfaces. In areas with intact kelp beds the sea urchins are frequently found in cryptic microhabitats. However, in areas where the kelp beds have been destroyed or are in the process of being destroyed, a high proportion of the urchin population is typically found occupying openly exposed microhabitats (Hagen 1983, 1987; Harrold & Reed 1985; Mann 1985).

Evidence from field studies suggests that changing patterns of microhabitat utilization, which coincide with the onset of destructive grazing of kelp, are governed by complex interactions among a multitude of causal factors including: urchin size, density and feeding history; season; predators; cryptic habitats; and the availability of drift algae (Bernstein *et al*. 1981; 1983).

In this chapter I contrast published findings on the microhabitat utilization of *Strongylocentrotus droebachiensis* with new results from a multifactorial laboratory experiment. First the null hypothesis of random spatial pattern is tested using the Poisson probability model as a statistical benchmark (Andrew & Mapstone 1987). Second, the overall cryptic behaviour of *S. droebachiensis* is considered, and

third, the usage of experimentally introduced spatial heterogeneity in the form of claypipe refuges is evaluated. The objective of these analyses is to identify determinants of spatial patterns and to identify preferences which are relevant in the context of sea urchin outbreak initiation.

4.2 Material and methods

Data for the three main analyses of this chapter were obtained from the multifactorial laboratory experiment (Section 2.1). Graphical analyses of spatial pattern are based on patterns of cumulative sea urchin occurrences. Cryptic behaviour is analysed numerically using quantitative data obtained for all 1439 tankdays in the behavioural dataset. Refuge usage is studied by graphical analysis of cumulative occurrences data, and by numerical analysis of quantitative data.

Graphical methods of data analysis are used extensively throughout this chapter, both as a supplement to conventional numerical statistical analyses, and as an independent analytical tool (Chambers *et al*. 1983).

4.2.1 Description of dataset

Spatial data were collected by recording the location of individual sea urchins at the end of each tank day. The locations were recorded as positions on a two dimensional map of the interior surface of the experimental tank. The map had a superimposed xy-coordinate grid which demarcated a total of 636 map locations (Fig. 2.2).

A quantitative measurement of the sea urchins spatial pattern inside the experimental tanks was obtained by summing the number of sea urchins recorded at each map location for all tank days in a particular treatment. As an example the resulting matrix of cumulative sea urchin occurrences for the entire dataset is listed in Table 4.2.

4.2.2 Data analysis

4.2.2.1 Spatial pattern

4.2.2.1.1 Construction of probability maps

Probability maps were constructed by using the observed mean number of sea urchins per subdivision, $\bar{x}$, as an estimate of the parametric mean, λ, of a Poisson distribution (Cliff & Haggett 1988; Sokal & Rohlf 1981). Thus, the probability, $P(X = x)$, of observing a certain number of, say x, urchins in a particular location is given by:

$$P(X = x) = \frac{\bar{x}^{x}}{e^{\bar{x}} \cdot x!}, \quad x = 0, 1, 2, 3, \ldots\ldots,$$

and the probability of observing no more than x urchins in a particular location is given by:

$$P(X \leq x) = \sum_{j=0}^{x} P(X = j).$$

Two range-defining x-values, x_{low} and x_{high}, are defined such that $P(X \leq x_{low}) \leq \alpha$ and $P(X \geq x_{high}) \leq \alpha$. These values are easily calculated using the above formula and a computer spreadsheet. Locations on the probability maps where the observed cumulative sea urchin occurrences are in the interval between x_{low} and x_{high} are coded as average. Values $\leq x_{low}$ are coded as significantly low, and values $\geq x_{high}$ are coded as significantly high.

4.2.2.1.2 Detection of departures from a random pattern

If the initial null hypothesis of this chapter is true, then the underlying spatial pattern is random, and the probability that a particular location on the probability map will exhibit a significant departure from the average value, either significantly low or significantly high, is $\frac{\alpha}{2}$. All probability maps in this chapter have been constructed by using a one-tailed significance level of $\alpha = 0.00001$. A lower bound for the probability of no significant departures in a

map comprising 636 locations under the null hypothesis is given by the Bonferroni inequality (Neter *et al.* 1985)

$$P \leq 1 - 636 \cdot \frac{0.00001}{2} = 1 - 0.00318 = 0.99682.$$

Therefore, even a single significant departure from the average value would be sufficient to reject the null hypothesis at the 0.005 level of significance. This calculation shows that graphical analysis of probability maps is a powerful technique for detecting non-randomness in the spatial pattern of sea urchins in laboratory tanks.

Additional tests for departures from the Poisson model were carried out by calculating the G-statistic for goodness of fit (Sokal & Rohlf 1981),

$G = 2\sum_{i=1}^{3} \ln\left(\frac{f_i}{\hat{f}_i}\right)$, where f_i and $\hat{f}_i$ are the observed and expected frequencies for the number of locations in the three groups, low, average and high (i = 1, 2, 3).

The expected Poisson frequencies for a tank map comprising 636 locations are calculated as follows:

$\hat{f}_i = 636 \sum_{x=a}^{b} \frac{\bar{x}^x}{e^{\bar{x}} \cdot x!}$, where the summation intervals [a, b] equal $[0, x_{low}]$, $[x_{low} + 1, x_{high} - 1]$, and $[x_{high}, \infty]$ for the three groups low, average, and high (i = 1, 2, 3).

This G-test has only one degree of freedom since one degree of freedom is subtracted because the mean of the sample data, $\bar{x}$, is used to calculate the expected frequencies (Sokal & Rohlf 1981).

4.2.2.2 Cryptic behaviour

4.2.2.2.1 Quantitative cryptic behaviour

Large sea urchins were recorded as cryptic when found hiding behind the vertical drainpipe, underneath kelp, or when found under or inside the claypipe refuges (Section 1.2). Small sea urchins were recorded as cryptic when found hiding in the aforementioned locations, as well as when found in the vertical tank grooves (Fig. 2.2). The percentage of cryptic individuals was calculated separately for each tankday. The data were successfully transformed using the angular transformation, and the resulting dataset was analysed in a 7-factor ANOVA.

4.2.2.2.2 Cryptic microhabitat usage

Usage of cryptic microhabitats is analysed graphically with subdivided histograms. Each histogram bar represents the number of cryptic sea urchins using each of the available cryptic microhabitats in a particular treatment, expressed as a percentage of the total number of cryptic urchins in the entire behavioral dataset, or "% of cryptic total" as indicated on the vertical axis of the histograms..

4.2.2.3 Refuge usage

The analysis of refuge usage was carried out on data for the 719 tankdays where refuges were present. Refuge usage was measured as a percentage of the final sea urchin density, and calculated separately for each tankday. The dataset was analysed in a 6-factor ANOVA.

4.3 Results

4.3.1 Spatial pattern

4.3.1.1 Testing for departure from a random spatial pattern

The logical first step in the analysis of the spatial pattern of a population is to test the null hypothesis of spatial randomness (Andrew & Mapstone 1987). The probability map Figure 4.1 shows that approximately two thirds of the tank locations were used by significantly lower or higher numbers of sea urchins than would be expected under H_0 (Table 4.1). Since only one significant departure from the Poisson model is sufficient to reject the null hypothesis with $\alpha = 0.005$ I conclude that sea urchins in the experimental tanks exhibited a non-random use of space.

The decision to reject the null hypothesis was confirmed by a test for goodness of fit. Comparing observed and expected frequencies for the number of locations in each of the three groups, low, average, and high (Table 4.1) yielded a highly significant G-value ($G = 9345.62 \gg \chi^2_{1,\ 0.001} = 10.83$).

This non-random spatial pattern of the sea urchins reflects a selective utilization of available surface area. Approximately two thirds of the sea urchins occurred in less than 14 % of the available space (the black areas in Fig. 4.1, Fig. 4.2, Table 4.1). The preferred areas included the

top corners and surrounding areas, the bottom corners, the vertical grooves, the top and bottom of the drainpipe, and locations in the general vicinity of the refuges (Fig. 4.1, Fig. 1.1). Conversely, the majority of locations in the experimental tanks were rarely occupied, and urchins were seldom found on featureless portions of vertical walls and tank bottom (Fig. 4.1, Table 4.2).

Table 4.1 Summary of statistics used to construct probability map and testing for goodness of fit. $\bar{x}$ is the mean number of urchins per location; Σx is the total number of sea urchins observed; f is the observed, and $\hat{f}$ is the expected number of locations. Individual level of significance, α = 0.00001. n = 1439 tankdays.

				Frequency	
	Mean	Sum	Range	Observed	Expected
Group	$\bar{x}$	Σx		f	$\hat{f}$
Significantly low number of urchins	4.83	1681	$0 \leq x \leq 12$	348	0.002495
Average number of urchins	28.21	5690	$13 \leq x \leq 63$	203	635.988948
Significantly high number of urchins	182.39	15385	$64 \leq x \leq 964$	85	0.008557
Total	35.78	22756	$0 \leq x \leq 964$	636	636.000000

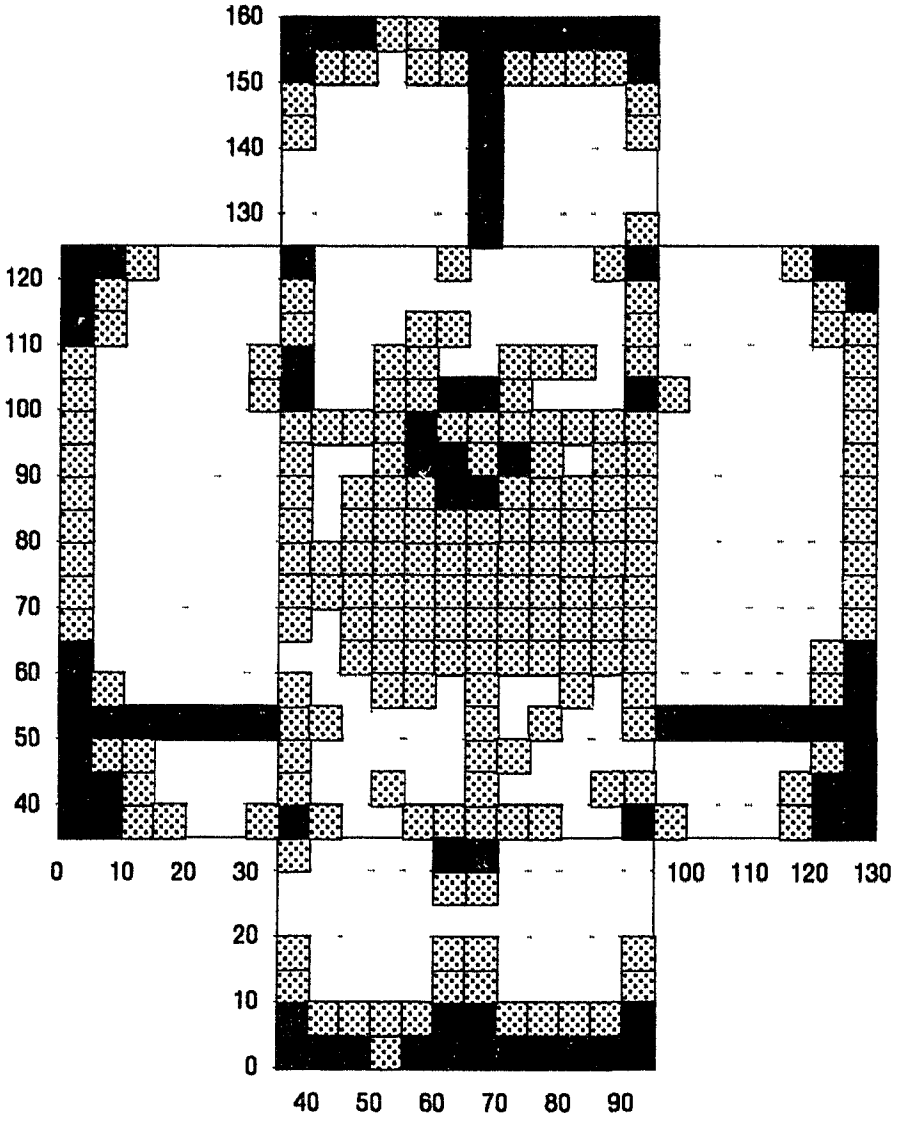

Fig. 4.1 PATTERN OF CUMULATIVE SEA URCHIN OCCURRENCES INSIDE EXPERIMENTAL TANKS. Key to symbols: ■ significantly high numbers of urchins, ▩ average numbers of urchins, significantly low numbers of urchins, n = 1439 tankdays.

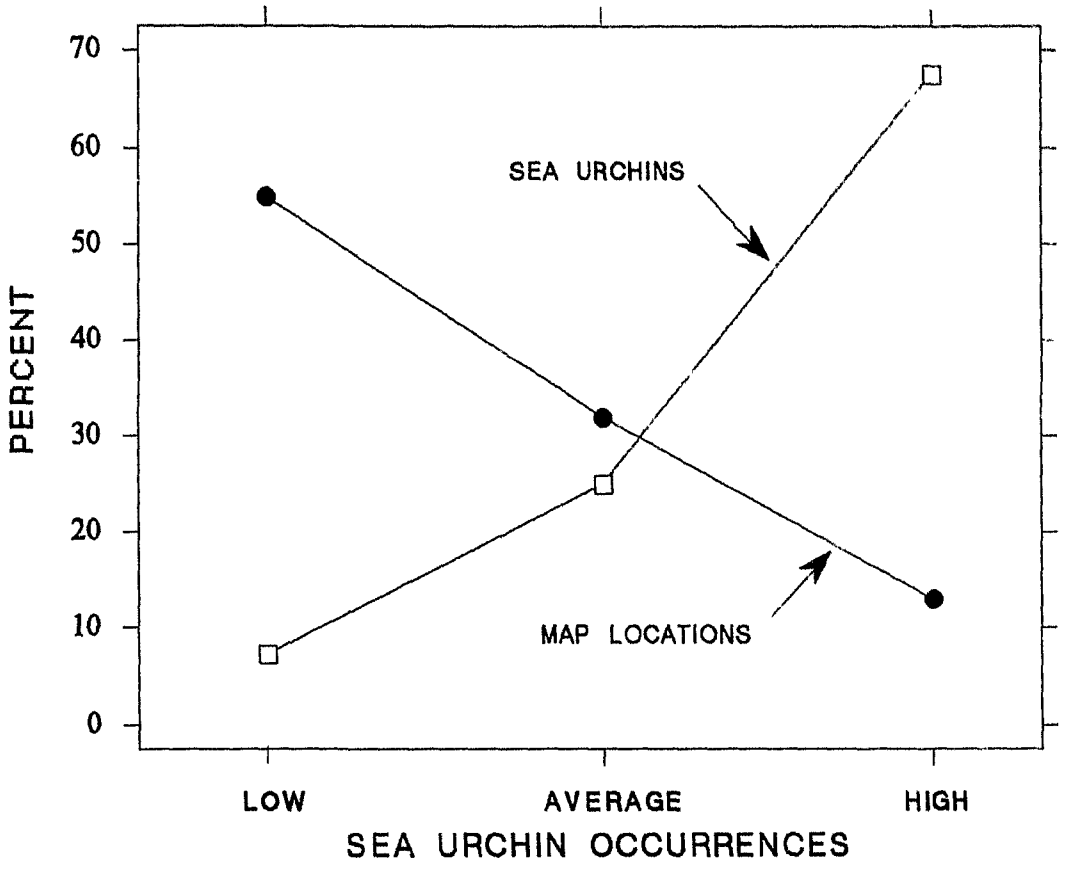

Fig. 4.2 SPACE UTILIZATION BY SEA URCHINS INSIDE EXPERIMENTAL TANKS. The proportional number of sea urchins in, and the proportional number of map locations in, the three groups; significantly low, average, and significantly high cumulative sea urchin occurrence. n = 480 tankdays per datapoint.

Table 4.2 Total cumulative number of sea urchin occurrences in the experimental tanks. X and Y correspond to positions on tank map. **n** = 1439 tankdays.

X	0	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95	100	105	110	115	120	125
Y																										
155								374	175	73	48	50	94	866	96	67	100	175	415							
150								141	51	18	9	13	21	420	20	13	21	46	174							
145								37	5	2	0	1	2	156	2	2	6	9	44							
140								14	0	0	2	1	1	78	1	3	1	1	14							
135								7	2	1	0	4	5	84	2	0	1	1	10							
130								7	1	2	3	4	1	102	1	1	1	2	9							
125								10	0	2	1	2	3	201	4	0	3	4	23							
120	270	105	24	1	0	2	8	109	9	7	7	9	15	10	9	4	8	17	111	6	4	1	5	14	79	233
115	150	36	8	1	2	0	5	14	5	4	6	1	2	10	7	6	7	6	23	6	5	3	3	8	43	118
110	67	17	2	1	0	2	7	24	7	9	8	13	15	12	10	11	9	7	27	3	4	1	2	3	19	57
105	44	10	1	1	2	1	14	75	8	9	27	32	12	11	29	30	15	5	56	11	1	1	0	1	10	39
100	45	11	1	2	2	4	20	204	8	6	17	36	96	88	46	9	8	7	197	17	3	1	0	1	8	35
95	37	8	4	2	1	1	4	36	47	25	26	81	51	54	60	19	29	59	32	6	5	2	1	4	11	40
90	44	14	3	7	4	2	5	14	11	10	26	74	65	62	76	30	10	14	19	7	5	5	2	2	10	49
85	57	13	7	3	1	4	7	15	8	20	17	61	80	84	52	24	16	14	28	8	5	8	1	2	7	40
80	41	11	2	5	4	10	6	13	11	22	29	59	34	35	44	20	23	14	22	8	4	4	1	5	5	57
75	29	6	2	2	2	3	10	24	20	19	26	41	26	31	50	30	15	14	18	4	2	2	1	0	8	40
70	37	7	2	3	3	6	8	15	15	26	27	51	27	39	58	36	16	16	16	3	2	2	4	2	5	39
65	30	7	5	3	5	1	7	15	10	17	32	45	33	36	28	28	26	19	18	8	2	3	1	1	8	47
60	66	8	2	4	1	3	4	10	11	21	17	17	20	24	21	27	18	13	13	7	5	4	0	3	16	67
55	91	14	4	3	1	1	3	17	9	12	17	24	12	16	12	10	16	11	14	11	5	3	2	3	22	94
50	964	463	196	143	107	109	230	29	15	8	9	15	12	15	11	19	5	5	18	251	152	79	98	168	459	954
45	140	54	13	2	7	2	9	22	6	8	10	9	5	22	15	9	11	8	11	6	7	2	1	11	45	171
40	201	88	28	3	2	4	10	32	8	8	13	11	8	15	5	9	10	13	20	6	5	3	2	19	75	202
35	341	147	52	14	9	10	27	153	26	10	10	19	22	34	21	17	3	8	116	13	2	3	7	37	134	308
30								20	6	2	4	2	92	91	7	8	2	2	12							
25								11	3	2	4	2	13	17	1	2	3	3	5							
20								6	2	1	1	3	7	3	4	1	2	2	10							
15								15	1	1	4	2	18	15	4	2	4	2	15							
10								43	12	2	2	5	35	33	7	5	6	12	57							
5								145	56	24	23	33	75	84	29	20	24	63	181							
0								352	140	69	61	84	163	165	90	64	97	174	399							

4.3.1.4 Effects of urchin size

The effects of urchin size on spatial pattern were examined by constructing separate probability maps for large (Fig. 4.3, Table 4.3) and small sea urchins (Fig. 4.4, Table 4.3). Both maps indicate a non-random use of space. The decision to reject the null hypothesis of random space utilization was confirmed by separate goodness of fit tests for each treatment. Comparing the observed and expected frequencies for the number of locations in the three groups, low, average, and high yielded highly significant G-values for both treatments (Table 4.3, c.f. Table 4.1).

The location-dependent significance-coding in the two maps was not identical (α = 0.0001, Table 4.4, Figs 4.3, 4.4). Comparing locations with significantly high sea urchin occurrences suggests a size-specific preference for vertical grooves in small urchins, whereas areas dominated exclusively by large urchins included the bottom corners, locations adjacent to the top corners, and the top and bottom locations by the drainpipe.

Table 4.3 Summary statistics for size-dependent spatial patterns. n is the number of tankdays, Σx is the total number of urchin occurrences, and $\bar{x}$ is the mean cumulative number of urchins per location in the treatment. x_{low} and x_{high} are threshold values for x, the observed cumulative number of sea urchins in a particular location, such that $P(X \leq x_{low}) \leq 0.00001$ and $P(X \geq x_{high}) \leq 0.00001$ if X has a random (Poisson) pattern. The G-value is for a goodness of fit test comparing the observed and expected frequencies for the number of locations in each of the three groups, significantly low, average and significantly high. The critical G-value is $\chi^2_{1,\ 0.001} = 10.83$.

Treatment	n	Σx	$\bar{x}$	x_{low}	x_{high}	G-value
Small urchins	720	11504	16.08	2	39	7052.33
Large urchins	719	11252	17.69	2	38	5820.60

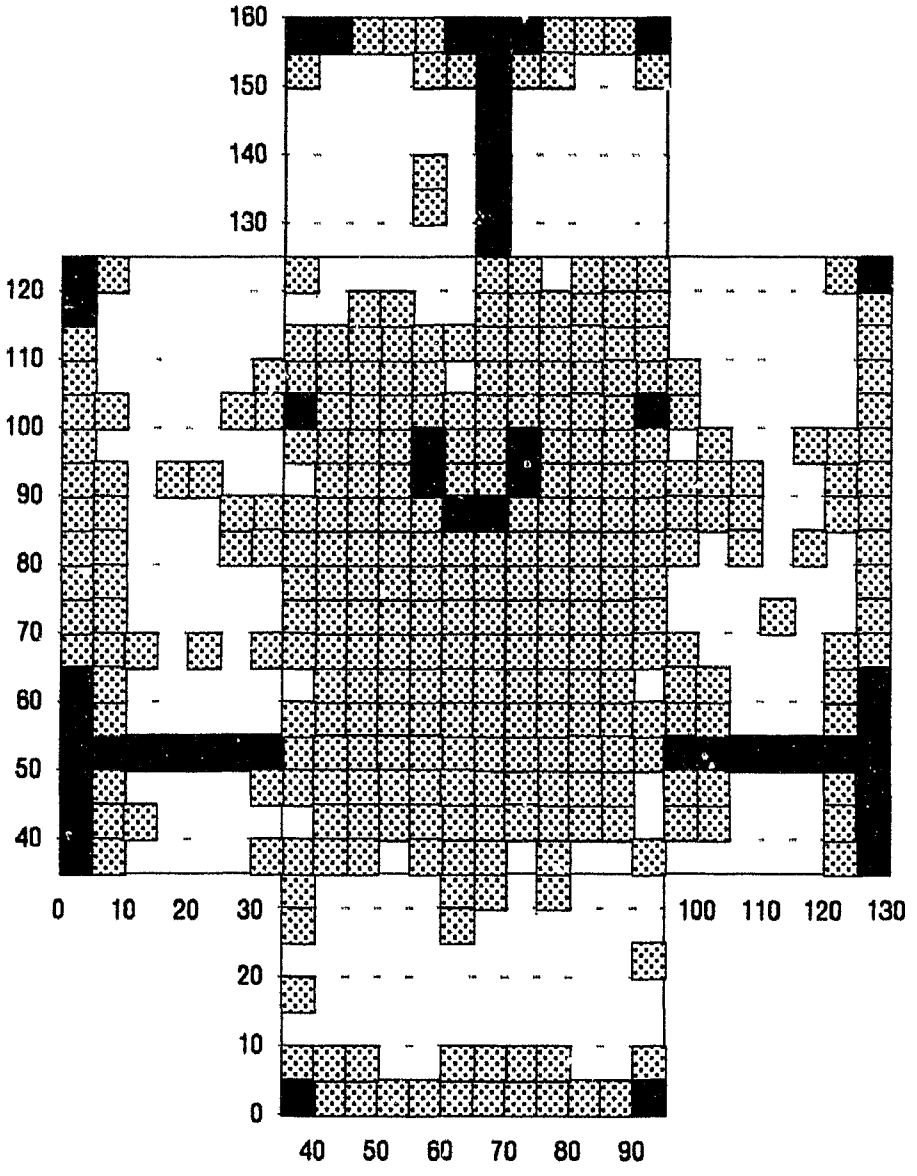

Fig. 4.3 PATTERN OF CUMULATIVE SMALL SEA URCHIN OCCURRENCES INSIDE EXPERIMENTAL TANKS. Key to symbols: ■ significantly high numbers of urchins, ▩ average numbers of urchins, significantly low numbers of urchins, **n** = 720 tankdays.

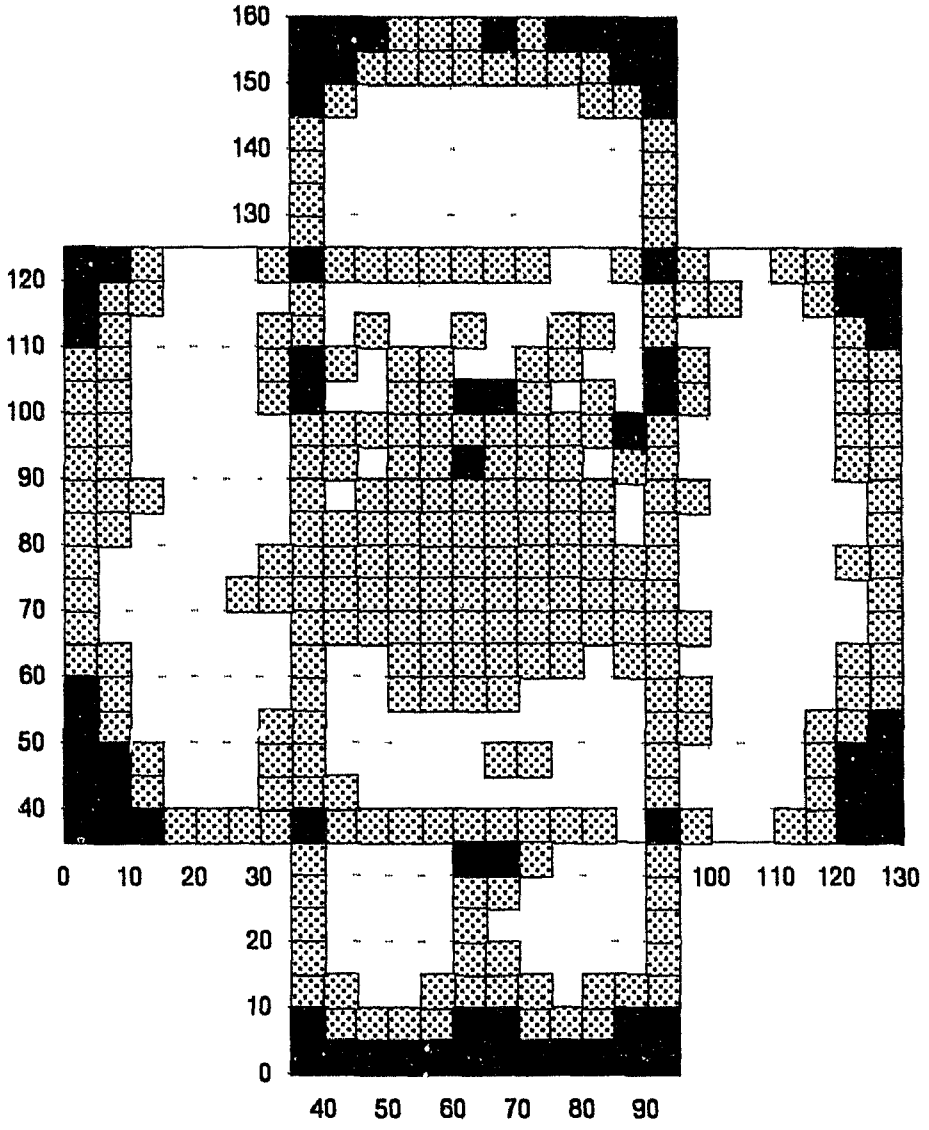

Fig. 4.4 PATTERN OF CUMULATIVE LARGE SEA URCHIN OCCURRENCES INSIDE EXPERIMENTAL TANKS. Key to symbols: ■ significantly high numbers of urchins, ▩ average numbers of urchins, significantly low numbers of urchins, **n** = 719 tankdays.

In Figure 4.5 the cumulative number of small urchins occurring in each location is plotted against the corresponding number for large sea urchins. The plot reveals two clusters of outliers, each consisting of three datapoints, where the number of small sea urchin occurrences is extremely high. The datapoints in the most extreme and the second-most extreme cluster are symmetrically located, respectively, at the topmost and second to topmost locations of the tree vertical grooves (Fig 4.6, Fig. 2.2).

Fig. 4.7 gives a more detailed picture of the size-specific spatial patterns. The topmost graph highlights the symmetry and magnitude of the small sea urchins preference for vertical grooves. Groove utilization is highest at the topmost locations, approximately halved at the second to topmost locations, approximately halved again at the bottom locations, and somewhat lower at the four intermediate groove locations. The bottom graph shows that large sea urchins are most abundant in the top corners and adjacent locations.

Table 4.4 Contingency table analysis of the effect of urchin size on spatial pattern. Tabulated figures represent number of map locations dominated by small urchins, equally dominated by small and large urchins, and dominated by large urchins. Dominance is rated according to a trinary coding scheme of observed urchin occurrence: *significantly low* < *average* < *significantly high*. **n** = 636 map locations, χ^2 = 323.64, $P \leq 0.0001$.

	Small	Equal	Large	Totals
Observed	91 (26.26 %)	378 (59.43 %)	167 (14.31 %)	636 (100 %)
Expected	0	636	0	636

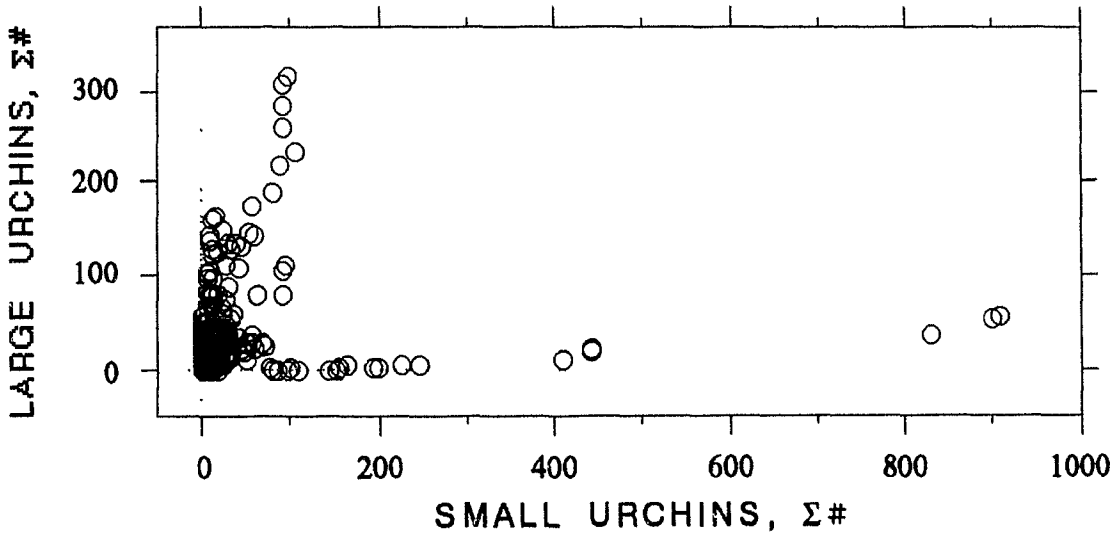

Fig. 4.5 CUMULATIVE OCCURRENCES OF SMALL AND LARGE SEA URCHINS INSIDE EXPERIMENTAL TANKS. The datapoints represent cumulative occurrences, **Σ#**, of small and large sea urchins at each tank map location. **n** = 636 map locations.

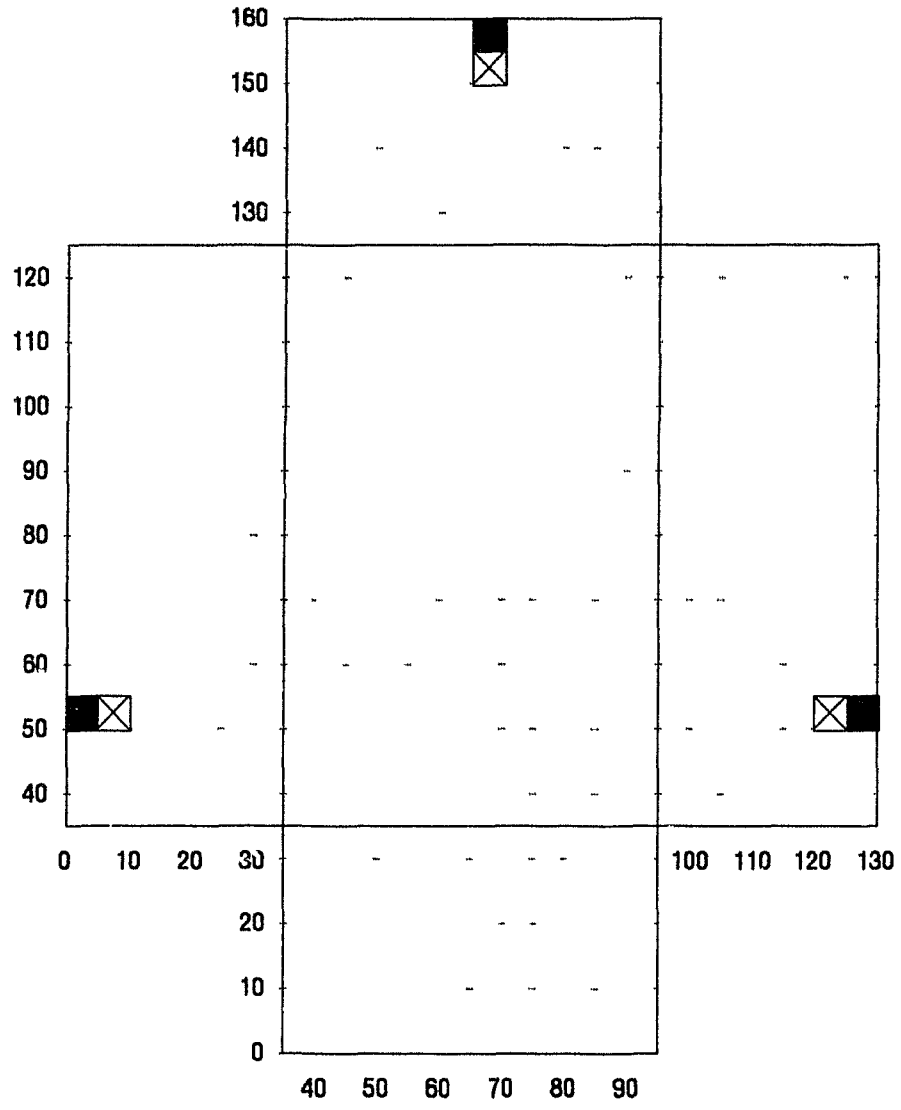

Fig. 4.6 LOCATIONS OF EXTREMELY HIGH CUMULATIVE OCCURRENCES OF SMALL SEA URCHINS. The locations are symmetrically positioned at the top of the three vertical grooves. Key to symbols: ■ member of cluster containing the 3 highest values, ☒ member of cluster containing the 3 second-highest values.

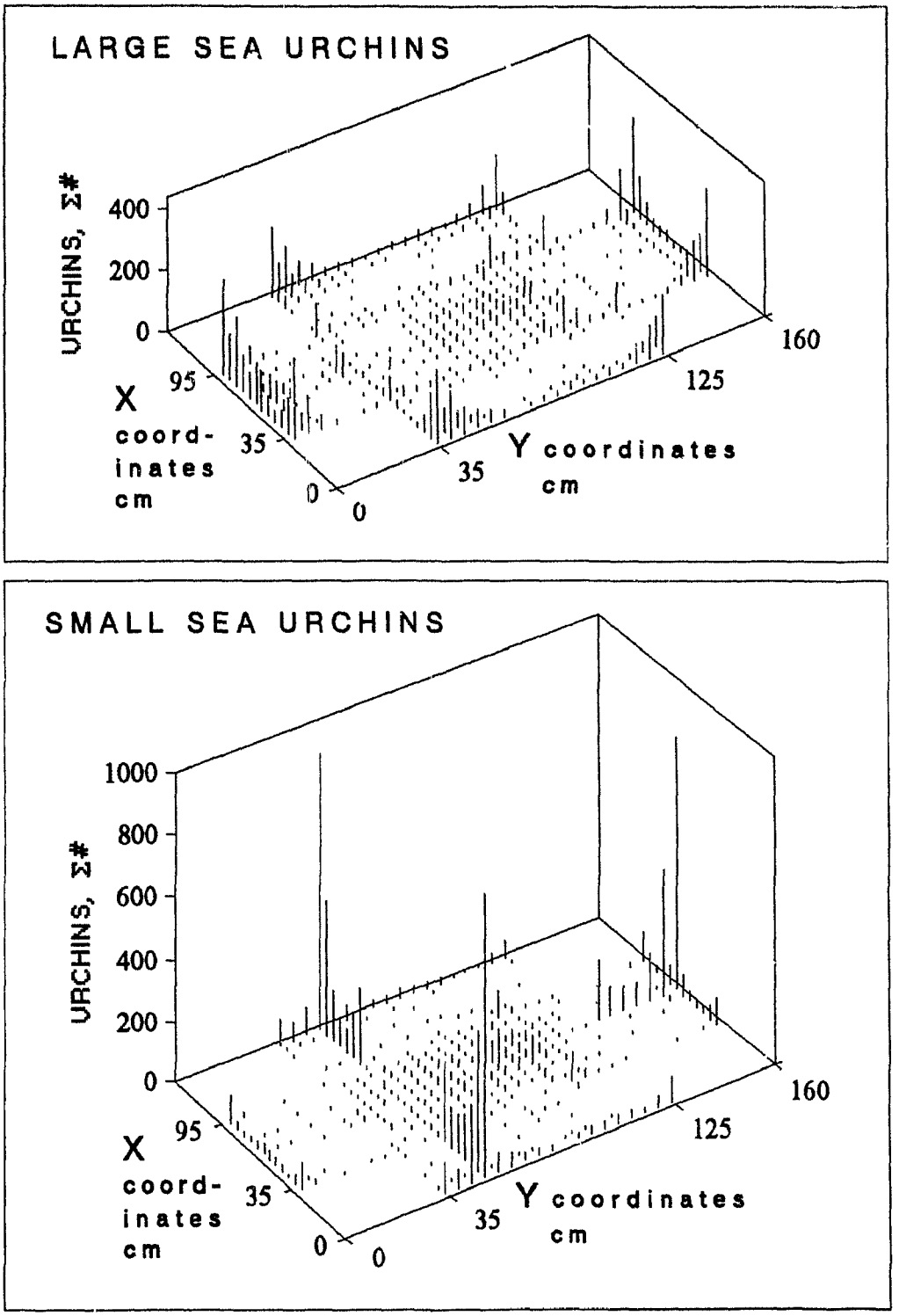

Fig. 4.7 SPATIAL PATTERN OF SEA URCHINS IN EXPERIMENTAL TANKS. The interior tank surface is mapped using a 5 cm coordinate grid in the XY-plane, and the cumulative occurrences, Σ#, of sea urchins are plotted as vertical lines projecting from the center of each tank map location.

4.3.2 Cryptic behaviour

4.3.2.1 Effects of urchin size

4.3.2.1.1 Cryptic behaviour

Sea urchin size is the most prominent main factor effect in the ANOVA table for the cryptic behaviour of *S. droebachiensis* (Table 4.5). The proportion of cryptic sea urchins decreases from 76 % to 32 % when sea urchin size increases from small to large (Appendix 3).

Sea urchin size is also involved in significant interactions with all the other experimental factors (Table 4.5). Therefore, the effects of the other experimental factors on large sea urchins, and on small sea urchins, will be considered separately in the remaining analyses of cryptic behaviour (Underwood 1981; Neter *et al.* 1985).

Table 4.5 ANOVA table for the analysis of cryptic behaviour. Degrees of freedom (df), mean squares (MS), F-values, and p-values for main effects and significant interactions. Prior to analysis the data were transformed using the angular transformation $\arcsin(\sqrt{\%\ \text{cryptic}})$. The Bonferroni family level of significance for the entire ANOVA is $\alpha \leq 0.05$, with $\alpha_i = 0.0004$ for each individual test. $n = 1439$ tankdays.

Source of variation	df	MS	F	p
Season	1	8.4	123.4	0.0001
Size	1	128.8	1891.2	0.0001
Prefeeding	1	2.8	40.7	0.0001
Density	2	1.7	25.0	0.0001
Refuges	1	4.4	64.6	0.0001
Food	1	24.1	354.3	0.0001
Predators	2	13.8	202.7	0.0001
Size × Season	1	1.2	18.0	0.0001
Size × Prefeeding	1	7.2	106.2	0.0001
Size × Density	2	1.1	16.6	0.0001
Size × Refuges	1	2.5	37.3	0.0001
Size × Food	1	5.9	86.2	0.0001
Refuges × Food	1	1.4	20.5	0.0001
Season × Predators	2	1.8	25.9	0.0001
Prefeeding × Predators	2	0.7	9.6	0.0001
Size × Refuges × Food	1	1.1	16.8	0.0001
Size × Season × Predators	2	1.7	24.3	0.0001
Error	1151	0.07		

4.3.2.1.2 Microhabitat usage

Cryptic sea urchins utilized four principal microhabitats: grooves, drainpipe, kelp, and refuges. Kelp and refuges were equally accessible to both sizegroups of sea urchins. Large sea urchins were too big to fit inside the vertical grooves which were used only by the small sea urchins. The cryptic drainpipe habitats were primarily used by large sea urchins because the distance between the drainpipe and the tank wall was greater than the diameter of the small sea urchins which found shelter only at its base. Sea urchins which were cryptic behind the drainpipe or underneath the refuges were occasionally using kelp as additional shelter.

While absolute usage of kelp and refuges was similar for both small and large sea urchins (Fig. 4.8), small urchin use of grooves outnumbered large urchin use of drainpipe habitats by a factor of 10 (Fig. 4.8). Thus, the major size-dependent difference in cryptic behaviour is a result of the small sea urchins access to, and preference for, the vertical grooves in the tank walls.

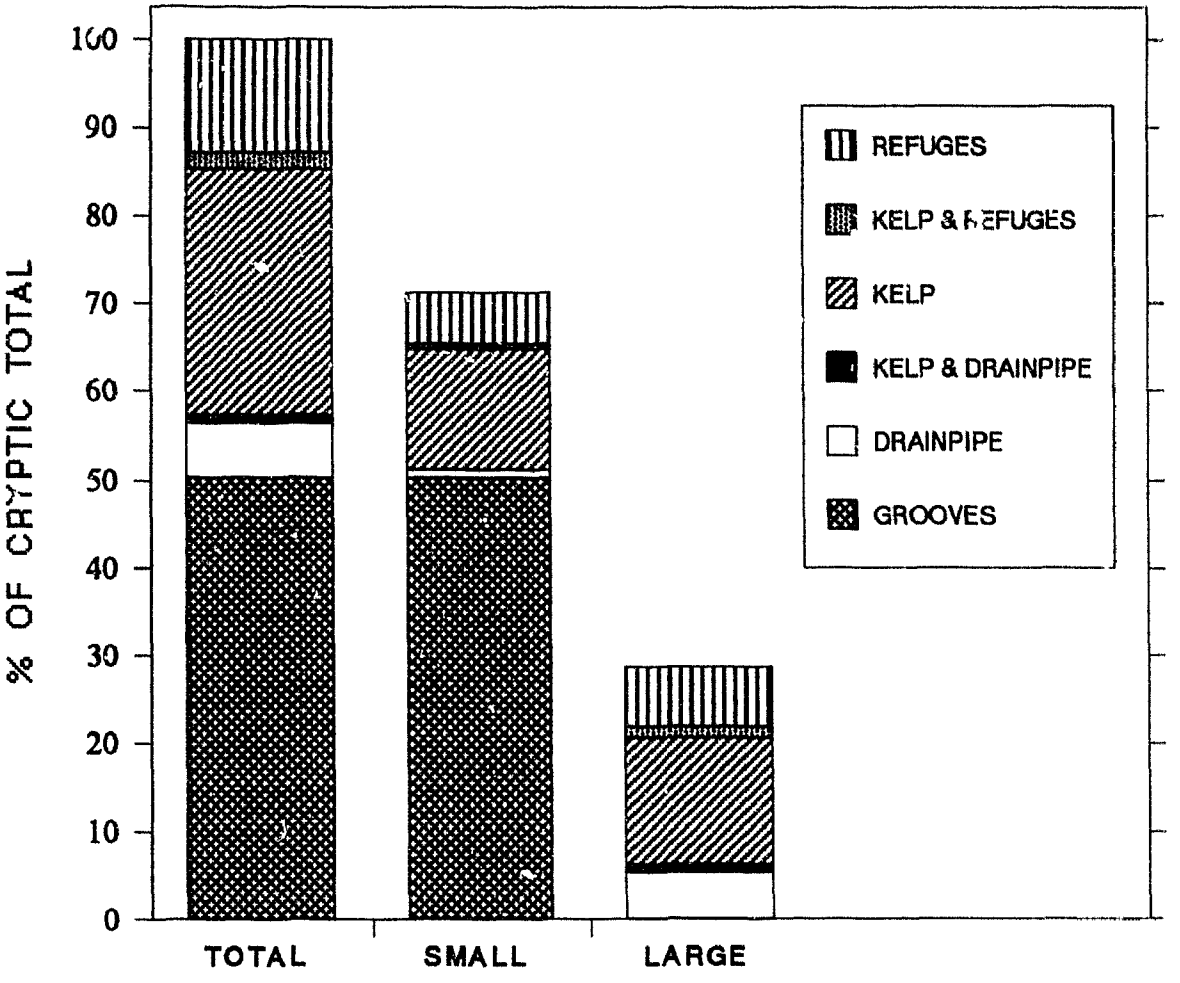

Fig. 4.8 SEA URCHIN USAGE OF CRYPTIC MICROHABITATS. Total usage of cryptic microhabitats and breakdowns for small and large sea urchins are plotted in separate columns. n_{total} = 1439 tankdays, n_{small} = 720 tankdays, n_{large} = 719 tankdays.

4.3.2.2 Effects of urchin density

4.3.2.2.1 Cryptic behaviour

Sea urchin density interacts significantly with sea urchin size (Table 4.5). Hence, the lines for small and large sea urchins in the size × density interaction plot are not parallel (Fig. 4.9). The overall effect of increasing sea urchin density is to decrease the proportion of cryptic individuals. Small urchins were more affected by density changes than were large urchins. The magnitude of the total decrease in the proportion of cryptic individuals when density increased from low to high, was approximately 11 % for small sea urchins and approximately 4 % for large sea urchins (Appendix 3).

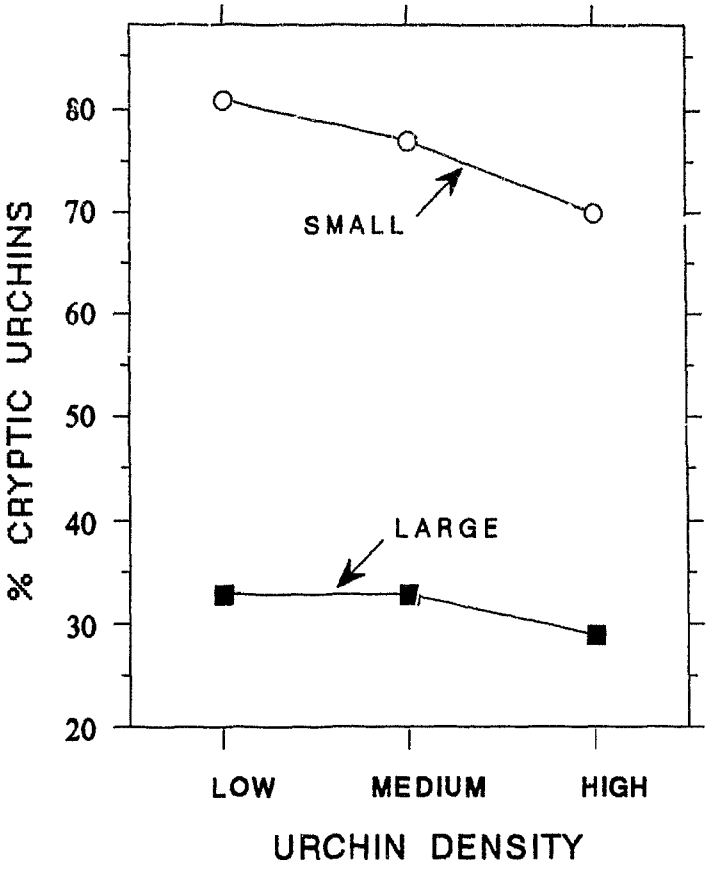

Fig. 4.9 EFFECTS OF SEA URCHIN DENSITY ON CRYPTIC BEHAVIOUR. n = 240 tankdays per datapoint.

4.3.2.2.2 Microhabitat usage

Total usage of all cryptic microhabitats increased when sea urchin density increased (Fig. 4.10A). Sea urchin density however had only minor effects on the proportional usage of different cryptic microhabitats (Fig. 4.10B).

The relative importance of grooves as a cryptic habitat for small sea urchins declined slightly with increasing density (Fig. 4.10B). This decline was compensated by a

slight increase in the relative usage of refuges (Fig. 4.10B).

The proportion of large sea urchins which used both drainpipe and kelp decreased as sea urchin density increased (Fig. 4.10B). This decrease was a result of reduced use of the drainpipe habitat. Relative kelp usage remained approximately constant at all three densities (Fig. 4.10B).

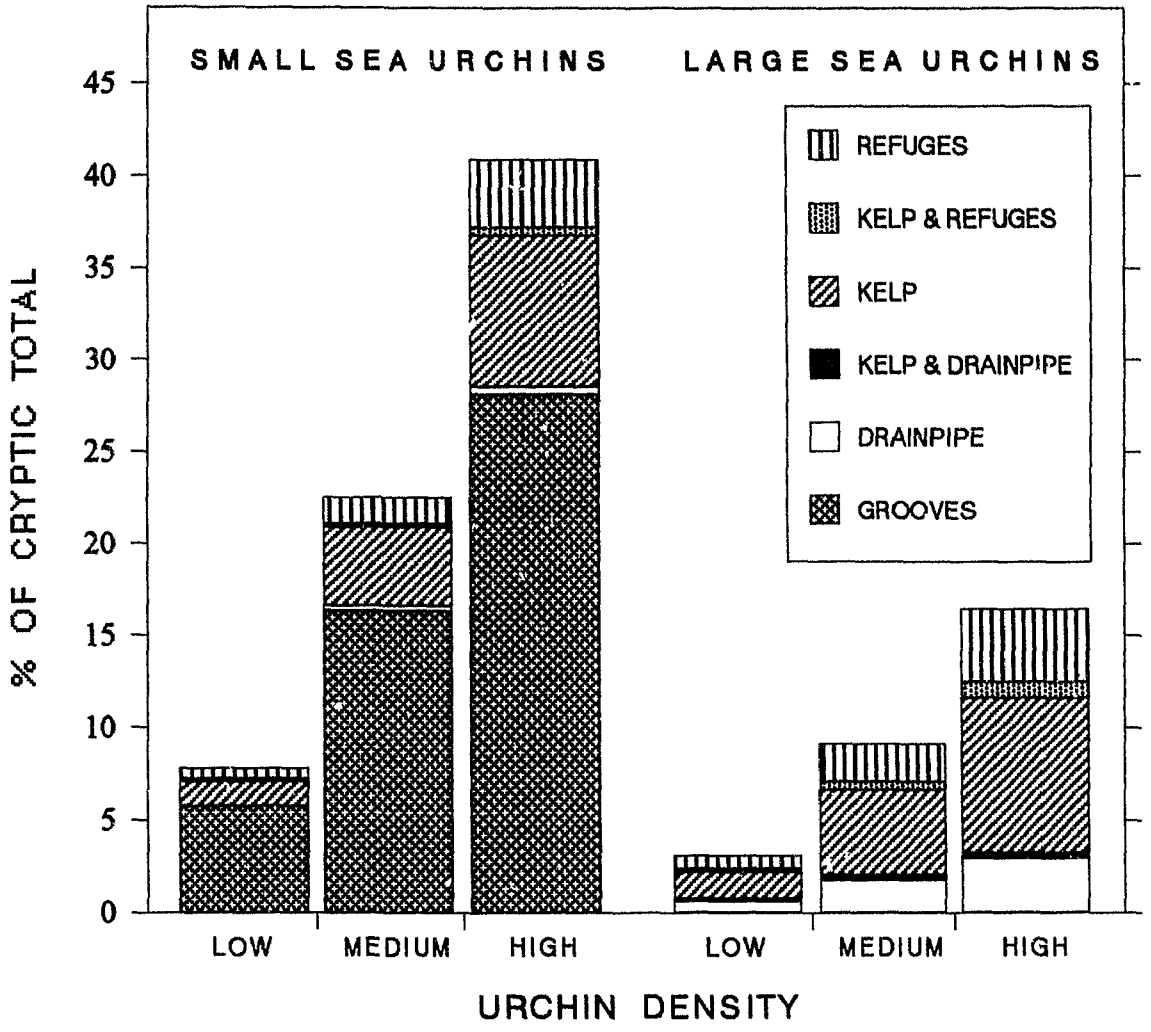

Fig. 4.10A EFFECTS OF SEA URCHIN DENSITY ON CRYPTIC MICROHABITAT USAGE. Usage of cryptic microhabitats is plotted separately for small and large sea urchins at low, medium, and high densities. **n** = 240 tankdays per treatment.

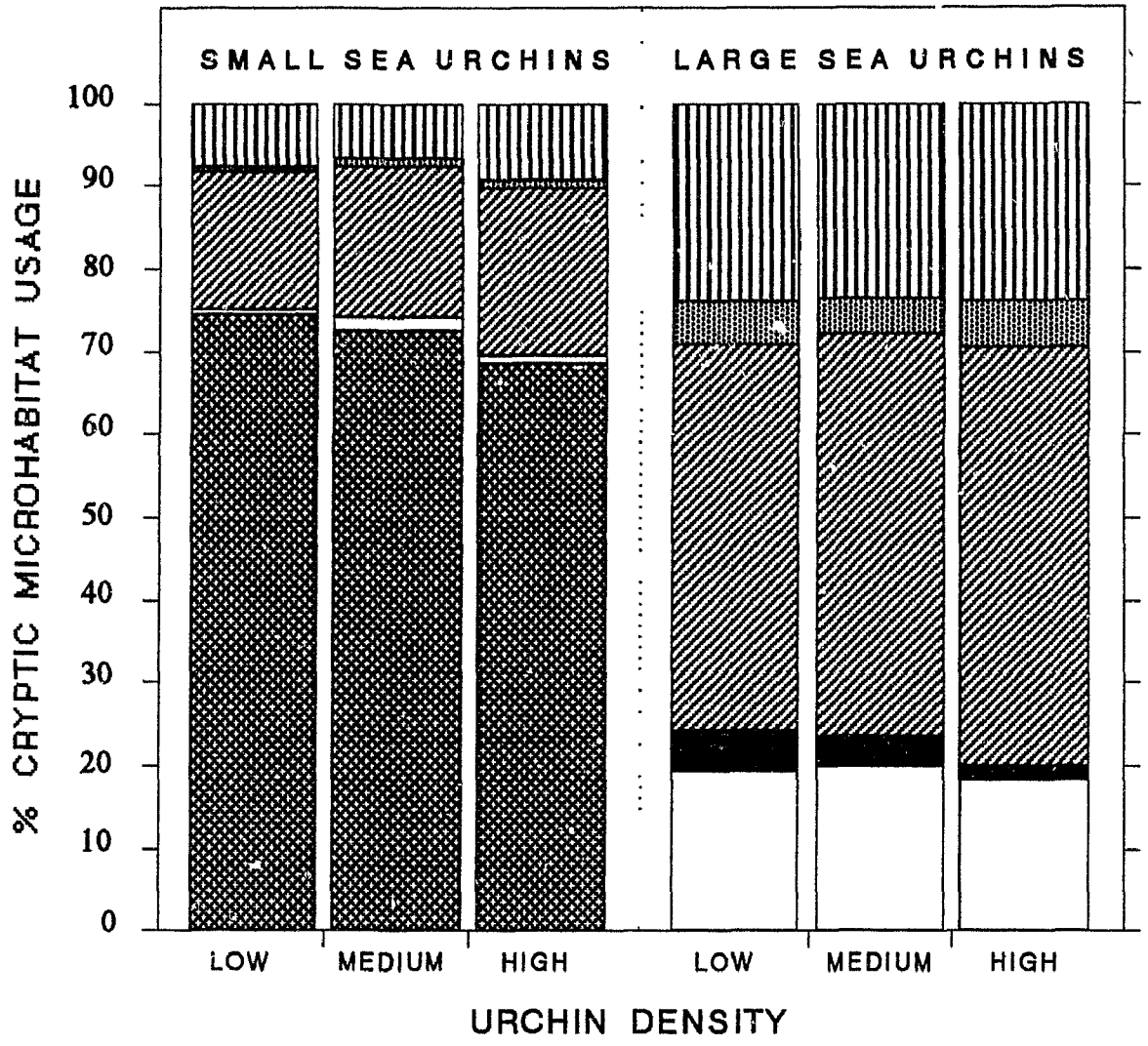

Fig. 4.10B EFFECTS OF SEA URCHIN DENSITY ON THE PROPORTIONAL USAGE OF CRYPTIC MICROHABITATS. Proportional usage of cryptic microhabitats is plotted separately for small and large sea urchins at low, medium, and high densities. n = 240 tankdays per treatment. Legend is the same as in Fig. 4.10A.

4.3.2.3 Effects of refuges and food

4.3.2.3.1 Cryptic behaviour

Significant two- and three-factor interactions among refuges, food and size indicate that the effects of any one factor depends on the level of the other two factors (Table 4.5). Separate addition of either refuges or kelp increased the proportion of cryptic sea urchins, but the effects were not additive (Appendix 3, Fig. 4.11).

Small urchins were relatively unaffected by the addition of either refuges or kelp. Nevertheless, they were considerably more cryptic than large urchins in all treatments. The greatest observed effect was an over 35 % increase in the cryptic behaviour of large urchins when kelp was introduced in the absence of refuges (Appendix 3; Fig. 4.11).

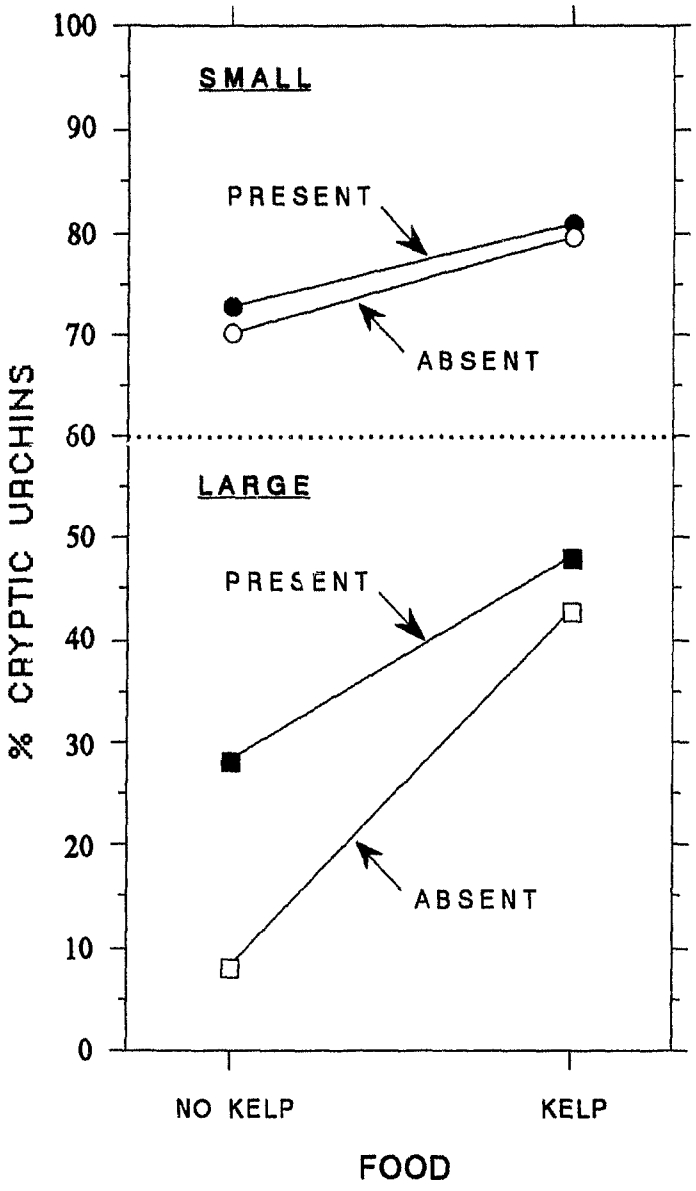

Fig. 4.11 EFFECTS OF REFUGES AND FOOD ON CRYPTIC BEHAVIOUR. n = 180 tankdays per datapoint.

4.3.2.3.2 Microhabitat usage

The vertical grooves in the tank walls were the principal cryptic microhabitat for small sea urchins (Fig. 4.12). The addition of either refuges or kelp decreased the small urchins use of these grooves, yet increased the total percentage of cryptic small sea urchins. Compared to refuges, kelp was the preferred cryptic habitat, however, the effects of kelp and refuges were not additive (Fig. 4.12).

The drainpipe provided the only available cryptic microhabitat for large sea urchins in the absence of refuges and kelp (Fig. 4.12). With the addition of either refuges or kelp the number of cryptic large sea urchins increased, while drainpipe usage remained approximately constant. Kelp was the large sea urchins preferred cryptic microhabitat, even in the presence of refuges. Again, the effects of kelp and refuges were not additive. A minor proportion of the cryptic large sea urchins used both kelp and refuges simultaneously (Fig. 4.12).

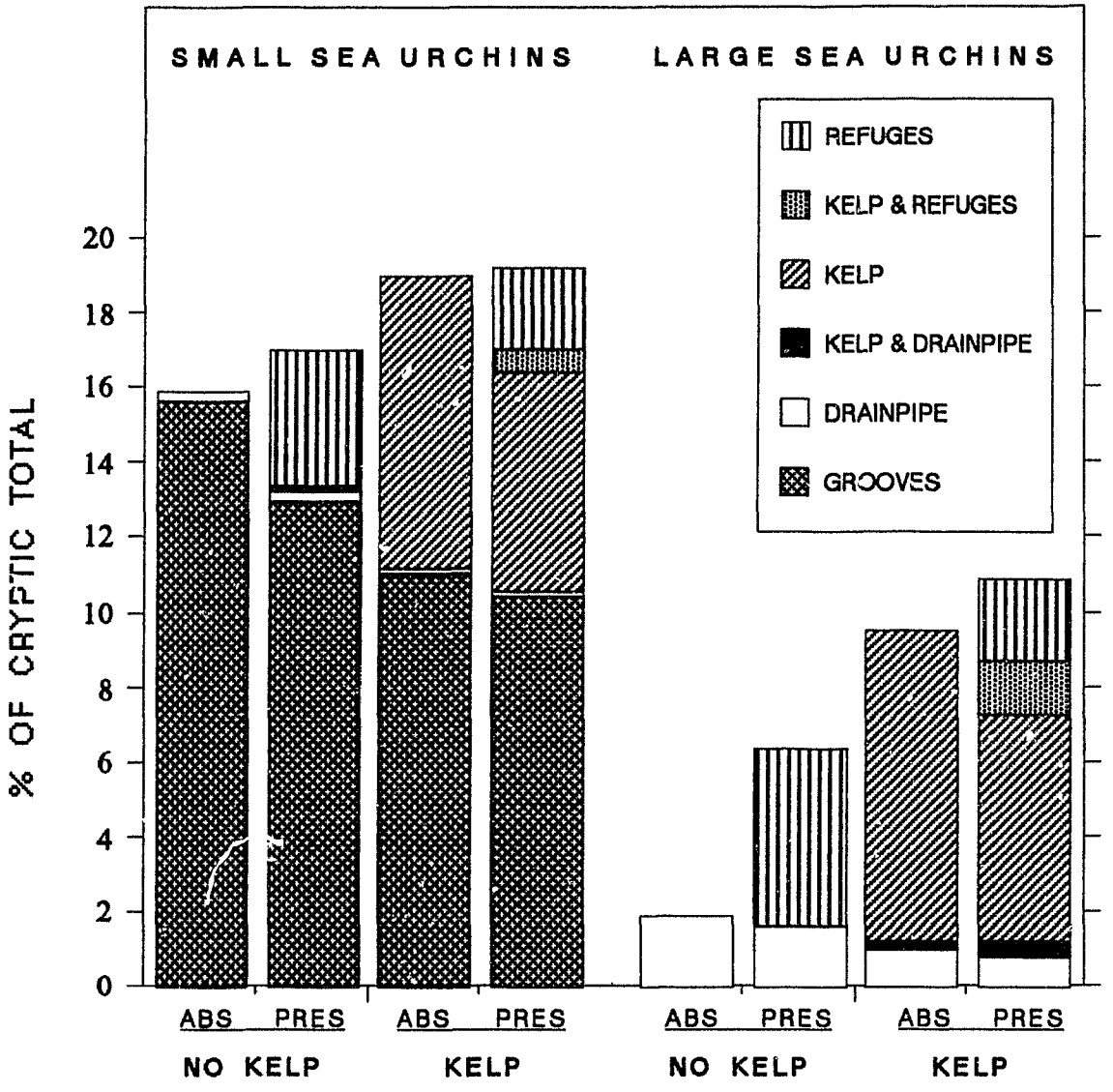

Fig. 4.12 EFFECTS OF REFUGES AND FOOD ON CRYPTIC MICROHABITAT USAGE. Usage of cryptic microhabitats is plotted separately for small and large sea urchins in the absence (ABS) and presence (PRES) of refuges in treatments with and without kelp. **n** = 180 tankdays per treatment.

4.3.2.4 Effects of season, prefeeding and predators

4.3.2.4.1 Cryptic behaviour

Season, size and predators interact significantly in a three-factor interaction, while prefeeding is involved in significant two-factor interactions with both size and predators (Table 4.5). The complex effects of these factors are illustrated in Fig. 4.13 and tabulated in Appendix 3.

The presence of predators, particularly wolffish, tended to make the urchins more cryptic, whereas starvation tended to make them less cryptic. However, approximately 90 % of the small well fed urchins remained cryptic in all summer treatments, and prefeeding had no discernable effect on large urchins in the absence of predators (Fig. 4.13, Appendix 3).

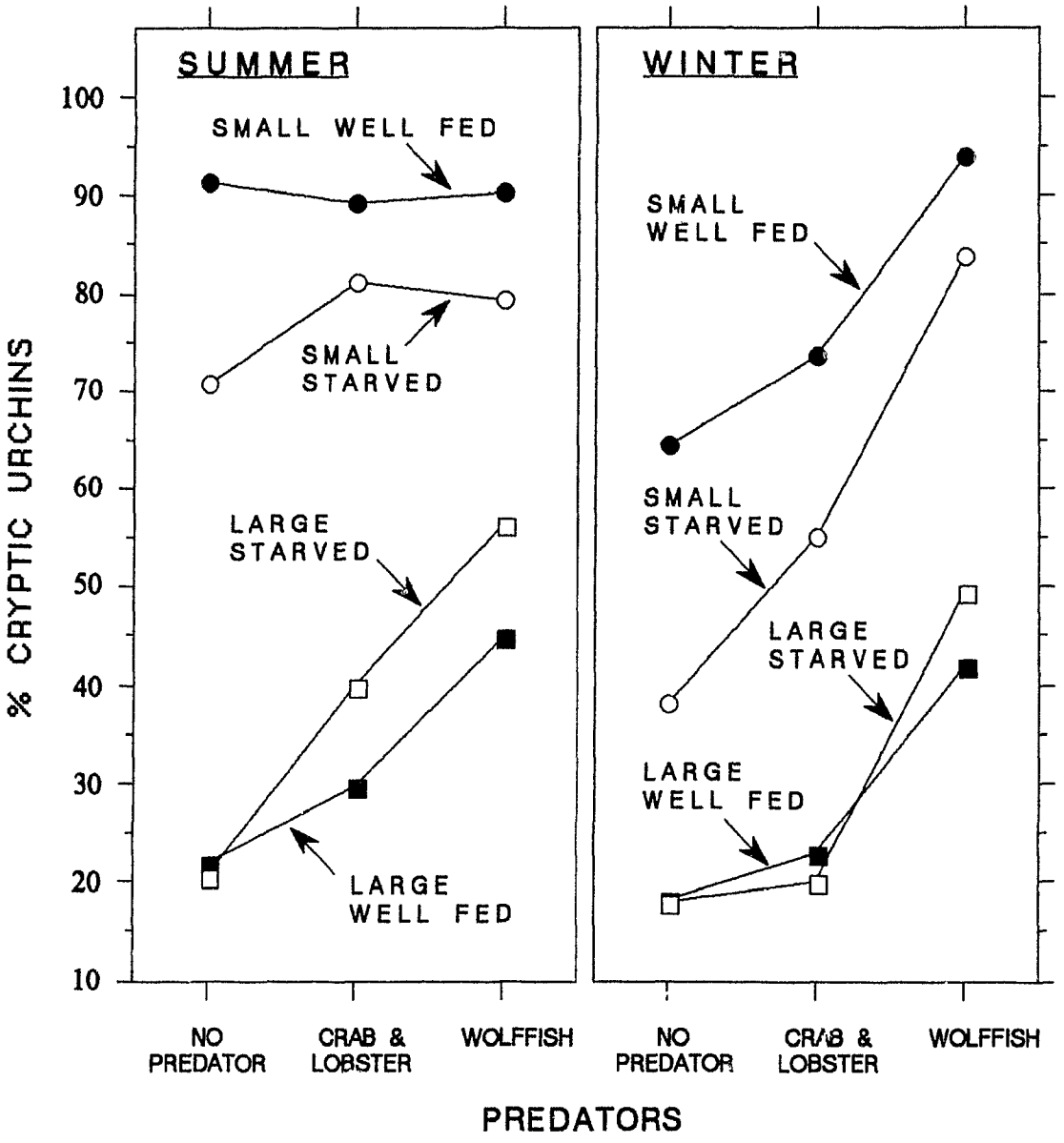

Fig. 4.13 EFFECTS OF SEASON, PREFEEDING AND PREDATORS ON THE CRYPTIC BEHAVIOUR OF SMALL AND LARGE *S. DROEBACHIENSIS*. n = 60 tankdays per datapoint.

4.3.2.4.2 Microhabitat usage

Small sea urchins usage of kelp as a cryptic microhabitat increased in the presence of wolffish irrespective of season or nutritional history (Figs 4.14A, 4.14B). The presence of wolffish also increased the small sea urchins use of refuges in all treatments under consideration, except when well fed in the summer season. Groove usage of small sea urchins decreased in the summer and increased in the winter when wolffish were present

When decapod predators were present, starved small sea urchins increased their usage of grooves, but decreased their use of refuges and kelp, whereas well fed small sea urchins decreased their refuge usage in the summer and increased their kelp usage in the winter (Figs 4.14A, 4.14B).

The large sea urchins usage of both refuges and kelp increased when predators were present (Figs 4.14A, 4.14B). The wolffish had the greater effect.

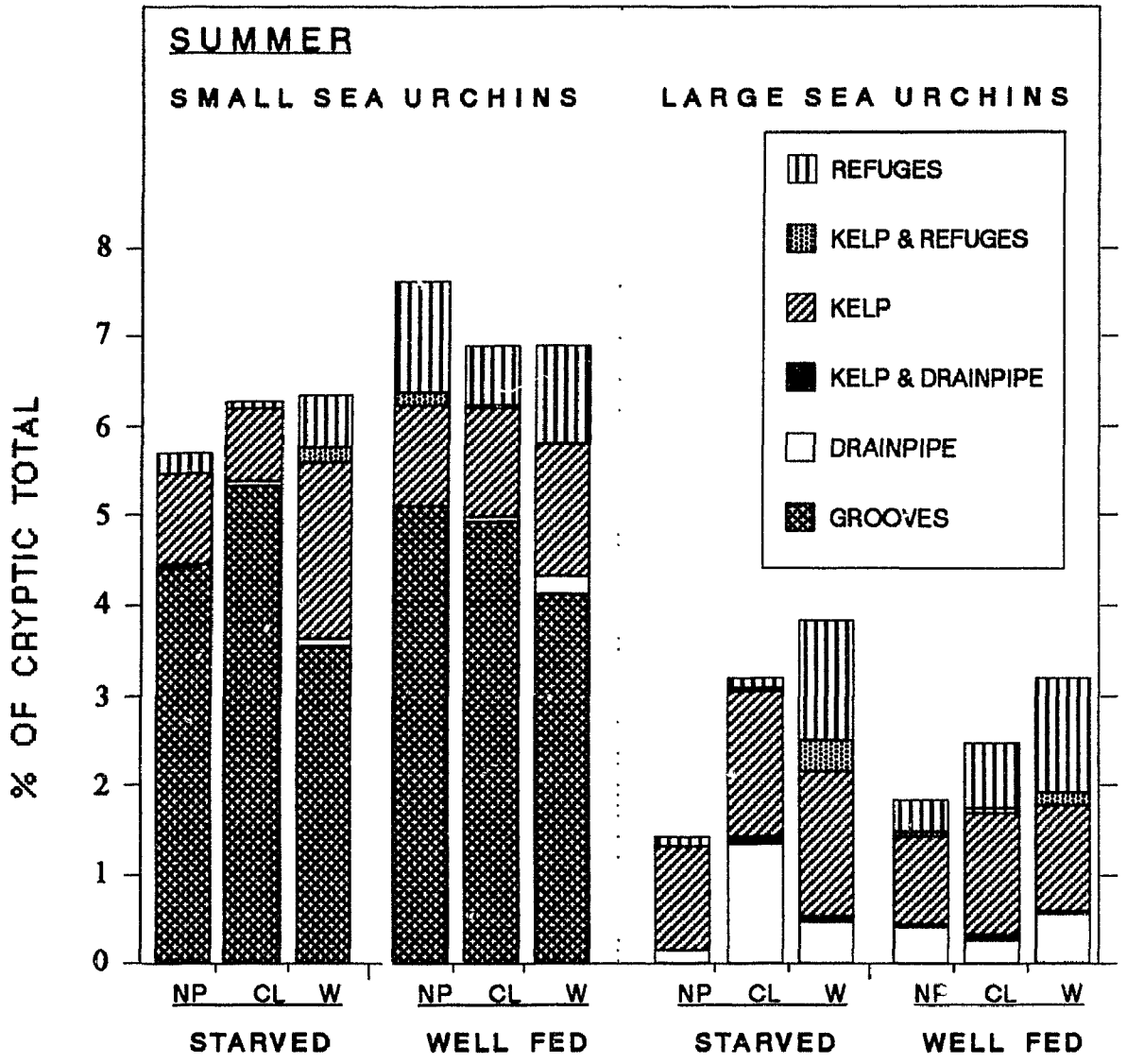

Fig. 4.14A EFFECTS OF SEASON, PREFEEDING AND PREDATORS ON CRYPTIC MICROHABITAT USAGE: SUMMER TREATMENTS. Usage of cryptic microhabitats is plotted separately for starved and well fed, small and large sea urchins with no predators (NP), crab & lobster (CL), and wolffish (W). **n** = 60 tankdays per treatment.

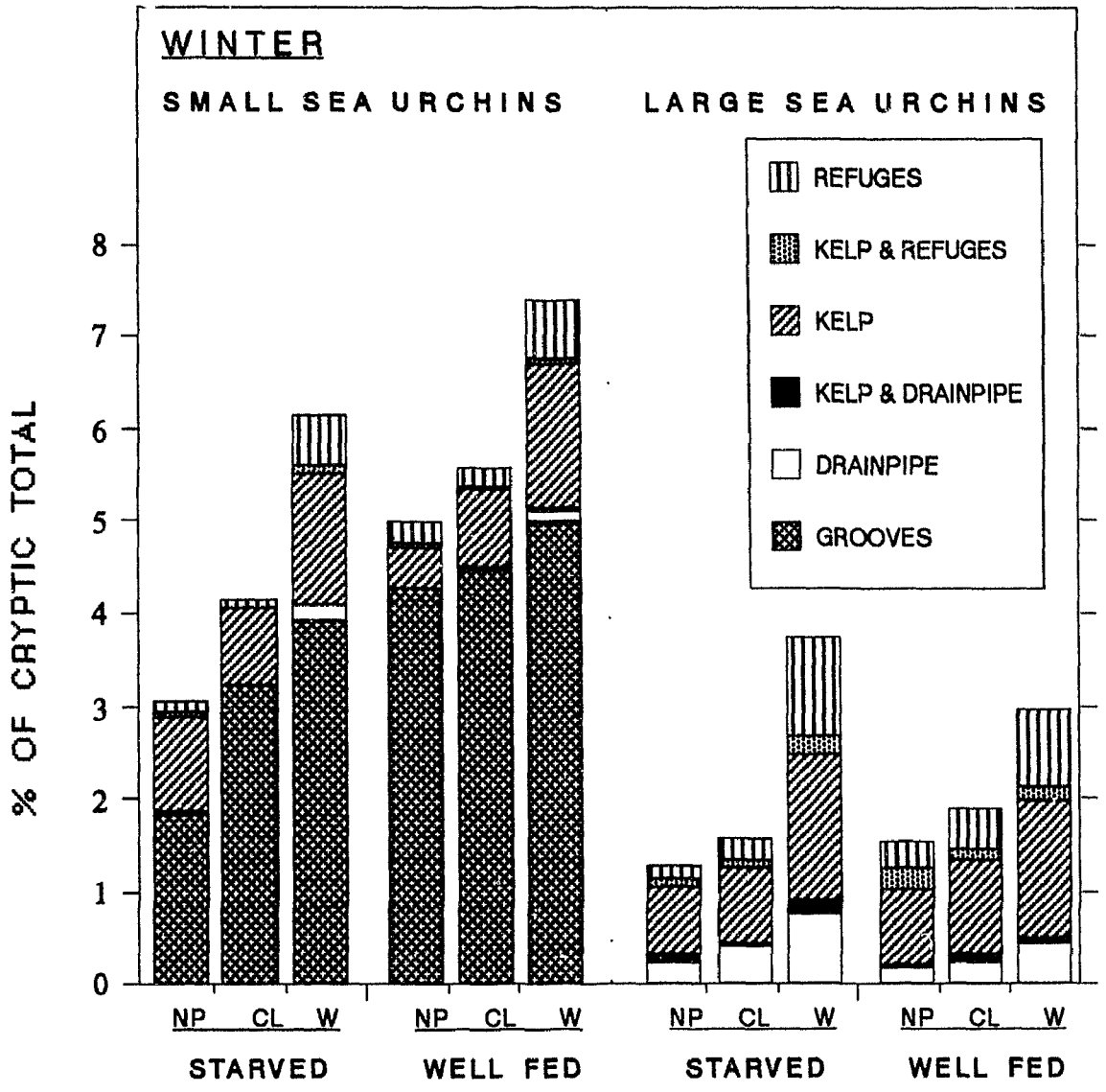

Fig. 4.14B EFFECTS OF SEASON, PREFEEDING AND PREDATORS ON CRYPTIC MICROHABITAT USAGE: WINTER TREATMENTS. Usage of cryptic microhabitats is plotted separately for starved and well fed, small and large sea urchins with no predators (NP), crab & lobster (CL), and wolffish (W). **n** = 60 tankdays per treatment.

4.3.2.4.3 Effects of acts of predation

There was no significant difference in cryptic behaviour between treatments where predation occurred and treatments where predation did not occur (Mann-Whitney U-test, $P > 0.05$; Fig. 4.15, Table 4.6; Mann *et al.* 1984).

Table 4.6 Effects of acts of predation on the cryptic behaviour of *S. droebachiensis*. Mean percentage of cryptic sea urchins in predator treatments where predation did, and did not, occur. The tabulated figures are treatment means. **n** = number of tankdays per treatment.

	No predation		Predation	
Predators:	% cryptic	n	% cryptic	n
Crab & lobster	50.5	305	52.7	197
Wolffish	69.5	239	64.9	271

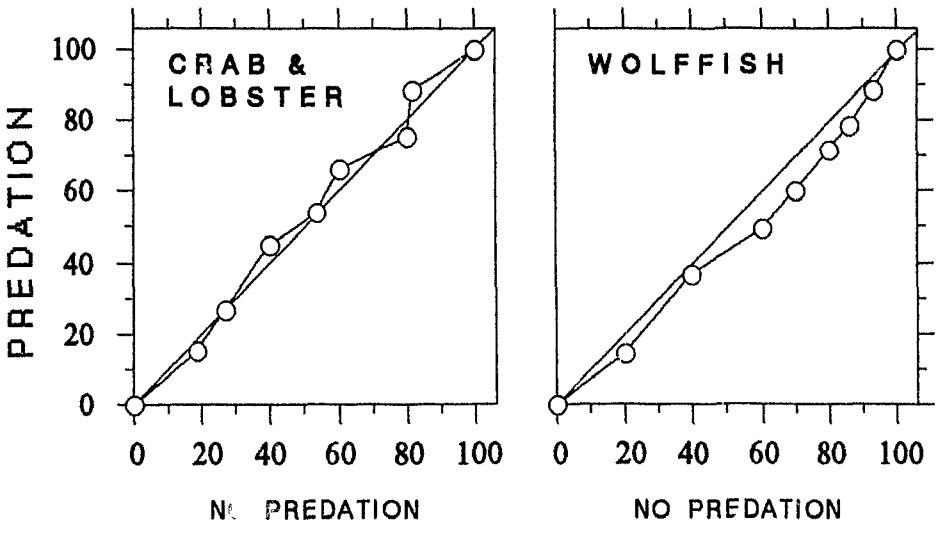

Fig. 4.15 EFFECTS OF ACTS OF PREDATION ON THE CRYPTIC BEHAVIOUR OF *S. DROEBACHIENSIS*. Data from treatments where no predation occurred are compared with data from treatments where predation did occur. Results for decapod predators and wolffish are plotted in separate percentile comparison graphs. Units are % cryptic sea urchins per tankday.

4.3.3 Refuge usage

4.3.3.1 Effects of refuges

The effects of refuges on space utilization were examined by constructing separate probability maps for treatments with and without refuges (Fig. 4.16, 4.17). Both maps indicate non-random spatial patterns. The decision to reject the null hypothesis of random space utilization was confirmed by separate goodness of fit tests for each treatment. Comparing the observed and expected frequencies for the number of locations in the three groups, low, average, and high yielded highly significant G-values for both treatments (Table 4.7).

The bottom corners are the only locations on the tank bottom which have significantly high sea urchin occurrences in the control treatments without refuges (Fig. 4.16). Treatments where refuges are present have 16 additional highly significant map locations on the tank bottom (Fig. 4.17). These locations are symmetrically located where the refuges meet the tank walls, and around the center piece of the refuges (Fig. 4.17; Fig. 2.2).

In Fig. 4.18 the cumulative number of small urchins occurring in each of the 16 most used refuge locations (Fig. 4.17) is plotted against the matching number for large urchins. The plot reveals two extreme values whose locations are symmetrically located on opposite sides of the tank where the refuges meet the tank walls (Figs 4.18, 4.19, Fig. 2.2).

Thus, the effect of adding claypipe refuges was to locally increase cumulative sea urchin occurrences in areas with increased spatial heterogeneity.

Table 4.7 Summary of spatial statistics for refuge usage. n is the number of tankdays, Σx is the total number of urchin occurrences, and $\bar{x}$ is the mean cumulative number of urchins per location in the treatment. x_{low} and x_{high} are threshold values for x, the observed cumulative number of sea urchins in a particular location, such that $P(x \leq x_{low}) \leq 0.00001$ and $P(x \geq x_{high}) \leq 0.00001$ if x has a random (Poisson) pattern. The G-value is for a goodness of fit test comparing the observed and expected frequencies for the number of locations in each of the three groups, significantly low, average and significantly high. The critical G-value is $\chi^2_{1,\ 0.001} = 10.83$.

Treatment	n	Σx	$\bar{x}$	x_{low}	x_{high}	G-value
Refuges absent	720	11399	17.92	2	38	5675.7
Refuges present	719	11357	17.86	2	38	6108.24

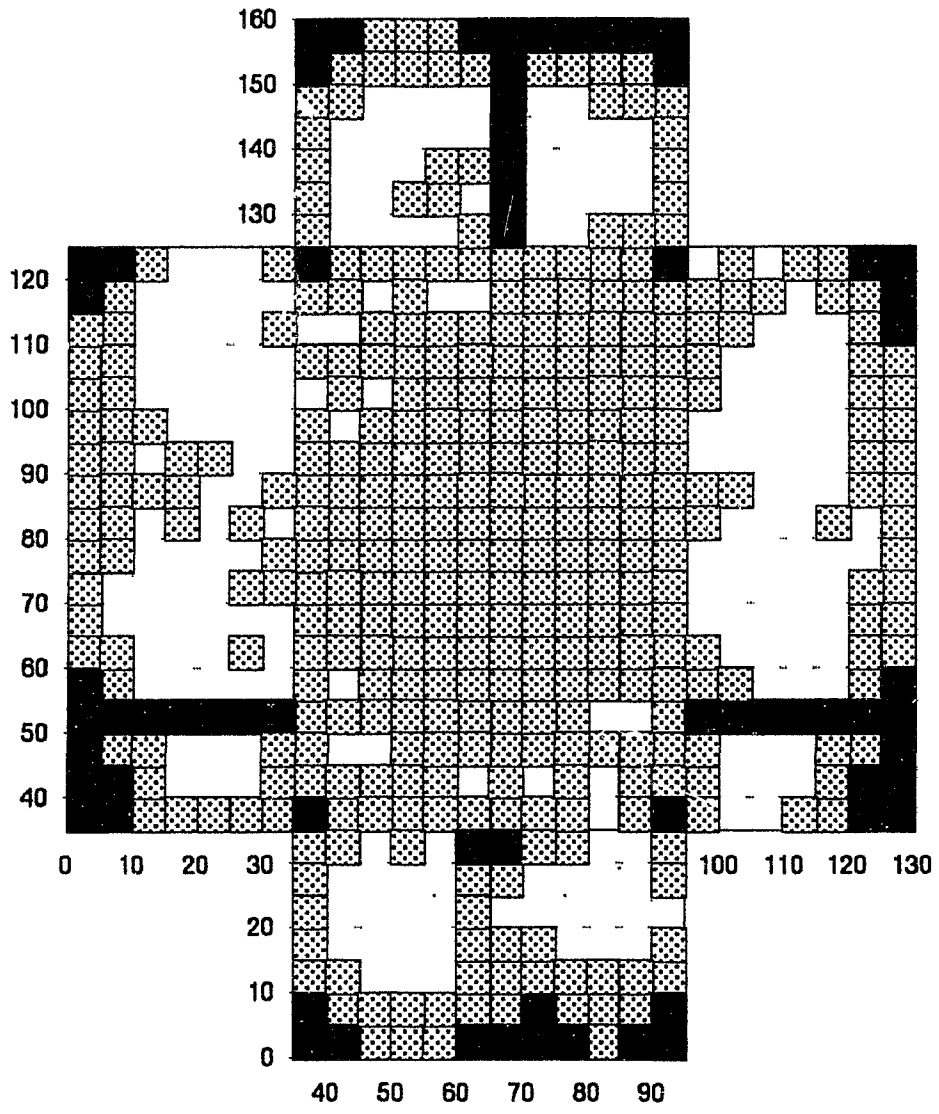

Fig. 4.16 PATTERN OF CUMULATIVE SEA URCHIN OCCURRENCES IN THE ABSENCE OF REFUGES. The only significantly high occurrences of sea urchins on the tank bottom are located in the four bottom corners. Key to symbols: ■ significantly high numbers of urchins, ▩ average numbers of urchins, significantly low numbers of urchins. **n** = 720 tankdays.

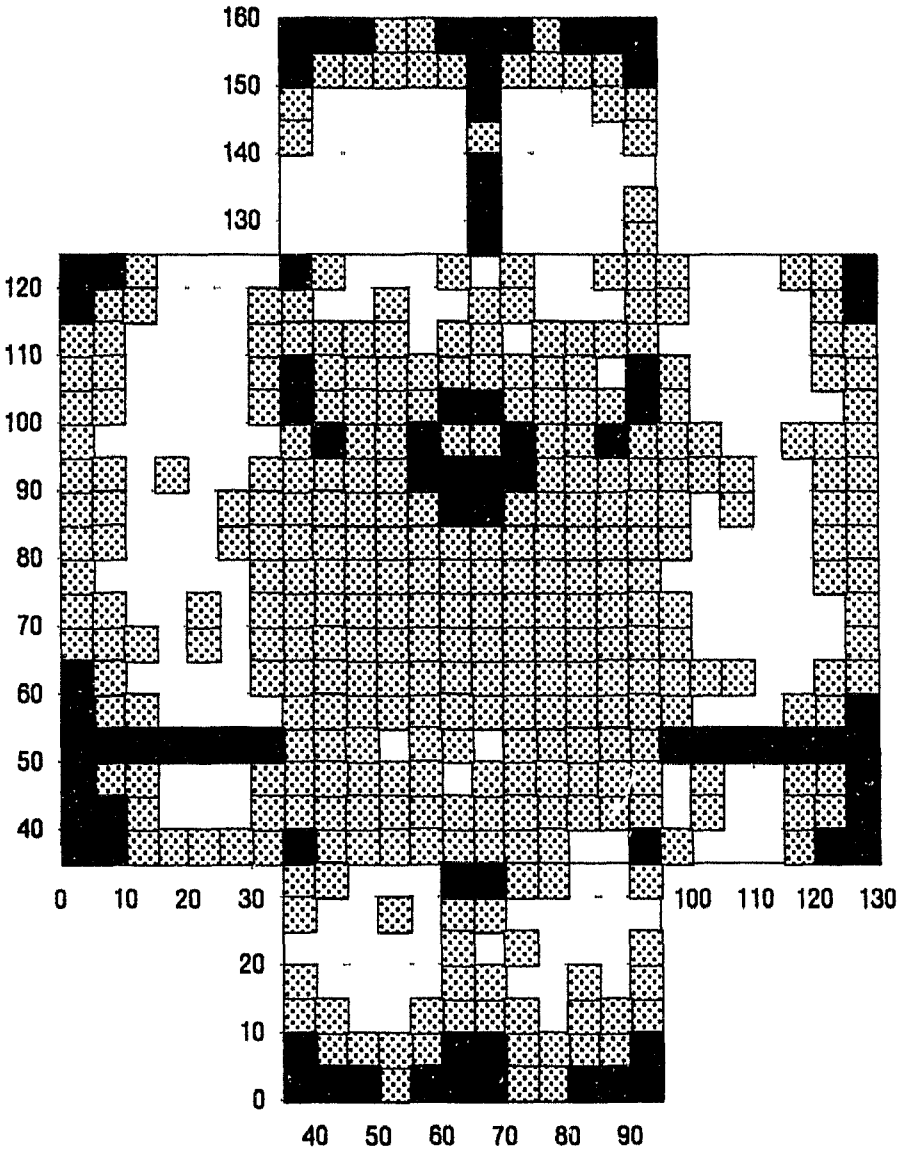

Fig. 4.17 PATTERN OF CUMULATIVE SEA URCHIN OCCURRENCES IN THE PRESENCE OF REFUGES. Areas of significantly high sea urchin occurrences on the tank bottom are located symmetrically around the center piece of the refuges, where the refuges meet the tank walls, and in three of the bottom corners. Key to symbols: ■ significantly high numbers of urchins, ▩ average numbers of urchins, significantly low numbers of urchins. n = 719 tankdays.

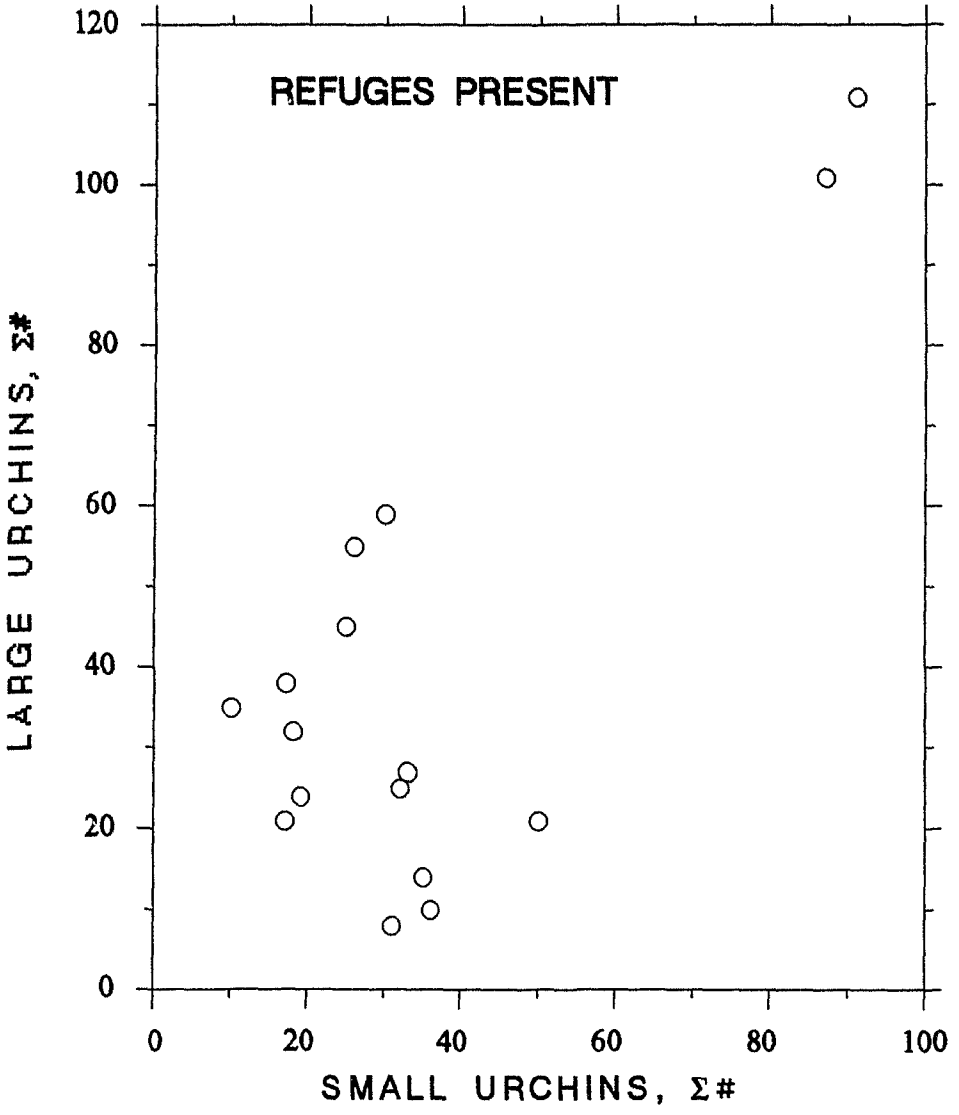

Fig. 4.18 CUMULATIVE OCCURRENCES OF SMALL AND LARGE SEA URCHINS IN THE VICINITY OF REFUGES. The datapoints represent significantly high cumulative occurrences, Σ#, of small and large sea urchins at the 16 map locations associated with the presence of refuges. **n** = 719 tankdays.

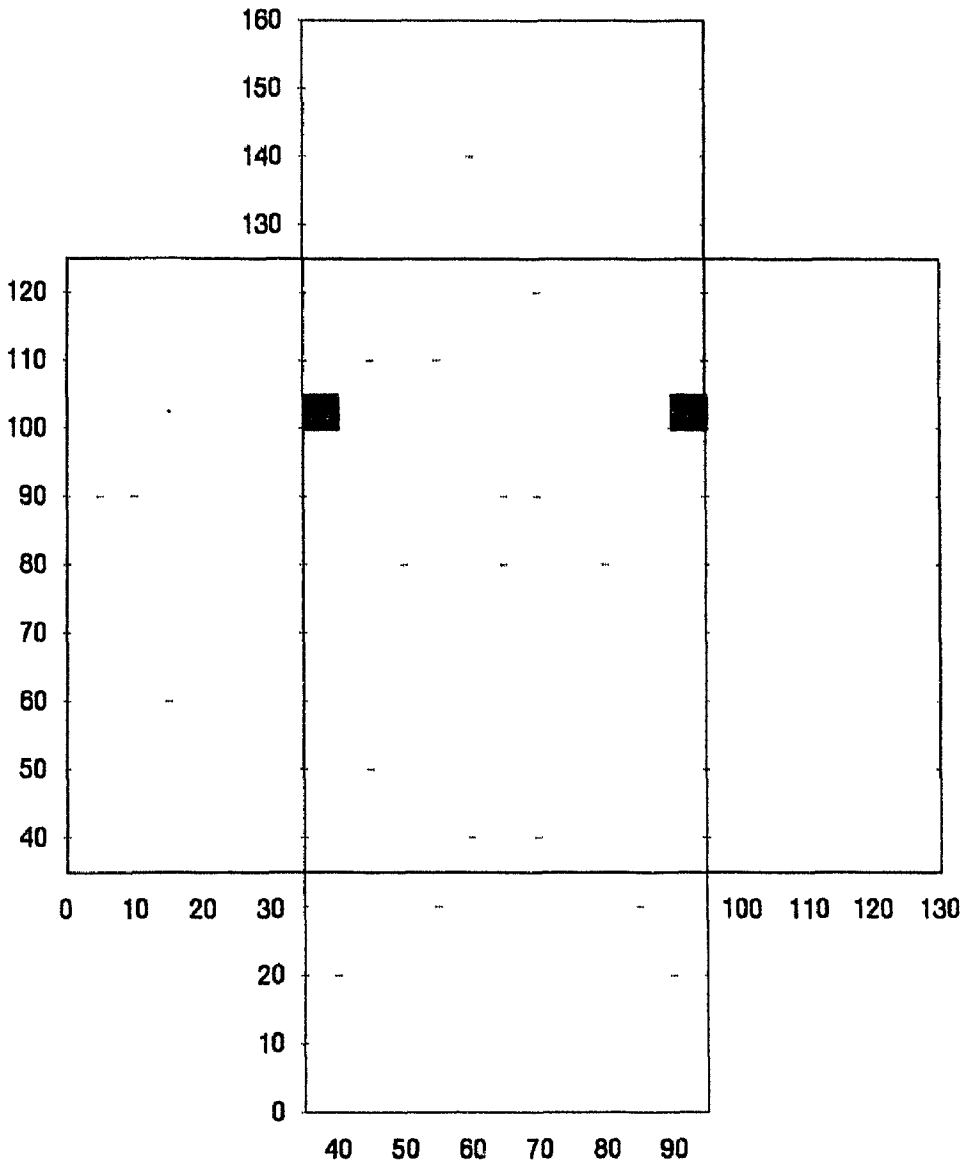

Fig. 4.19 LOCATIONS OF THE HIGHEST CUMULATIVE OCCURRENCES OF SEA URCHINS IN THE VICINITY OF REFUGES. Key to symbols: ■ the 2 most frequently occupied refuge locations.

4.3.3.2 Treatment effects

The refuge usage of *S. droebachiensis* was determined by two groups of two significant interacting main factors, one consisting of season and prefeeding, and the other consisting of urchin size and predators (Table 4.8). Sea urchin density and food had no significant effects on refuge usage.

Table 4.8 ANOVA table for refuge usage. Degrees of freedom (df), mean squares (MS), F-values, and p-values for significant main effects and interactions. Prior to analysis the data were transformed using the angular transformation $\arcsin(\sqrt{\%\text{ refuge usage}})$. The Bonferroni family level of significance for the entire ANOVA is $\alpha \leq 0.05$, with $\alpha_i = 0.0008$ for each individual test. $n = 719$ tankdays.

Source of variation	df	MS	F	p
Season	1	1.2	20.3	0.0001
Size	1	1.6	26.4	0.0001
Prefeeding	1	3.0	49.6	0.0001
Predators	2	6.7	109.8	0.0001
Season × Prefeeding	1	1.1	18.3	0.0001
Size × Predators	2	1.3	20.7	0.0001
Error	575	0.061		

4.3.3.2.1 Season and prefeeding

Well fed urchins exhibited a clear seasonal response pattern, with high refuge usage in the summer and low refuge usage in the winter (Appendix 3, Fig. 4.20). In comparison, season had little effect on the refuge usage of starved sea urchins, which had lower refuge usage than well fed urchins at all times, although the magnitude of the difference was minimal in the winter season (Appendix 3, Fig. 4.20).

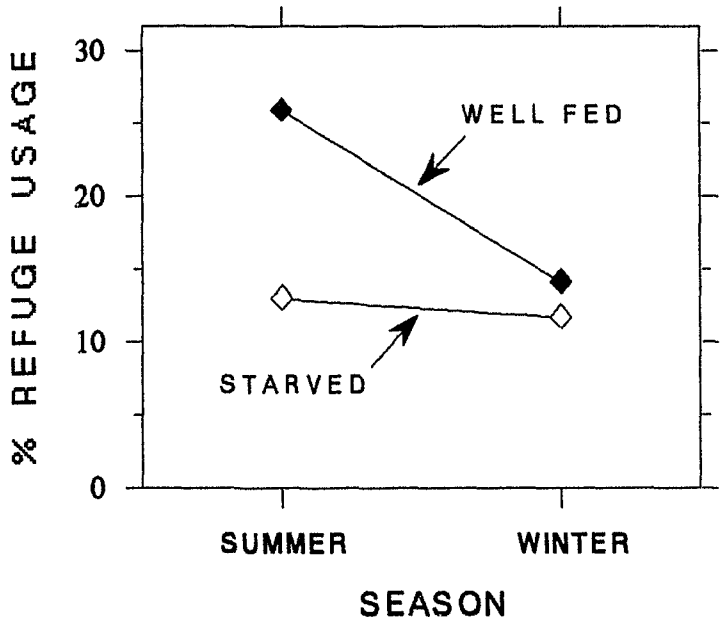

Fig. 4.20 EFFECTS OF SEASON AND PREFEEDING ON THE REFUGE USAGE OF *S. DROEBACHIENSIS*. n = 180 tankdays per datapoint.

4.3.3.3.2 Urchin size and predators

Although refuge usage for both sizegroups of sea urchins increased in the presence of wolffish, large urchins demonstrated the greater increase (Appendix 3, Fig. 4.21). In control treatments large urchins had the lower refuge usage, yet in the presence of wolffish, refuge usage by the large urchins increased beyond that of the small urchins.

Decapod predators had opposite effects of small magnitude on the two sizegroups of sea urchins (Table 13, Fig. 4.21). Small urchins decreased, while large urchins increased their refuge usage in the presence of decapod predators. Although the small urchins had the higher refuge usage in the control treatments, their refuge usage decreased below that of the large urchins in the decapod predator treatments.

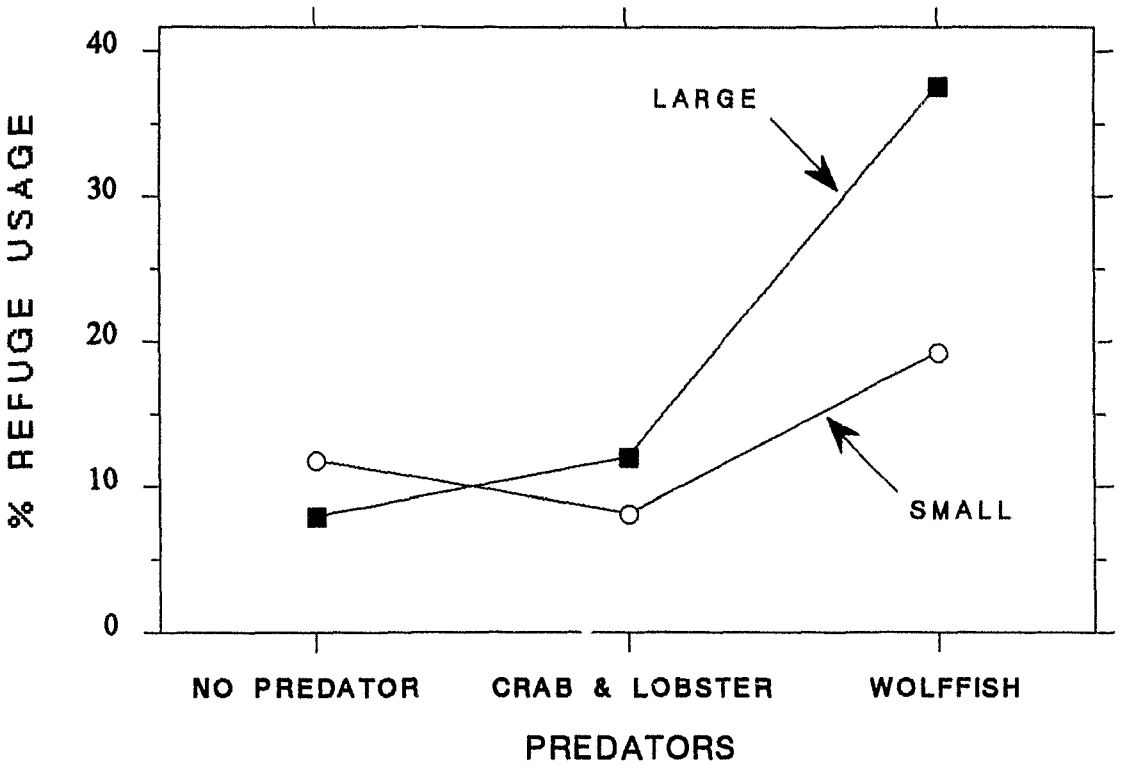

Fig. 4.21 EFFECTS OF URCHIN SIZE AND PREDATORS ON THE REFUGE USAGE OF *S. DROEBACHIENSIS*. n = 120 tankdays per datapoint.

4.4 Discussion

4.4.1 Spatial pattern

Sea urchins occurred in non-random spatial patterns under experimental conditions in laboratory tanks and exhibited a strong preference for areas of locally increased spatial heterogeneity. The most striking evidence of this effect was the high magnitude and near perfect symmetry of the small sea urchins preference for the two topmost locations of the three vertical grooves.

Size-dependent differences in microhabitat preference were related to the scale of spatial heterogeneity. Small urchins exhibited a strong preference for vertical grooves in the tank walls, which were of the same magnitude as the size of the small urchins. Similarly, large urchins exhibited a preference for larger microhabitats, such as the top and bottom locations by the drainpipe. The small urchins were capable of unrestricted movement behind the drainpipe and did not exhibit a preference for locations in this vicinity. The bottom corners of the tank were highly preferred by large urchins, whose size was of the same magnitude as the rounded curvature of the corners.

Sea urchins in nature frequently occupy microhabitats with a high degree of spatial heterogeneity (Keats *et al.* 1985b), and will even actively excavate burrows in flat rock substrata (Fewkes 1889, 1890; Otter 1932). Thus it would

appear that sea urchins in nature, and in laboratory tanks, both prefer locations where surface contact is maximized. Urchins occupying heterogeneous microhabitats would presumably increase their fitness by being more difficult to dislocate by wave surge or predators.

The preceding observations inspired the formulation of the following hypotheses: i) sea urchins prefer microhabitats with a high degree of spatial heterogeneity, and ii) the presence of predators will increase the usage of spatially heterogeneous microhabitats. These hypotheses are tested in the next two subsections by examining the cryptic behaviour and refuge usage of *S. droebachiensis*.

4.4.2 Cryptic behaviour

The cryptic behaviour of *S. droebachiensis* under laboratory conditions demonstrated a trend towards a less cryptic lifestyle in response to increasing body size. Size-specific differences in cryptic behaviour were linked to the small sea urchins utilization of vertical grooves in the tank walls. The large sea urchins had outgrown these microhabitats and were restricted to cryptic spaces behind the drainpipe in the absence of experimentally introduced shelter in the form of kelp or claypipe refuges.

The proportion of cryptic sea urchins decreased with increasing density. Therefore, the absolute density of

exposed sea urchins increased at a slightly higher rate than the total population density when the latter was experimentally inflated.

Hypothesis i, that sea urchins prefer microhabitats with a high degree of spatial heterogeneity, was tested by examining the effects of kelp and claypipe refuges on the proportion of cryptic sea urchins. The presence of either element increased the proportion of cryptic sea urchins. Thus, the null hypothesis of no treatment effects is rejected. Note however, that the effects of kelp and refuges were not additive. Kelp, which is known to induce positive chemotaxis in *S. droebachiensis* (Garnick 1978; Mann *et al.* 1984), had the larger effect and was the most highly preferred habitat when both kelp and refuges were present. Note also that small urchins, which had access to cryptic microhabitats in the form of vertical grooves in the tank walls (Section 4.4.1, Chapter 6), were less affected by the introduction of additional spatial heterogeneity than were the large urchins.

Hypothesis ii, that the presence of predators will increase the usage of spatially heterogeneous microhabitats, was tested by comparing the proportion of cryptic sea urchins in treatments with predators and in control treatments without predators. The presence of predators, especially Atlantic wolffish, made large urchins more cryptic, while the effect of decapod predators was slight, particularly in the

winter season. Small sea urchins were also more cryptic in the presence of predators, except when well fed in the summer season. At this time a high proportion of the small urchins were cryptic whether predators were present or not. The effect of predators was independent of whether an act of predation had actually occurred (Mann *et al.* 1984).

Consequently hypothesis ii was rejected in its original form and modified as follows: iia) large sea urchins increase their usage of cryptic microhabitats in the presence of predators. The complex effects of predators on the cryptic behaviour of small sea urchins is not given further consideration at this point because the main focus of this chapter is on the formation of exposed destructive feeding aggregations which are composed of large sea urchins.

Bernstein *et al.*'s (1981, 1983) suggestion that sea urchins will hide more readily in the presence of fish predators is in agreement with hypothesis iia. These authors attributed increased hiding of large sea urchins in the summertime to the seasonal presence of predatory fishes, especially wolffish. This argument is supported by my results which showed that the percentage of cryptic large sea urchins increased in the presence of predators, notably wolffish, while in the absence of predators there was only a slight seasonal difference in cryptic behaviour.

Hypothesis iia is not supported by Bernstein *et al.*'s (1981, 1983) results for decapod predators. They presented evidence of reduced hiding for large sea urchins in the presence of decapod predators at high urchin densities. However, no such response was apparent for large sea urchins at the urchin densities employed in this study.

Previously published results from field studies suggest that starvation caused by scarcity of drift algae is correlated with a less cryptic behaviour, presumably caused by the hungry urchins active pursuit of food (Bernstein *et al.* 1983; Harrold & Reed 1985; Mattison *et al.* 1977; Dean *et al.* 1984). Absence of kelp made large urchins significantly less cryptic in my experiment too, although starved large urchins were noticeably less cryptic than well fed large urchins only in the winter decapod treatments.

4.4.3 Refuge usage

Hypothesis i, that sea urchins prefer microhabitats with a high degree of spatial heterogeneity, was tested by examining the usage of microhabitats in the presence and absence of claypipe refuges. The null hypothesis of no refuge effect was rejected and 16 locations with significantly high numbers of sea urchins were identified with the presence of refuges.

Vadas *et al.* (1986) proposed an alternative mechanism for the relationship between local sea urchin abundance and

spatial heterogeneity in laboratory tanks. They interpreted groupings of sea urchins in the corners of laboratory tanks and around intake hoses and drainpipes as artifacts caused by abrupt changes of topographic features which purportedly inhibited random dispersal of the urchins. In my experimental tanks, however, claypipe refuges, bottom corners or other areas of locally increased microspatial heterogeneity did not appear to restrict the ability of sea urchins to move freely. Furthermore, urchins occupying spatially heterogeneous microhabitats were often difficult to remove from the tanks, presumably because they had a larger available attachment area than urchins on featureless portions of the tank surface. It is therefore proposed that the observed preference for spatially heterogeneous microhabitats is a result of increased available attachment area rather than inhibition of dispersal.

Hypothesis iia, that large sea urchins increase their usage of cryptic microhabitats in the presence of predators, was tested by comparing refuge usage in the presence of decapod predators or wolffish with control treatments without predators. Large sea urchins increased their refuge usage in the presence of both decapod predators and wolffish. Consequently hypothesis iia was not rejected.

The effect of nutritional history or prefeeding on refuge usage has been assessed in field studies of Californian sea urchin populations (Harrold & Reed 1985; Mattison *et al.*

1977). A high proportion of the urchins in California occupied refugial microhabitats when kelp availability was high, while space occupancy shifted towards exposed microhabitats when kelp was scarce. These observations are in agreement with my results for refuge usage, which was significantly higher when the sea urchins were well fed than when they were starved.

CHAPTER 5 FEEDING BEHAVIOUR

5.1 Introduction

The feeding behaviour of sea urchins is closely linked to the mechanisms by which these animals control benthic community structure. Sea urchins are capable both of overgrazing kelp beds and of preventing kelp recolonization in overgrazed areas (Wharton & Mann 1981; Hagen 1987). Overgrazing occurs when the sea urchins switch from a passive detritivorous role, where they feed on drift algae and have negligible impact on community structure, to an aggressive herbivorous mode of feeding where they decimate entire kelp beds (Breen & Mann 1976a; Harrold & Reed 1985; Mann 1985). A barren post-overgrazing community configuration can then be indefinitely sustained by the browsing activity of actively foraging sea urchins (Lang & Mann 1976; Johnson & Mann 1982).

Evidence from field studies suggests that the behavioural switch from passive detritivores to aggressive herbivores is triggered when the ratio of available kelp biomass to urchin biomass decreases (Harrold & Reed 1985; Johnson & Mann 1988). However, other factors including urchin size, the presence of predators, availability of cryptic habitats, feeding history, and season may also be important (Bernstein *et al.* 1981; 1983; Mann 1985). Here I study the effects of these purported causal factors on the feeding behaviour of *S. droebachiensis* under controlled experimental conditions in laboratory tanks.

5.2 Results

5.2.1 Effects of season, urchin size and prefeeding

Sea urchin size and prefeeding had significant main effects on the feeding behaviour of *S. droebachiensis* (Table 5.1). These two factors interacted significantly and were also involved in a three-factor interaction with season. There was no other significant effect of season.

The proportion of feeding urchins was highest when the urchins were starved (Fig. 5.1; Appendix 3). The relatively parallel lines in the winter section of the interaction plot indicate that winter prefeeding had uniform effects on both sizegroups of sea urchins (Fig. 5.1). However, in the summer season the lines slope in different directions indicating that prefeeding had less effect on small and more effect on large sea urchins as compared to the winter season. The proportion of feeding large urchins was higher than the proportion of feeding small urchins in all treatments except when well fed in the summer season.

Table 5.1 ANOVA table for the analysis of feeding behaviour. Degrees of freedom (df), mean squares (MS), F-values, and p-values for significant main effects and interactions. The Bonferroni family level of significance for the entire ANOVA is $\alpha \leq 0.05$, with $\alpha_i = 0.0008$ for each individual test. $n = 719$ tankdays per treatment.

Source of variation	df	MS	F	p
Size	1	1.523	27.490	0.0001
Prefeeding	1	4.729	85.358	0.0001
Refuges	1	0.864	15.590	0.0001
Predators	2	1.020	18.416	0.0001
Size × Prefeeding	1	0.84	15.152	0.0001
Prefeeding × Predators	2	0.686	12.385	0.0001
Season × Size × Prefeeding	1	0.660	11.921	0.0006
Error	575	0.055		

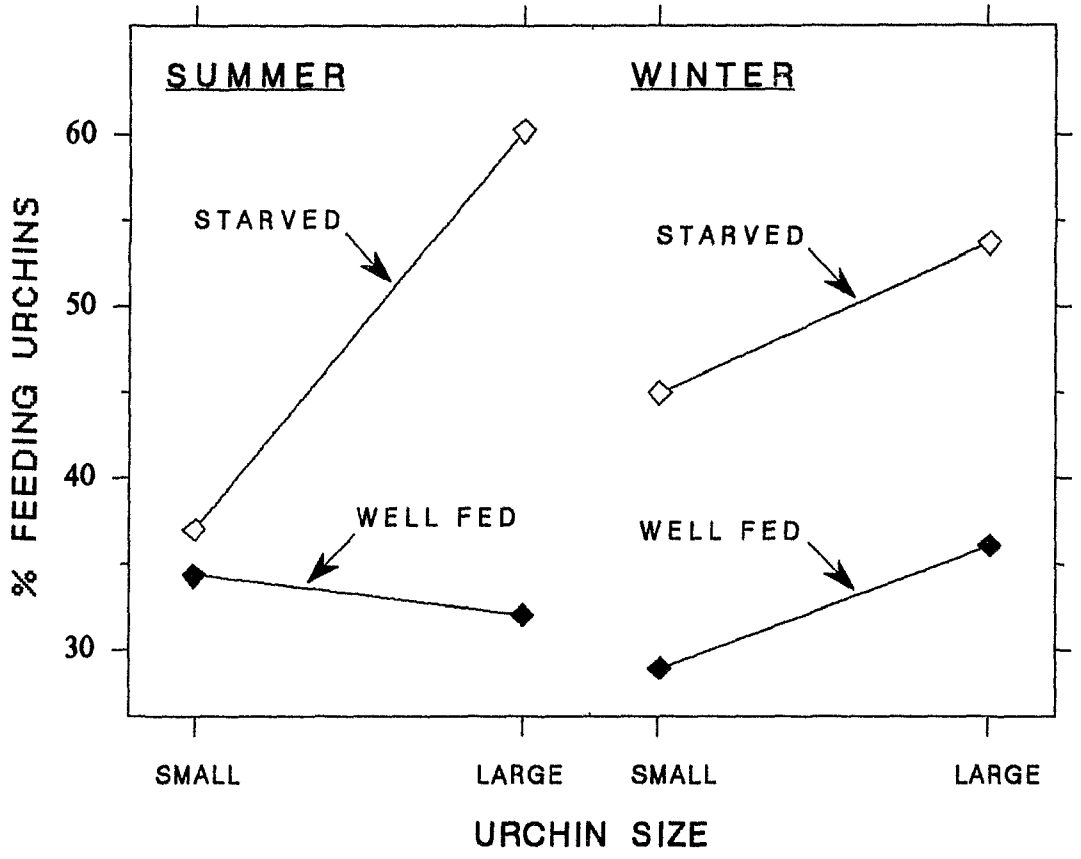

Fig. 5.1 EFFECTS OF SEASON, SIZE AND PREFEEDING ON THE FEEDING BEHAVIOUR OF *S. DROEBACHIENSIS*. **n** = 90 tankdays per datapoint.

5.2.2 Effects of refuges

The main factor effect for refuges is significant, but refuges do not interact significantly with other experimental factors (Table 5.1). Fewer sea urchins were feeding when refuges were present. The effect of refuges however was of comparatively low magnitude with 44.37 % of the sea urchins feeding in the absence, and 37.45 % feeding in the presence of refuges.

5.2.3 Effects of predators and prefeeding

The main treatment effect for predators is significant, and predators do interact significantly with prefeeding (Table 5.1). Hence the non-parallel appearance of the lines for starved and well fed sea urchins in Fig. 5.2. Decapod predators decreased the proportion of feeding starved urchins and increased the proportion of feeding well fed urchins (Fig. 5.2, Appendix 3). Wolffish increased the proportion of feeding well fed sea urchins more than the decapods did, but had little effect on the feeding behaviour of starved urchins.

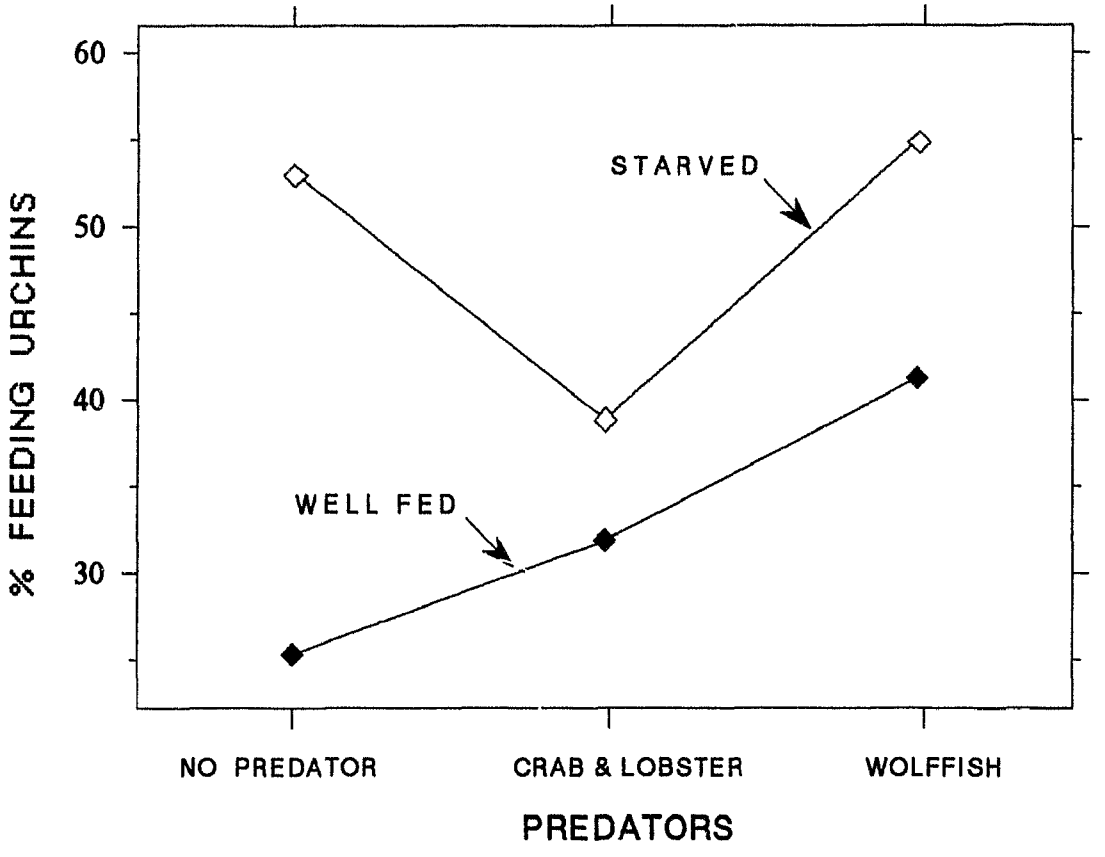

Fig. 5.2 EFFECTS OF PREDATORS AND PREFEEDING ON THE FEEDING BEHAVIOUR OF *S. DROEBACHIENSIS*. **n** = 120 tankdays per datapoint.

5.2.4 Destructive feeding aggregations in the laboratory

Destructive feeding aggregations are made up of sea urchins in the aggressive herbivore mode of feeding (*sensu* Mann 1985). Urchins in this feeding mode are characterized by being exposed and non-solitary. In the laboratory less than 20 % of the feeding sea urchins fit this description (Fig. 5.3A). Most of these exposed, non-solitary sea urchins were large and had been starved prior to observation. They occurred predominantly in high density treatments without predators (Fig. 5.3B).

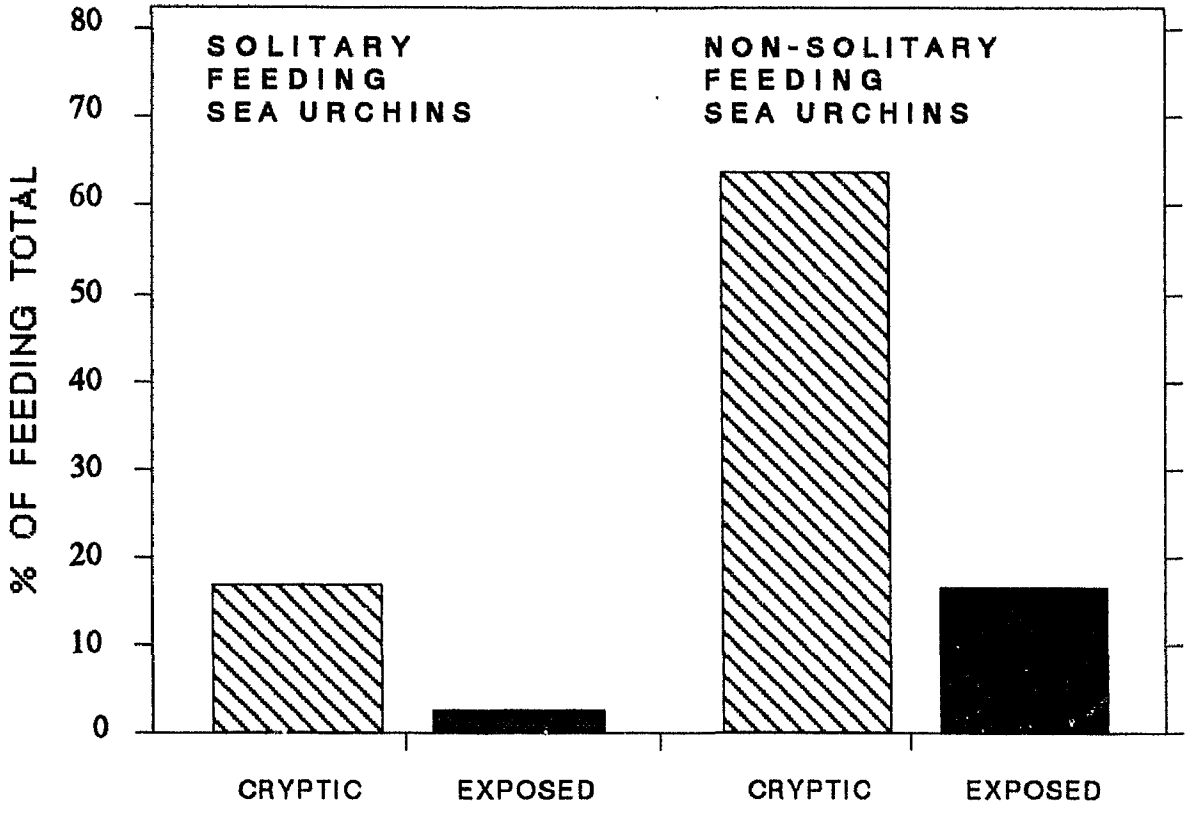

Fig. 5.3A DESTRUCTIVE FEEDING AGGREGATIONS IN THE LABORATORY. Total number of feeding sea urchins subdivided into groups of solitary/non-solitary and cryptic/exposed individuals.

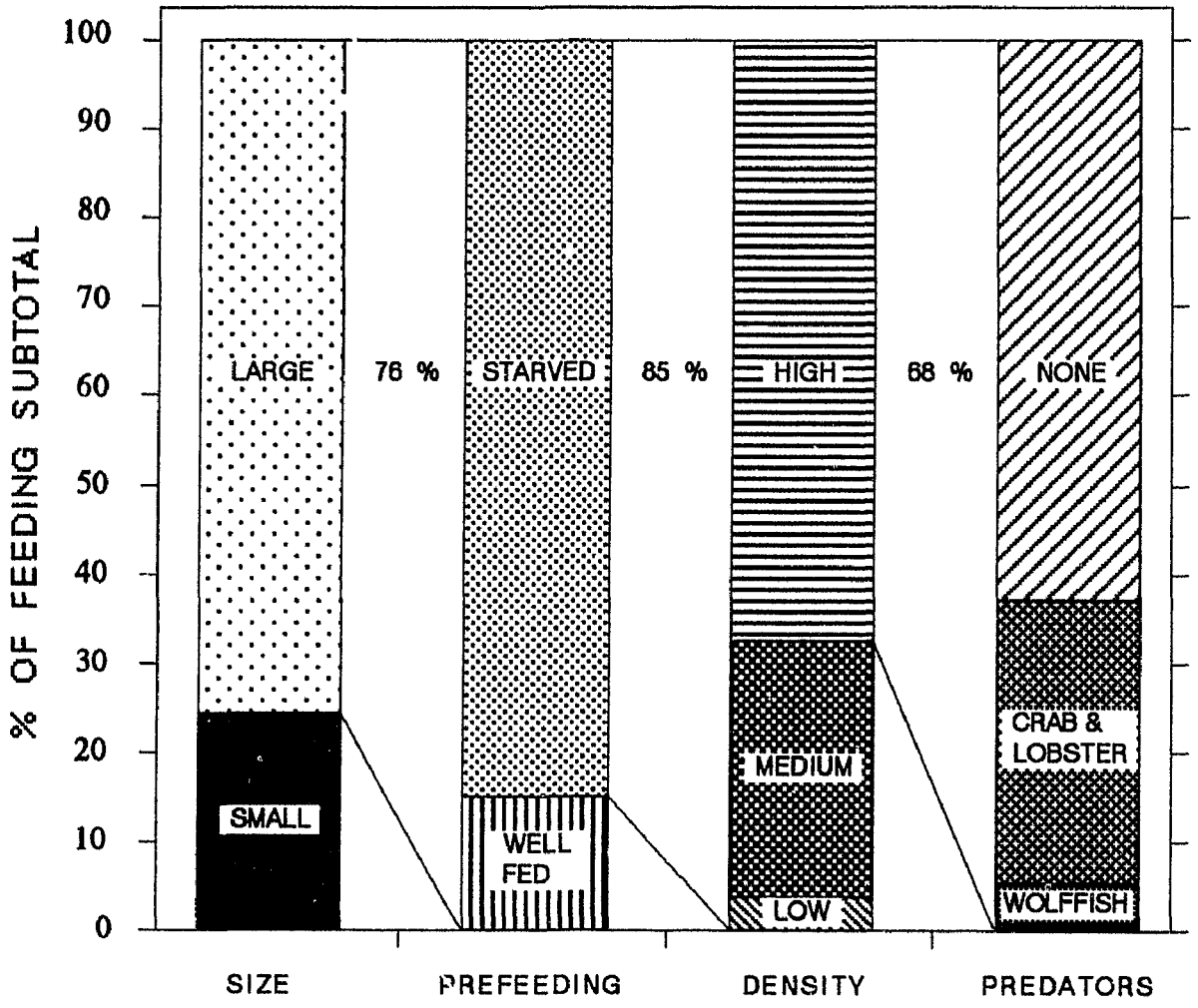

Fig. 5.3B DESTRUCTIVE FEEDING AGGREGATIONS IN THE LABORATORY. Total number of feeding, non-solitary, and exposed sea urchins are subdivided according to size in the leftmost column. Successive subdivisions of majority fractions are indicated by slanted lines and percentages.

5.3 Discussion

Prefeeding was the single most important determinant of the collective feeding behaviour of *S. droebachiensis*. This factor interacted significantly with season, size and predators. The magnitude of the prefeeding effect varied considerably at different levels of these variables, although the proportion of feeding starved urchins was consistently higher than the proportion of feeding well fed urchins. Prefeeding had similar effects on small and large urchins in the winter season but in the summer, starved large urchins had approximately twice the feeding activity of well fed large urchins, while only a minor prefeeding-related difference was evident for small urchins.

Increased feeding activity of large urchins in the summer might be interpreted as a post spawning phenomenon (Himmelman *et al.* 1983), or related to the seasonal increase in seawater temperature (Miller & Mann 1973). However, prefeeding, rather than gonadal cycle or seawater temperature, would still appear to be the major determining factor, as only starved large urchins exhibited increased feeding activity in the summer.

Prefeeding had profound effects on the sea urchins' feeding activity in the presence of predators. The proportion of feeding starved urchins decreased when decapod predators were present, but appeared unaltered in the presence of

wolffish. Well fed urchins however increased their feeding activity in the presence of predators, particularly wolffish.

Most of the feeding sea urchins were cryptic and non-solitary, presumably corresponding to a passive detritivore mode of feeding (*sensu* Mann 1985). Although less common, non-solitary exposed feeding, which presumably corresponds to an aggressive herbivore mode of feeding (*sensu* Mann 1985), did occur. Non-solitary, exposed feeding was most frequently observed in treatments with large, starved sea urchins at high density in the absence of predators.

CHAPTER 6 DISCUSSION OF BEHAVIOURAL ASPECTS OF OUTBREAK INITIATION

The formation of destructive feeding aggregations of *S. droebachiensis* is regarded as the proximate cause of kelp bed destruction (Mann 1977; Bernstein *et al.* 1983). It represents the transition from a typical kelp bed environment, where the urchins are presumably scarce, non-crowded, and cryptic, to a situation where the urchins are locally abundant, aggregated, and exposed. In this laboratory study I have investigated this transition process by quantifying the aggregation behaviour, microhabitat utilization and feeding behaviour of *S. droebachiensis* in response to changes in size, density, season, prefeeding, refuges, food, and predators.

My results suggest that large sea urchins have a basic tendency to aggregate in response to increasing population density (Table 6.1). This tendency was inhibited by the presence of wolffish, and to a lesser extent by the presence of refuges. Only when the urchins were small, or at low density, did they have random or non-crowded patterns of aggregation.

Microhabitat utilization of sea urchins in the laboratory was characterized by non-random spatial patterns. Urchins occurred most frequently in areas of locally increased microspatial heterogeneity, and were seldom found on featureless portions of the tank surface.

Small urchins were more cryptic than large urchins. This difference was related to the large urchins' lack of access to the narrow vertical grooves in the tank walls which constituted the small urchins' principal cryptic microhabitat (Section 4.4.1), and may therefore be regarded as a spurious result caused by experimental artifact. Consequently the results for small and large urchins are best assessed independently.

Large urchins were most exposed at high density, in the absence of refuges, food and predators (Table 6.1). Utilization of cryptic microhabitats by large urchins was related to availability, and increased when additional spatial heterogeneity in the form of kelp or claypipe refuges was introduced. The proportion of cryptic large urchins also decreased at lower urchin densities and in the presence of predators, particularly wolffish. The effect of predators was partly an indirect result of predatory reduction of urchin density, and partly a result of increased utilization of cryptic microhabitats, as indicated by significantly increased levels of refuge usage in the presence of predators.

The proportion of feeding urchins was highest when the the urchins were large and had been starved prior to experimentation. The feeding activities of large urchins increased in the summer season, and when refuges and decapod predators were absent.

Thus, the formation of destructive feeding aggregations, as described by high levels of aggregation, exposure and feeding, can apparently be mimicked in the laboratory by increasing the population density of starved, large *S. droebachiensis* in the absence of refuges and predators (Table 6.1). A similar conclusion was reached by examining the characteristics of non-solitary, exposed and feeding urchins (Section 5.2.4).

Table 6.1 Mimicking destructive feeding aggregations of *S. droebachiensis* in the laboratory. Factor levels which maximized aggregation, exposure and feeding activity are listed. Factor levels corresponding to major causal effects are capitalized, minor causal effects are in lowercase, and unimportant factors are indicated by dashes.

Experimental factor	Aggregation	Exposure	Feeding
Season	-	-	summer
Size	LARGE	LARGE	LARGE
Prefeeding	-	-	STARVED
Density	HIGH	high	-
Refuges	absent	ABSENT	absent
Food	-	NO KELP	
Predators	NO WOLFFISH	NO WOLFFISH	
	decapods	no decapods	no decapods

Apparent successful mimicry of destructive feeding aggregations in the laboratory does not establish a functional correspondence between the artificial and natural phenomena, nor does it constitute proof that the formation of such aggregations are regulated by similar mechanisms under field and laboratory conditions. It does, however, provide a basis for comparison of results from field and laboratory.

It has been inferred from field experiments that decapod predators facilitate formation of destructive feeding aggregations in high density populations of *S. droebachiensis* (Bernstein *et al.* 1983; Mann 1985), but this inference was only partially supported by data from the present study. The presence of decapod predators appeared to facilitate formation of destructive feeding aggregations in the winter by making large urchins more aggregated and less cryptic. However, in the summer, the decapod predators made large urchins less active feeders and more cryptic. The equivocal nature of my results inspired scrutiny of the original publication (Bernstein *et al.* 1983), which revealed that the alleged role of decapod predators was based on uncorrected significance levels in a multifactorial analysis of variance (Section 3.4.2).

It has also been inferred from field experiments that decapod predators do not elicit formation of aggregations by *S. droebachiensis* (Vadas *et al.* 1986). These inferences,

however, were not substantiated by a reanalysis of the original data (Section 3.4.2).

Contrary to postulates by Vadas *et al.* (1986) the presence of kelp, while obviously necessary for the formation of destructive feeding aggregations, had little effect on the aggregation behaviour of sea urchins in the laboratory. These authors, however, based their argument, that sea urchin aggregations form only in the presence of food, on a narrow definition of the term aggregation which excluded non-feeding aggregations.

Field observations suggest that destructive grazing of kelp proceeds in narrow transition zones between intact kelp beds and adjacent barren grounds. The width of such transition zones varies from concentrated grazing fronts less than one meter wide, to infiltration areas several meters wide (Breen & Mann 1976a; Breen 1980; Wharton & Mann 1981; Bernstein & al. 1981; Hagen 1983). Sea urchin densities inside kelp beds undergoing destruction are, as a rule, extremely low [Miller & Mann (1973) reexamined by Bernstein & Mann (1982); Breen & Mann 1976a; Hagen 1983], and the large urchins in the transition zones are probably migrants from high density populations of starved urchins in adjacent barren areas (Lang & Mann 1976). It would therefore seem that conditions resembling an urchin-dominated barren ground must be present in the vicinity of a kelp bed prior to the initial formation of destructive feeding aggregations, *i.e.* a habitat

patch unsuitable for kelp but with a high density of starved large urchins,.

While high density populations of starved large urchins are conclusively capable of aggregating along the edges of kelp beds in sufficient numbers to perpetuate a process of destructive grazing, there is no direct evidence to suggest that the initial formation of destructive feeding aggregations occurs spontaneously inside a kelp bed. Furthermore, the notion that destructive grazing is initiated by resident kelp bed populations of sea urchins (*e.g.* Mann 1982; Bernstein *et al.* 1983) would seem to be negated by results from a field experiment where transplantation of up to 400 urchins to the interior of a kelp bed failed to induce formation of destructive feeding aggregations (Breen 1974; Breen & Mann 1976a). The possibility outlined above, that a structural dichotomy between low urchin density kelp beds and adjacent urchin-dominated habitats must exist prior to the onset of destructive grazing, can therefore not be excluded at present.

This dual-habitat hypothesis of outbreak initiation is consistent with the observed urchin behaviour in the laboratory. My results suggest that the formation of destructive feeding aggregations is determined by two opposing influences; a basic intrinsic tendency towards increased aggregation, exposure and feeding activity in response to large body size, high population density, and

starvation, *i.e.* conditions resembling an urchin-dominated barren ground; and a secondary environmentally determined trend towards random patterns of aggregation, cryptic lifestyle and passive detritivorous feeding. The single most important extrinsic factor is the presence of Atlantic wolffish, but increased microspatial heterogeneity, a prehistory of plentiful food supply, the presence of decapod predators, and winter conditions also decreased the basic tendency to form exposed feeding aggregations (Table 6.1).

Studies of other strongylocentrotid species have shown that the presence of high density urchin populations in the vicinity of kelp beds is a labile situation where destructive grazing may be initiated or terminated by fluctuations in the supply of non-attached food (Mattison *et al.* 1977; Duggins 1981; Dean *et al.* 1984; Harrold & Reed 1985). However, this kind of environmentally controlled indeterminacy exists only at intermediate urchin densities. Destructive grazing is impossible at low urchin densities and unavoidable at high urchin densities. The factors determining the numerical abundance of *S. droebachiensis* are therefore of ultimate importance for the persistence of either kelp beds or urchin-dominated barren grounds. These factors will be addressed next.

PART II

PREDATOR CONTROL OF SEA URCHIN POPULATIONS: NUMERICAL ASPECTS OF OUTBREAK PREVENTION AND TERMINATION

The concept of predator control of sea urchin populations is closely linked with the predator hypothesis of Mann & Breen (1972) which states that reduction of predator densities may trigger explosive growth of sea urchin populations thereby leading to destructive grazing of kelp beds. Breen (1974) formalized this scenario by constructing a simulation model for the effects of predators on sea urchin populations. In Breen's model, predator control is defined in terms of predator biomass, sea urchin biomass, and sea urchin recruitment. Sea urchins in the model are "controlled" as long as their biomass is less than a certain value derived from field observations at the edge of kelp beds undergoing destruction. A lower limit for predator control of the urchins is set at the recruitment level required to initiate kelp bed destruction in the absence of predators, and an upper limit is set at the recruitment level required to initiate kelp bed destruction at a fixed level of predation. Thus, at a given level of predation the modelled sea urchin population is controlled as long as urchin recruitment is contained inside a specified interval.

The minimum urchin biomass required to destroy kelp, lies at the core of Breen's (1974) definition of predator control. As mentioned above, the estimates of this critical sea urchin biomass were obtained from measurements at the edge of kelp beds in a zone of locally increased sea urchin density where destructive grazing was actually taking place. Breen's approach is, therefore, based on post fact observation of urchin biomass in established destructive feeding aggregations, rather than based on estimates of the sea urchin biomass required for the initial formation of such aggregations. Later studies have instead attempted to estimate urchin density prior to the onset of destructive grazing by measuring sea urchin density in recently created barren grounds (Mann 1977; Wharton & Mann 1981).

Bernstein *et al.* (1981, 1983) pointed out that the critical sea urchin density required to initiate formation of destructive feeding aggregations was not fixed, but depended on the sea urchins behavioural responses to external factors including the presence of predators. Hence, definitions of predator control which are based on a critical sea urchin density threshold should take into consideration that this threshold is not necessarily constant for different times and places.

The term predator control can also be used in another context, *i.e.* with reference to the level of predation that would be required to terminate a sea urchin dominated barren

condition (Bernstein *et al.* 1981). It is critical to differentiate between these two kinds of predator control in order to prevent or eliminate confusion. For example, confusion results when Miller (1985a), in a reappraisal of the predator hypothesis, fails to distinguish between the two kinds of predator control; and when criticized in terms of prevention of destructive grazing (Keats 1986), retorts in terms of termination of barren grounds (Miller 1986).

In this section I present new estimates of predation rates and examine the numerical responses of predators to changes in sea urchin density (Chapter 7). This information is then incorporated into a new simulation model (Chapter 8), together with pertinent results on the sea urchins' behavioural responses (Section 1). The model is then used to analyse various aspects of predator control including: outbreak prevention, in response to steady recruitment conditions or recruitment pulses; and outbreak termination.

CHAPTER 7 PREDATION AND DISEASE-RELATED MORBIDITY

7.1 Introduction

The original predator hypothesis, that the recent large-scale outbreak of *S. droebachiensis* in Eastern Canada was a result of reduced predation on sea urchins following depletion of local lobster stocks, has been much debated. (Mann & Breen 1972; Breen & Mann 1976b; Pringle *et al.* 1982; Wharton & Mann 1981; Miller 1985a; Elner & Campbell 1987; Breen 1987). As unequivocal testing of this hypothesis in the field is not practically feasible (Breen 1980; Mann 1982), evaluation of the numerical impact of lobster predation on sea urchin populations has been limited to indirect testing by extrapolation from estimated predation rates (Breen 1974; Breen & Mann 1976b; Evans & Mann 1977; Miller 1985a; Elner & Campbell 1987).

Estimating predation rates is complicated by the fact that the predation pressure on sea urchins in nature fluctuates in response to a number of variables including availability of refuges and alternative prey, urchin density, seawater temperature, and the relative body sizes of the sea urchins and their predators (Breen 1974; Evans & Mann 1977; Witman 1985). These variables must be quantified before the robustness of current predation rate estimates can be assessed.

Irrespective of the accuracy of predation rate estimates, the qualitative impact of predation on sea urchin populations cannot be predicted with certainty if a keystone predator effect (*sensu* Paine 1969) is present (Mann & Breen 1972). The only way a keystone predator effect can be detected is through controlled density manipulations in the field. This has yet to be done for sea urchin predators in the North Atlantic. Therefore, in the absence of conclusive evidence to the contrary (Miller 1985a; Elner & Campbell 1987), the original hypothesis that the American lobster, *Homarus americanus*, is a keystone predator of S. *droebachiensis* in Nova Scotia has yet to be refuted (Mann & Breen 1972; Breen 1987). Further estimation of predation rates on sea urchins may still provide useful information by yielding more robust estimates and aiding in the formulation of alternative hypotheses, but estimation cannot substitute for rigorous field experiments.

In this chapter I analyse predation and disease-related morbidity data from the multifactorial laboratory experiment described in Chapter 2. I present evidence in support of Keats (1986) proposition of a functional predator response to increased urchin abundance (Breen 1974), and analyse my results in comparison with other estimates of predation rates. The critical temperature hypothesis of Scheibling and Stephenson (1984) is also considered.

7.2 Methods

Data on predation in the laboratory were recorded as the number of urchins consumed per tankday. As the predation data could not be transformed to meet the assumptions of ANOVA, non-parametric and graphic statistical methods were used as indicated in the appropriate tables.

Hypotheses tested included: comparisons between the two predator treatments for all urchins combined, and separately for large and small urchins; and all null hypotheses of the form, size × predator × X, where X ∈ {season, prefeeding, density, food, refuges, temperature}. The non-parametric approach used precluded exact adjustment of test results to compensate for the total number of individual tests performed. Thus, the true possibility of making type I errors may be higher than indicated by the reported significance levels.

Type 2 and 3 predator functional response curves were expressed in the "Holling form" (May 1981, Table 5.1). They were fitted using the SYSTAT statistical program. Only the shape of the curves was considered. No attempt was made to interpret the biological meaning of the response curve parameters.

Decapod predator treatments contained one rock crab and one lobster per tank. Neither predator had the movement of its claws impeded. No attempt was made to formally isolate

the effects of the two decapod predators on the experimental sea urchin population.

Only urchins that appeared healthy and mobile were used in the experiment. At the end of each tankday the number of immobile urchins with a morbid appearance was recorded.

7.3 Results

7.3.1 Predation

7.3.1.1 Effects of predators and urchin size

Decapod predators and Atlantic wolffish had significantly different patterns of predation (Table 7.1). For small urchins, the mean diurnal predation rate was about 1 urchin per tankday for both decapod predators and wolffish, but the predators differed greatly in their consumption of large urchins (Fig. 7.1; Tables 7.1, 7.2). The decapod predators consumed only 0.67 large urchins per tankday, while the wolffish consumed 2.18 large urchins per tankday (Table 7.2).

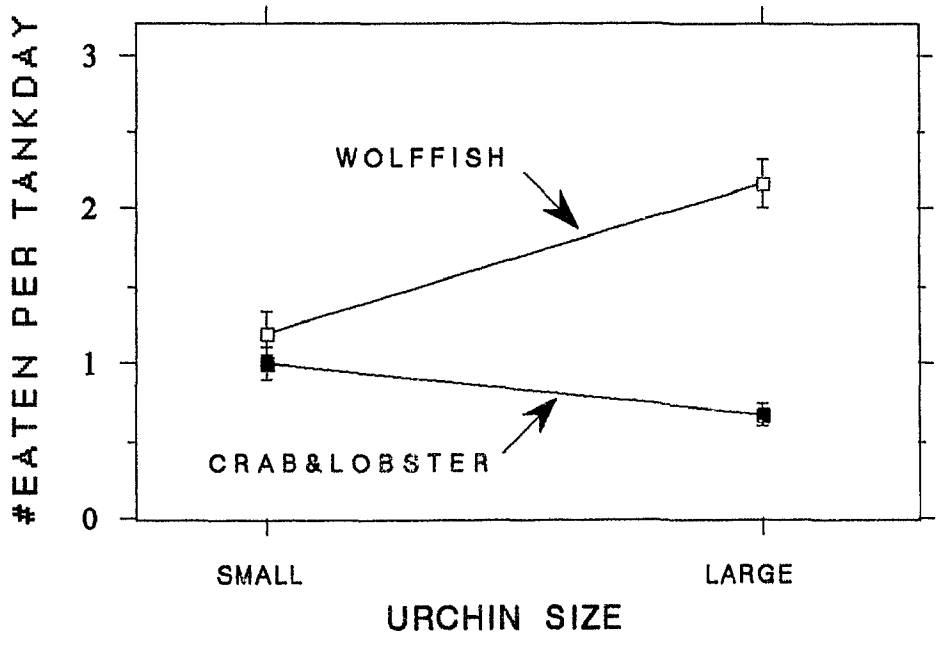

Fig. 7.1 MEAN NUMBER OF SMALL AND LARGE *S. DROEBACHIENSIS* EATEN BY DECAPOD PREDATORS AND ATLANTIC WOLFFISH. Error bars represent standard errors of the means.

Table 7.1 Effects of predators and sea urchin size on diurnal predation rates.

Effect	#Eaten per tankday	Test
Null hypothesis	P - value	
Predators		
H_0: crab & lobster = wolffish	0.013	Kolmogorov-Smirnov
Predators × Size		
Crab & lobster:		
H_0: small = large	0.3486	Kolmogorov-Smirnov
Wolffish:		
H_0: small = large	0.0191	Kolmogorov-Smirnov

Table 7.2 Mean number of small and large sea urchins eaten per tankday by decapod predators and Atlantic wolffish. S.E. - standard error of the mean.

Treatment	#Urchins	#Eaten	%Eaten	#Tankdays	Mean #eaten per tankday	S.E.
Crab & lobster						
Small sea urchins	4195	253	6,03	251	1.008	0.1022
Large sea urchins	4215	168	3.99	251	0.6693	0.074
Subtotal	8410	421	5.01	502	0.8386	0.0635
Wolffish						
Small sea urchins	4140	301	7,27	250	1.204	0.142
Large sea urchins	4250	583	13.72	268	2.1754	0.1584
Subtotal	8390	884	10.54	518	1.7066	0.1088
Grand total	16800	1305	7.77	1020	1.2794	0.0649

7.3.1.2 Effects of urchin density

The mean number of sea urchins eaten per tankday increased significantly with increasing urchin density (Fig. 7.2; Tables 7.3, 7.4). This response was strongest for wolffish consumption of large urchins which increased from 1.12 urchins per tank-day at low density to 3.54 urchins per tank day at high density (Table 7.4).

The mean proportion of the available sea urchins that was eaten dropped by approximately 50 % when sea urchin density was increased from 5 to 30 animals per tank in all predator ×

urchin size combinations except decapod predation on small urchins (Tables 7.3, 7.4; Fig. 7.3). Here the mean proportion of sea urchins that were eaten increased by almost 1 % between medium and high density after an initial decrease of approximately 2.5 % between low and medium density (Table 7.4; Fig 7.3).

Experimental factors other than urchin size and population density had no significant effects on predation rates of small and large sea urchins by decapod predators and Atlantic wolffish when individually tested by Kolmogorov-Smirnov tests.

Table 7.3 Effects of sea urchin density on diurnal predation rates. P - values are corrected for ties.

Effect	#Eaten per tankday P - value	Test
Crab & lobster		
Small sea urchins:		
H_0: low = medium = high	0.0001	Kruskal Wallis
Large sea urchins		
H_0: low = medium = high	0.002	Kruskal-Wallis
Wolffish		
Small sea urchins:		
H_0: low = medium = high	0.0001	Kruskal Wallis
Large sea urchins		
H_0: low = medium = high	0.0001	Kruskal-Wallis

Table 7.4 Mean number of small and large sea urchins eaten per tankday at different densities by decapod predators and Atlantic wolffish. S.E. - standard error of the mean.

Treatment	#Urchins	#Eaten	%Eaten	#Tankdays	Mean #eaten per tankday	S.E.
Crab & lobster						
Small sea urchins:						
Low density	415	32	7.71	83	0.3855	0.0782
Medium density	1260	66	5.24	84	0.7857	0.1428
High density	2520	155	6.15	84	1.8452	0.2325
Large sea urchins:						
Low density	420	29	6.91	84	0.3452	0.0872
Medium density	1215	56	4.61	81	0.6914	0.0988
High density	2580	83	3.22	86	0.9651	0.1699
Wolffish						
Small sea urchins:						
Low density	420	47	11.19	84	0.5595	0.1102
Medium density	1260	96	7.62	84	1.1429	0.2478
High density	2460	158	6.42	82	1.9268	0.3161
Large sea urchins:						
Low density	500	112	22.40	100	1.1200	0.1486
Medium density	1290	181	14.03	86	2.1047	0.2498
High density	2460	290	11.79	82	3.5366	0.3591

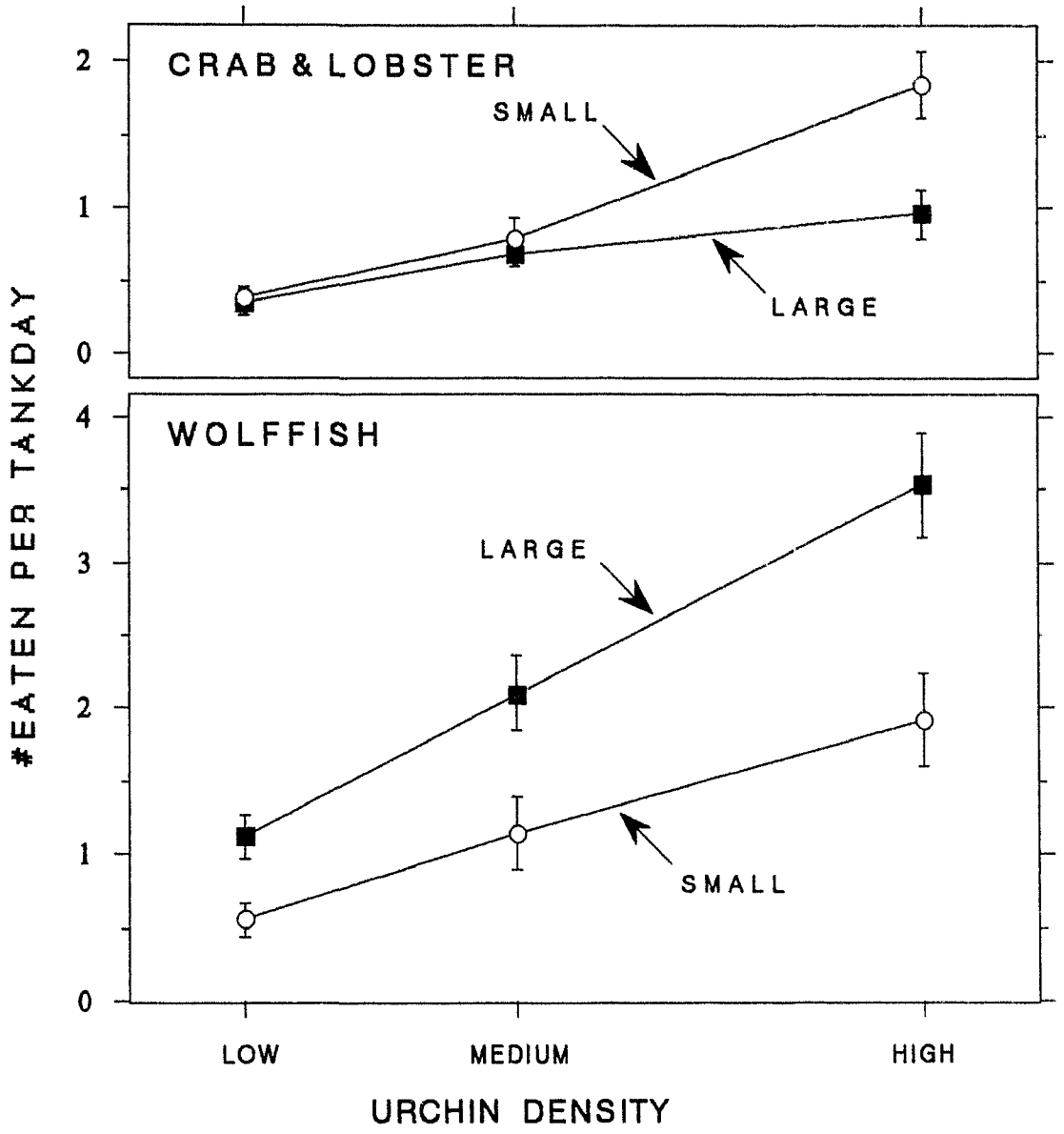

Fig. 7.2 MEAN NUMBER OF SMALL AND LARGE *S. DROEBACHIENSIS* EATEN BY DECAPOD PREDATORS AND ATLANTIC WOLFFISH AT DIFFERENT SEA URCHIN DENSITIES. Error bars represent standard errors of the means.

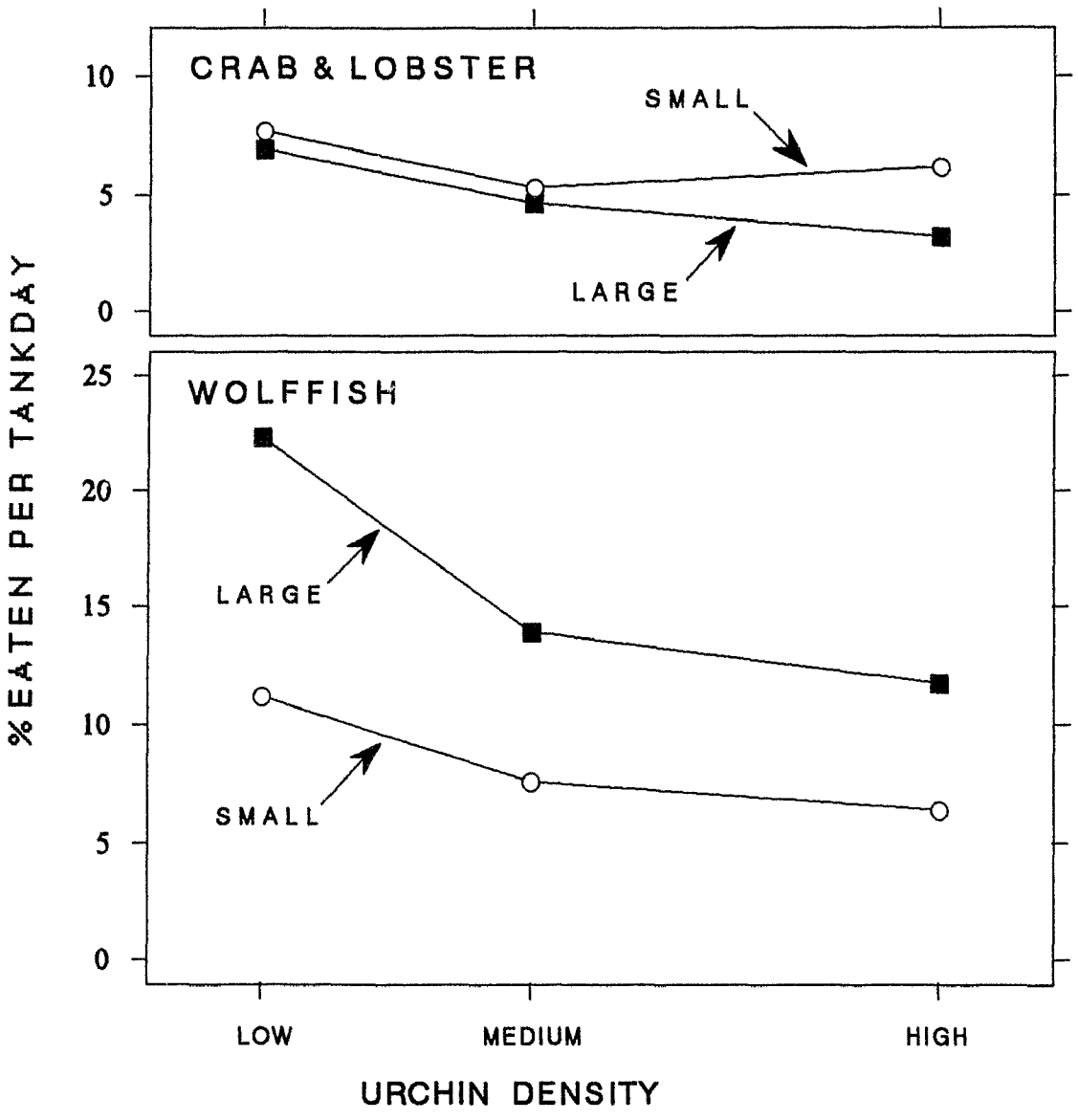

Fig. 7.3 PERCENTAGE SMALL AND LARGE *S. DROEBACHIENSIS* EATEN BY DECAPOD PREDATORS AND ATLANTIC WOLFFISH AT DIFFERENT SEA URCHIN DENSITIES.

7.3.1.3 Crab mortality

The decapod predator treatments consisted of a total of 502 tankdays during which 421 sea urchins and 29 rock crabs were consumed (Table 7.5). However, the proportional consumption of available prey was almost identical; 5.78 % of the available crabs were eaten compared with 5.01 % of the available urchins (Table 7.6); and consumption of crabs did not change significantly when the relative abundance of urchins and crabs was altered by changing sea urchin density from 5:1 to 30:1 (Table 7.6; Chi-square test, P = 0.4679).

The mean number of sea urchins eaten per tankday was approximately twice as high in replicates where the crab had not been eaten (Fig. 7.4, Table 7.5).

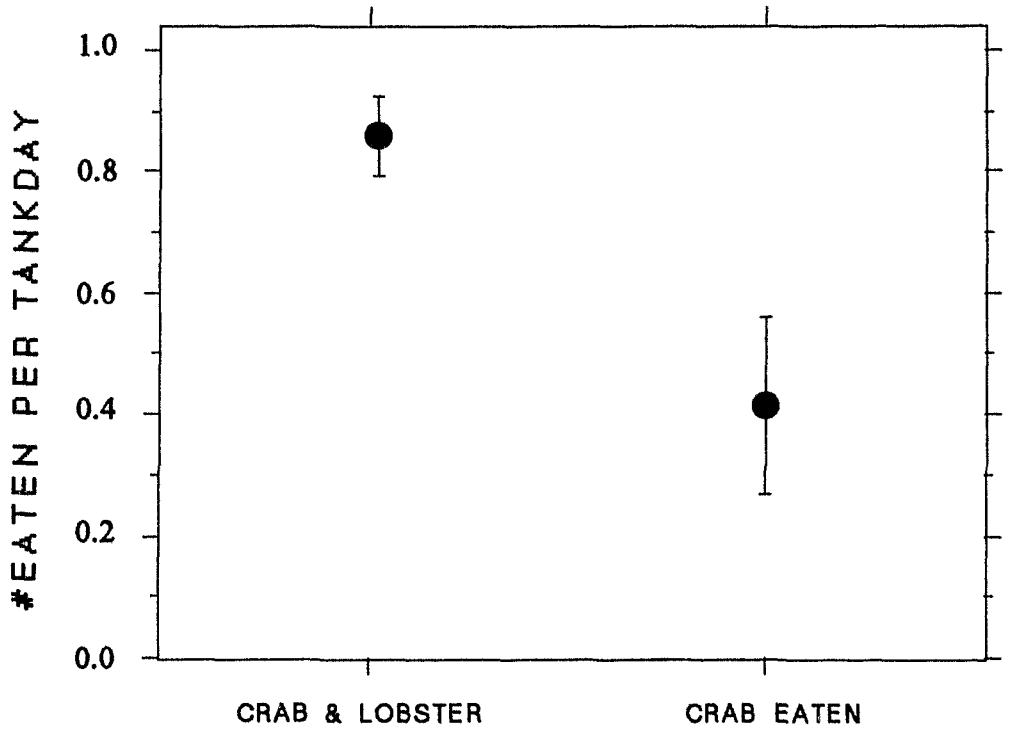

Fig. 7.4 MEAN PREDATION RATES OF *S. DROEBACHIENSIS* BY DECAPOD PREDATORS, AND BY LOBSTERS WHICH HAD ALSO EATEN THE ROCK CRAB. Error bars represent standard errors of the means.

Table 7.5 Predation of sea urchins by decapod predators, and by lobsters which had also eaten the rock crab. S.E. - standard error of the mean.

Treatment	#Urchins	Consumption of urchins #	%	#Tankdays	Mean #urchins eaten per tankday	S.E.
Crab & lobster	7970	409	5.13	472	0.867	0.0667
Crab eaten	440	12	2.73	29	0.414	0.1448
Total	8410	421	5.01	502	0.8386	0.0635

Table 7.6 Predation of sea urchins and rock crabs by lobsters. Total consumption of sea urchins and crabs is listed as numbers eaten (#), and as percentages of available prey of the respective species that were eaten (%).

Urchin density	Numerical ratio of urchins:crabs available	Consumption of urchins #	%	Consumption of crabs #	%	Numerical ratio of urchins:crabs eaten
Low	5:1	61	7.31	10	5.99	6.10:1
Medium	15:1	122	4.93	12	7.27	10.17:1
High	30:1	238	4.67	7	4.14	34.00:1
Total	16.75:1	421	5.01	29	5.78	14.52:1

7.3.1.4 Effects of temperature

Wolffish predation on large sea urchins was negatively correlated with seawater temperature (Fig. 7.6; $P < 0.01$ Spearman & Kendall rank correlation coefficients). There was no significant relationship between seawater temperature and predation by wolffish on small sea urchins, or by decapod predators on either sizegroup of urchins (Figs 7.5, 7.6).

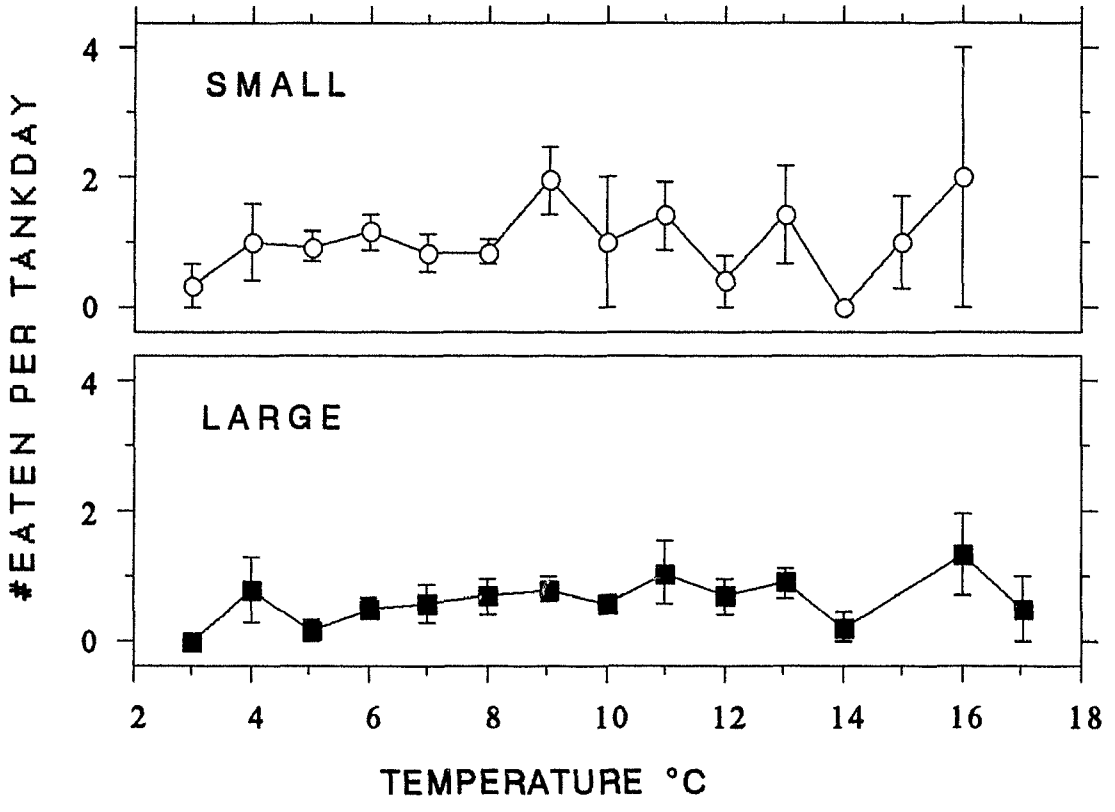

Fig. 7.5 RELATIONSHIP BETWEEN SEAWATER TEMPERATURE AND SEA URCHIN PREDATION BY DECAPOD PREDATORS. Mean number of sea urchins eaten per tankday is plotted separately for small and large urchins. Error bars represent standard errors of the means.

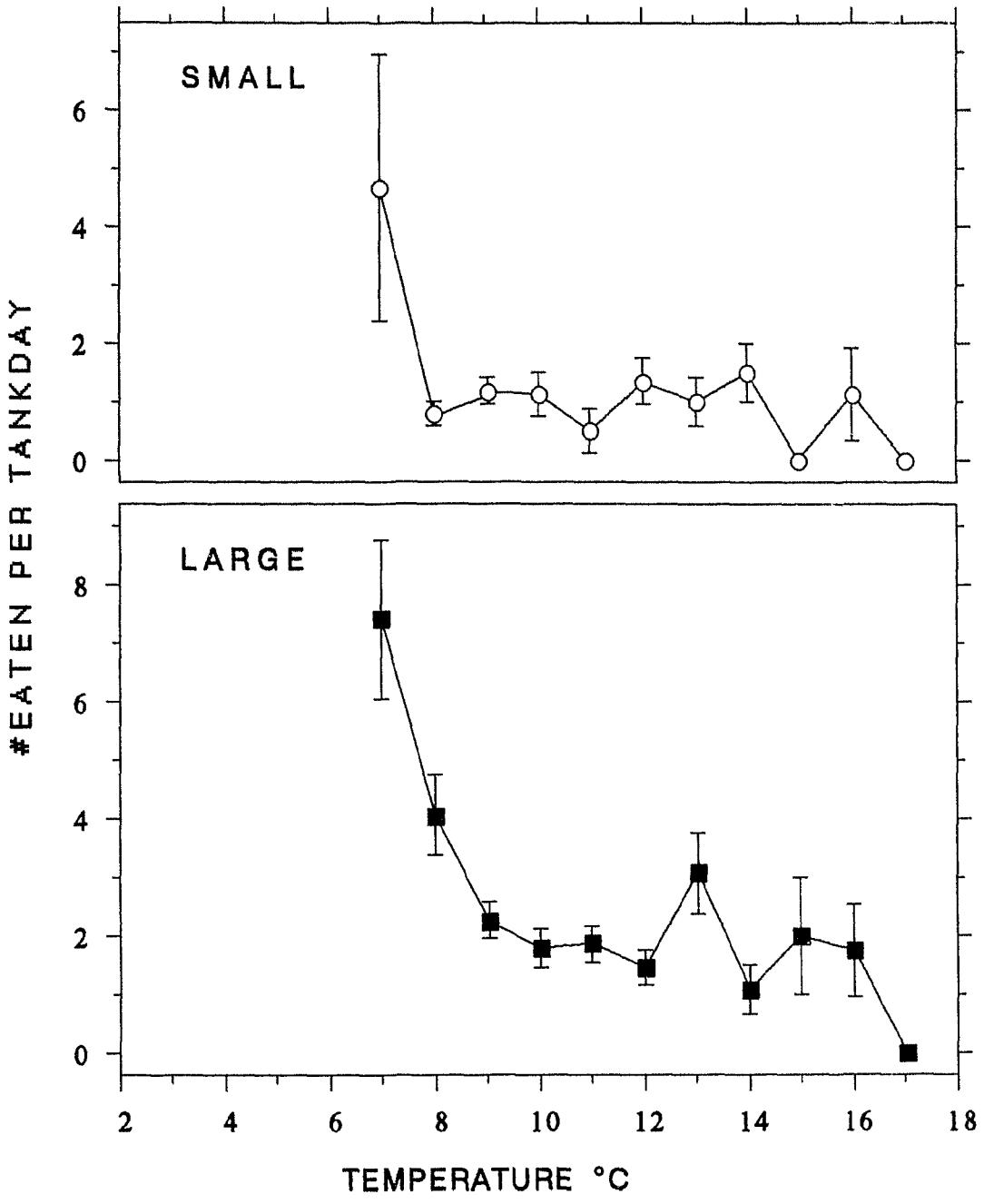

Fig. 7.6 RELATIONSHIP BETWEEN SEAWATER TEMPERATURE AND SEA URCHIN PREDATION BY ATLANTIC WOLFFISH. Mean number of sea urchins eaten per tankday is plotted separately for small and large urchins. Error bars represent standard errors of the means.

7.3.2 Disease-related morbidity

Total disease-related morbidity of *S. droebachiensis* was approximately 1 % of the experimental sea urchin population, with more than 90 % of the observed morbidity taking place at high temperatures (≥ 9 °C; Table 7.8). However, when the two sizegroups of sea urchins were tested separately the effect of temperature remained significant only for the large urchins (Table 7.7; Fig. 7.7 & Table 7.8). Mean diurnal morbidity-rates were close to zero at temperatures below 8 °C, higher above 9°C, and peaked at 16°C (Fig. 7.8).

Morbid urchins exhibited symptoms of amoeboid disease, *Paramoeba invadens* Jones (1985), rather than bacterial disease (Jones & Scheibling 1985).

Table 7.7 Effects of sea urchin size and seawater temperature on the diurnal morbidity rates *S. droebachiensis*. Morbidities at low (< 9 °C) and high (≥ 9 °C) temperatures are compared.

Effect	%Morbidity per tankday	Test
	P - value	
Small sea urchins		
H_0: low = high	0.2245	Kolmogorov-Smirnov
Large sea urchins		
H_0: low = high	0.0267	Kolmogorov-Smirnov
Total		
H_0: low = high	0.0073	Kolmogorov-Smirnov

Table 7.8 Diurnal disease-related morbidity rates of small and large *S. droebachiensis*. S.E. - standard error of the mean.

Temperature Size	#Urchins	Morbid urchins #	%	#Tankdays	Mean % morbidity per tankday	S.E.
Low temperature (< 9°C)						
Small	6835	14	0.21	410	0.31	0.01
Large	3370	1	0.03	187	0.02	0.02
Subtotal	10205	15	0.15	597	0.22	0.07
High temperature (≥ 9°C)						
Small	5615	52	0.8	341	0.95	0.17
Large	9110	183	2.01	573	2.12	0.25
Subtotal	14725	235	1.6	914	1.68	0.17
Total	24930	250	1.00	1511	1.10	0.11

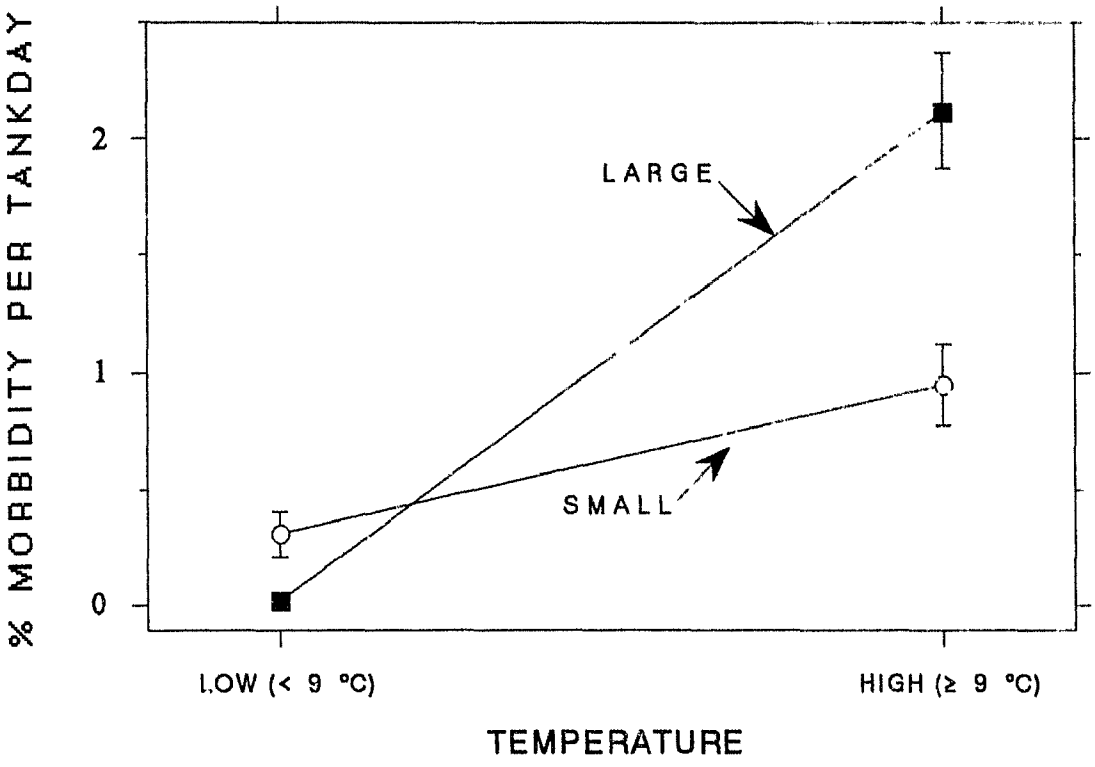

Fig. 7.7 MEAN % DISEASE-RELATED MORBIDITY PER TANKDAY OF SMALL AND LARGE *S. DROEBACHIENSIS* AT LOW AND HIGH TEMPERATURES. Error bars represent standard errors of the means.

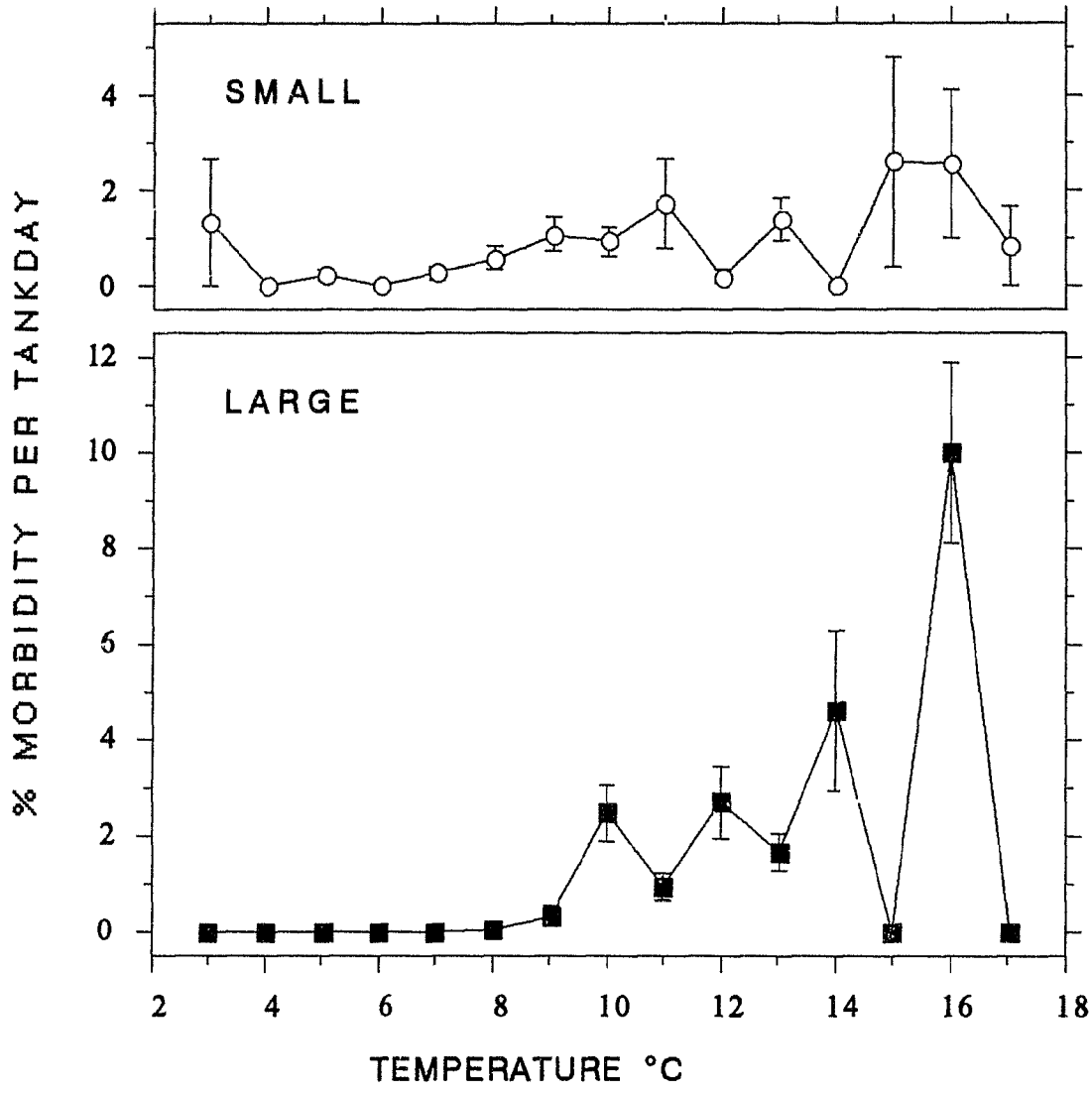

Fig. 7.8 RELATIONSHIP BETWEEN SEAWATER TEMPERATURE AND DISEASE-RELATED MORBIDITY OF SMALL AND LARGE *S. DROEBACHIENSIS*. Error bars represent standard errors of the means. (*NB* Vertical scale differs from Fig. 7.7.)

7.4 Discussion

7.4.1 Functional predator responses

In this study both decapod predators and Atlantic wolffish exhibited functional responses to increasing sea urchin abundance (*sensu* Holling 1959). That is, the number of successful attacks on the sea urchins increased in response to increases in their density. Functional responses are also evident in the data from Breen (1974) and Evans & Mann (1977) (Fig. 7.9).

Miller (1985a), however, attempted to assess the numerical impact of lobster predation on populations of *S. droebachiensis* by calculating a flat average predation rate irrespective of urchin density. Keats (1986) questioned the lack of attention given to numerical responses in Miller's (1985a) review and noted that "... lobster predation on urchins as calculated by Miller is meaningless in the context within which it has been applied.".

Functional responses are commonly classified in three distinct categories according to the shape of the curve that arises when the number of prey killed is plotted against the number of available prey (Holling 1959). In a Type 1 functional response the predator eats a constant proportion of the available prey until the prey density reaches a certain limit beyond which the total consumption of prey remains constant. The resulting curve is a straight line

approach to a horizontal line which represents the predators maximum consumption capacity. Breen (1974) implied that lobster predation on *S. droebachiensis*, in his simulation model, could be described as a Type 1 functional response. However, inspection of a plot of Breen's (1974) data for lobster predation reveals that the proportion of urchins eaten is not constant, but decreases when sea urchin density increases (Fig. 7.9). The pattern is therefore inconsistent with a Type 1 functional response.

A Type 2 functional response is characterized by a curvilinear asymptotic approach to a maximum feeding capacity. In this response the proportion of prey killed is a strictly decreasing function of available prey density. My data for wolffish, and for decapod predation on large sea urchins, are consistent with a Type 2 functional response. Breen's (1974) data for lobster predation are also consistent with a Type 2 functional response (Fig. 7.9).

A Type 3 functional response has a sigmoid response curve. The proportion of prey killed decreases asymptotically after an initial increase, thus producing a characteristically humped plot. The percentage of small sea urchins in this study that were eaten by decapod predators decreased, and then increased, as sea urchin density increased from low to medium to high. This pattern is indicative of a Type 3 functional response. Data on lobster

predation of large sea urchins from Evans & Mann (1977) also clearly indicate a Type 3 functional response (Fig. 7.9).

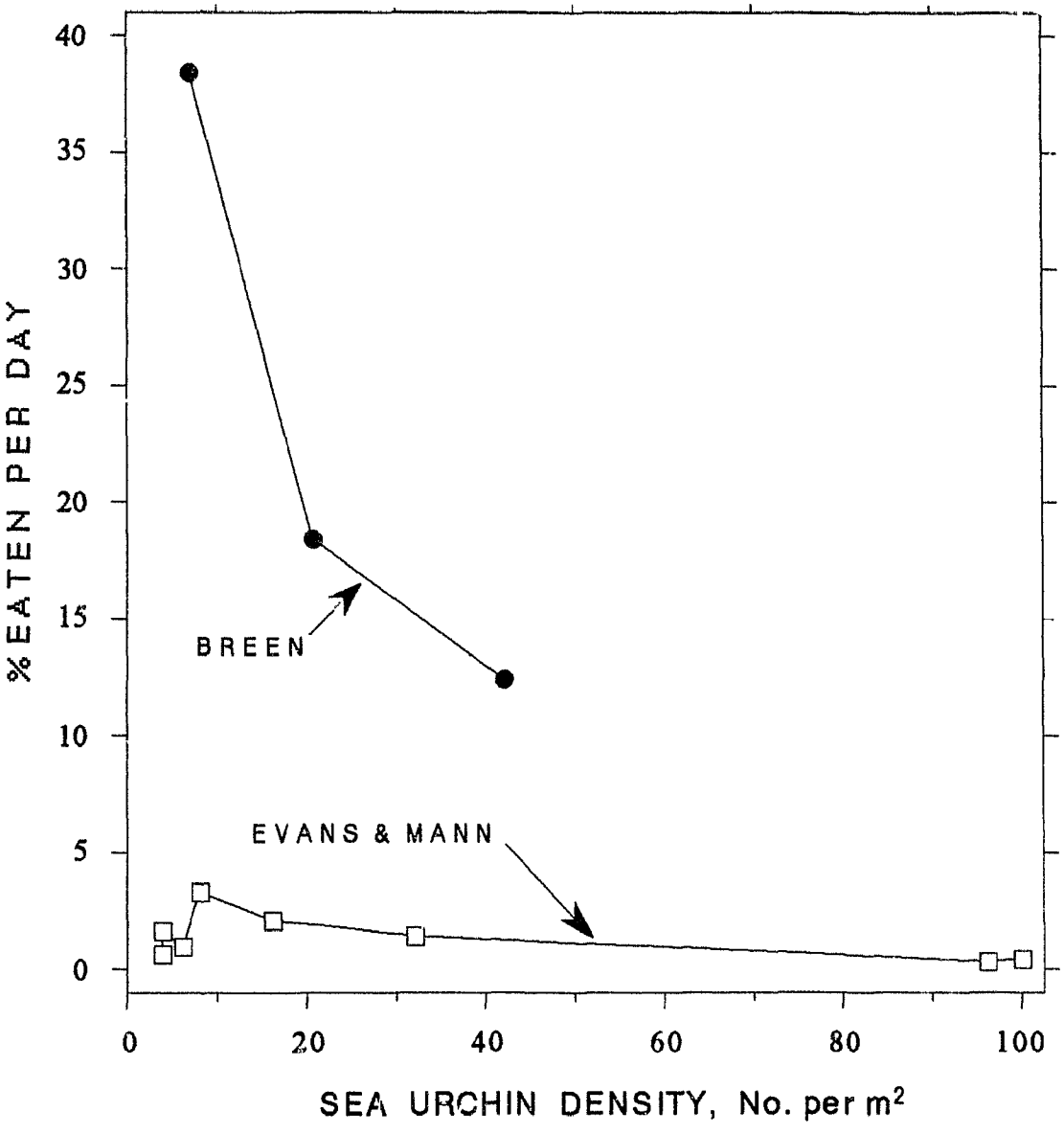

Fig. 7.9 RELATIONSHIP BETWEEN SEA URCHIN DENSITY AND PREDATION BY LOBSTERS. Sea urchin density is plotted against the percentage of the available sea urchins that were eaten per lobster per day. Key to symbols: ● Breen (1974, experiment 3); □ Evans & Mann (1977). Units on horizontal axis are number of individuals per square meter.

In Fig 7.10B, Type 3 functional response curves are successfully fitted to my own data on decapod predation of small and large urchins, and to data from Breen (1974) and Evans & Mann (1977). Fig. 7.10A illustrates an attempt to fit Type 2 functional response curves to the same datasets. As the Type 2 curve fitting procedure did not converge for the data on small urchins, no curve is drawn for this dataset. The remaining datasets appear to be reasonably well described by either type functional response curve (Figs 7.10A, 7.10B).

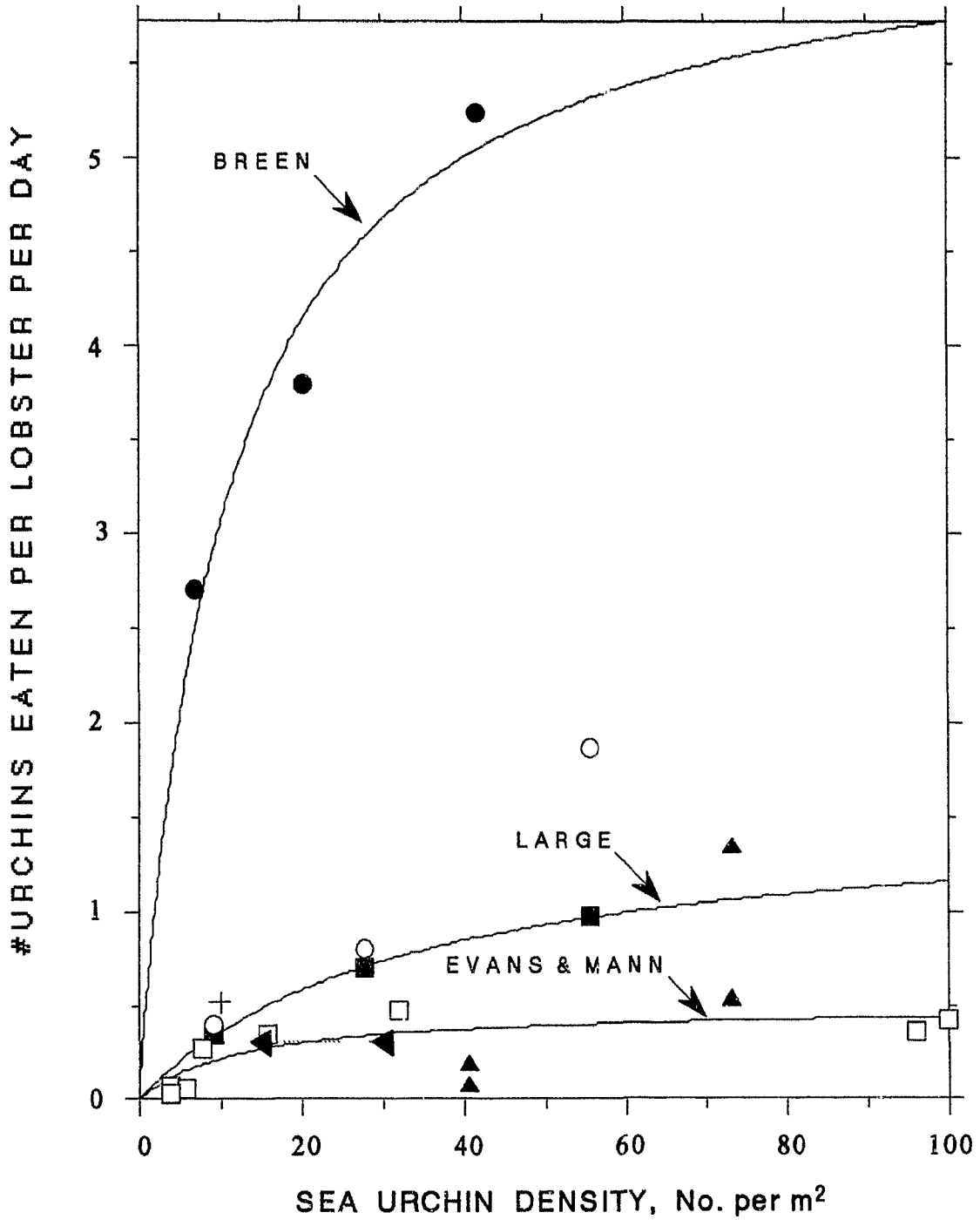

Fig. 7.10A RELATIONSHIP BETWEEN SEA URCHIN DENSITY AND LOBSTER PREDATION INTERPRETED AS TYPE 2 FUNCTIONAL RESPONSES. Key to symbols: ● Breen (1974, experiment 3); ○ small and ■ large sea urchins (Table 7.4); □ Evans & Mann (1977); + Breen (1974, experiment 1). Plausible intervals for observations from ◀ Himmelman & Steele (1971) and ▲ Elner (1980) are indicated by dotted lines (Appendix 1).

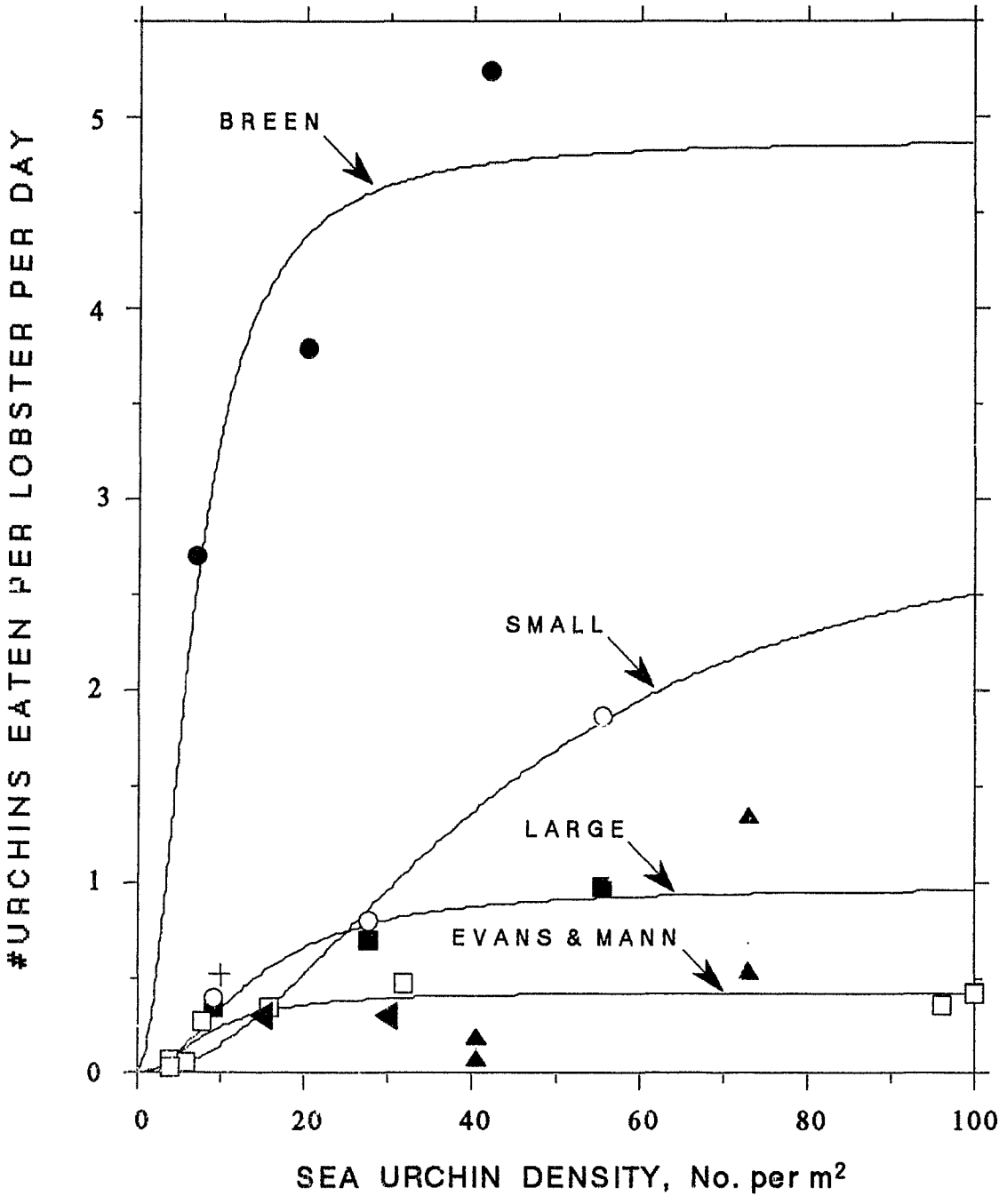

Fig. 7.10B RELATIONSHIP BETWEEN SEA URCHIN DENSITY AND LOBSTER PREDATION INTERPRETED AS TYPE 3 FUNCTIONAL RESPONSES. Key to symbols: ● Breen (1974, experiment 3); ○ small and ■ large sea urchins (Table 7.4); □ Evans & Mann (1977); + Breen (1974, experiment 1). Plausible intervals for observations from ◀ Himmelman & Steele (1971) and ▲ Elner (1980) are indicated by dotted lines (Appendix 1).

7.4.2 Predation rate estimates

Aside from particulars on the possible shapes of the functional response curves, the apparent numerical discrepancies among the different datasets obviously deserve some comment (Figs 7.10A, 7.10B). My estimates for decapod predation on small and large sea urchins are intermediate between the curves for Breen (1974, experiment 3) and Evans & Mann (1977). The seemingly inflated values from Breen (1974, experiment 3) may have been caused by the lack of alternative prey, since the single estimate from another experiment where alternative prey were present, is close to the values from other studies (Breen 1974, experiment 1; Figs 7.10A, 7.10B). It is also possible that bias may have been introduced by the linear regression procedure used in the conversion from biomass units, as the figures for this experiment were the only ones that could not be converted directly to number of urchins eaten per predator per day (Breen 1974, experiment 3; Appendix 1).

The curve through my results for large urchins lies above the curve through Evans & Mann's (1977) results (Figs 7.10A, 7.10B). This incongruity may be related to differences in our experimental setups. The most conspicuous difference was that Evans & Mann (1977) had pegged the claws of the rock crabs that were used as alternative prey, whereas I used natural rock crabs that did not have the movement of their claws impeded. For the treatments in my experiment where the rock

crab had been eaten, the mean number of consumed urchins was approximately halved. Thus the discrepancy between our feeding rate estimates may be attributed to the added effect of crab predation on the sea urchins in my experiments (Drummond-Davis *et al.* 1982; Elner 1980; Breen 1974). However, this hypothesis was not supported by regular observations of decapod feeding behaviour in the experimental tanks. The rock crabs played a fugitive, subordinate role to the lobsters, and appeared to function only as lobster food. Therefore, an alternative hypothesis is that the capture of crabs reduced the lobsters diurnal consumption of sea urchins. If that is the case, the discrepancy between my and Evans & Mann's (1977) predation rate estimates is best explained as a result of increased consumption of rock crabs by lobsters in their experiments due to increased vulnerability of the crabs caused by artificial impediment of their claws.

Other quantitative estimates of lobster feeding by Elner (1980) and Himmelman & Steele (1971) fall within the same size range as previous estimates by Evans & Mann (1977) and my results for large sea urchins. Elner & Campbell (1987) found urchin remains in 133 out of 917 lobsters from barren grounds where urchin densities ranged from 29 to 90 individuals/m^2, but this result gives no reliable estimate of actual feeding rates. This is partly because only the hard parts of the urchins, which lobsters apparently tend not to

ingest, can be reliably identified in lobster stomachs, and partly due to the paucity of data on the gastric residence time of sea urchin remains in lobster stomachs (Breen 1987).

The decapod predators in my experiment ate more small urchins than large urchins, particularly at high sea urchin densities. Lobsters attacking large urchins appeared clumsy and one successful act of predation required several attempts (Evans & Mann 1977). In contrast wolffish, which had higher feeding rates than the decapod predators, were capable of crushing several large urchins in few minutes with seemingly little effort.

Several authors have debated the influence of seawater temperature and food preferences on the number of sea urchins eaten by lobsters (Breen 1974; Evans & Mann 1977; Elner 1980; Miller 1985a; Elner & Campbell 1987). In my experiment the lobsters consistently consumed approximately 5 % of the available urchins and crabs irrespective of their relative proportions, and there was no significant relationship between seawater temperature and lobster predation rates. The lobsters ate fewer urchins in experiments where the crab had been eaten, but this had little influence on the overall average consumption of urchins. These results suggests that sea urchin density, rather than seawater temperature or relative prey abundance, is the critical determinant of the rate of sea urchin consumption by lobsters.

Wolffish predation on *S. droebachiensis* has been estimated in the laboratory by Breen (1974), and in the field by Keats *et al.* (1986). Breen's (1974) results were based on two weeklong observations of a single wolffish: one in which the fish ate 15 of 20 available urchins in addition to several alternative prey items; and another without alternative prey, in which the fish ate 31 of 35 available urchins. The resulting diurnal predation rate estimates of 2.14 and 4.43 urchins per day are comparable with my mean diurnal predation rate estimates of 2.1 and 3.5 urchins per day at medium and high sea urchin densities (15 and 30 urchins per tank; Table 7.4, Fig. 7.2).

Examination of the gut contents of wolffish from urchin-dominated areas in Newfoundland suggested that *S. droebachiensis* was its most important food item (Keats *et al.* 1986). However, as the gastrointestinal evacuation rate for wolffish is still unknown, the estimated predation rates are lacking in precision and a meaningful comparison with my results is not possible.

7.4.3 Disease-related morbidity

Most of the observed disease-related sea urchin morbidity in the multifactorial experiment occurred at temperatures above 9°C. This result is consistent with Scheibling & Stephenson's (1984) hypothesis of temperature-dependent disease-related mortality of *S. droebachiensis*.

CHAPTER 8 A SIMULATION MODEL

8.1 Introduction

Earlier attempts to model interactions among kelp, sea urchins, and predators in the North Atlantic include several conceptual models (Wharton & Mann 1981; Hagen 1983; Scheibling 1984; Johnson 1984; Johnson & Mann 1988), as well as three quantitative models: an energy flow model (Miller *et al.* 1971), a theoretical interaction model (Mohn & Miller 1987), and a simulation model (Breen 1974, 1980; Breen & Mann 1976b). These models possess varying degrees of realism, and differ in their ability to generate testable hypotheses.

The conceptual models summarize available knowledge and suggest hypothetical interactions. They draw attention to the pivotal role of sea urchins in mediating the transformation between kelp beds and urchin-dominated barren grounds, but differ in the prominence they give to predation and other plausible regulatory mechanisms.

The three quantitative models approach the subject matter from three different angles. Miller *et al.*'s (1971) static energy flow model describes a kelp bed in which urchins consume only about 7% of the annual production. The kelp bed was, in fact, in the early stages of a sea urchin outbreak, but the model did not predict its imminent destruction (Mann 1977).

Mohn & Miller's (1987) model is a theoretical attempt to describe the dynamic interactions among kelp, sea urchins and predators, in terms of a slightly modified version of the Lotka-Volterra equations. In this model the urchins are assumed to be homogeneously distributed, although an aggregated distribution is one of the essential features of the overgrazing process (Mann 1977). The model also assumes a smooth, reciprocal relationship between the kelp and urchins biomasses, which implies the existence of a kelp-urchin equilibrium at intermediate biomasses. This is contrary to the nonlinear threshold effects which characterize real overgrazing situations (Harrold & Pearse 1987).

Breen's (1974) model simulates the effect of predation on sea urchin population dynamics and attempts to test the hypothesis that predators are capable of preventing destructive grazing of kelp. It includes detailed information on urchin growth and size-specific feeding preferences of decapod predators, but does not include effects of urchin behaviour.

In this chapter I use a simulation model based on the results from previous chapters to study the impact of predation on sea urchin outbreak dynamics. First I estimate the predator densities required to prevent sea urchin outbreaks in response to both constant levels of sea urchin recruitment, and in response to recruitment pulses. Second, I estimate predator densities required to terminate outbreaks.

8.2 Methods

8.2.1 Model description

The computer program for the model is written in the programming language "Think's Lightspeed Pascal" from Symantec Corporation, and implemented on an Apple Macintosh II microcomputer (Appendix 3). The model simulates the effect of sea urchin grazing on fleshy macroalgae, as well as the effects of predation on juvenile and adult sea urchins (Fig. 8.1).

8.2.1.1 Age structure and recruitment

The urchin population consists of two age classes, juveniles and adults. New recruits enter the juvenile urchin population in the spring approximately one year after being spawned and fertilized. They remain members of the juvenile population until the fall of the following year, when they become members of the adult urchin population.

The juvenile and adult urchin populations of the simulation model correspond to the small and large size-classes in the multifactorial experiment (Chapter 2). The assigned age categories of juvenile for the size-range 5 - 19 mm diameter, and adult for the ≥ 20 mm diameter, are based on recent estimates of sea urchin growth rates in the field (Raymond & Scheibling 1987).

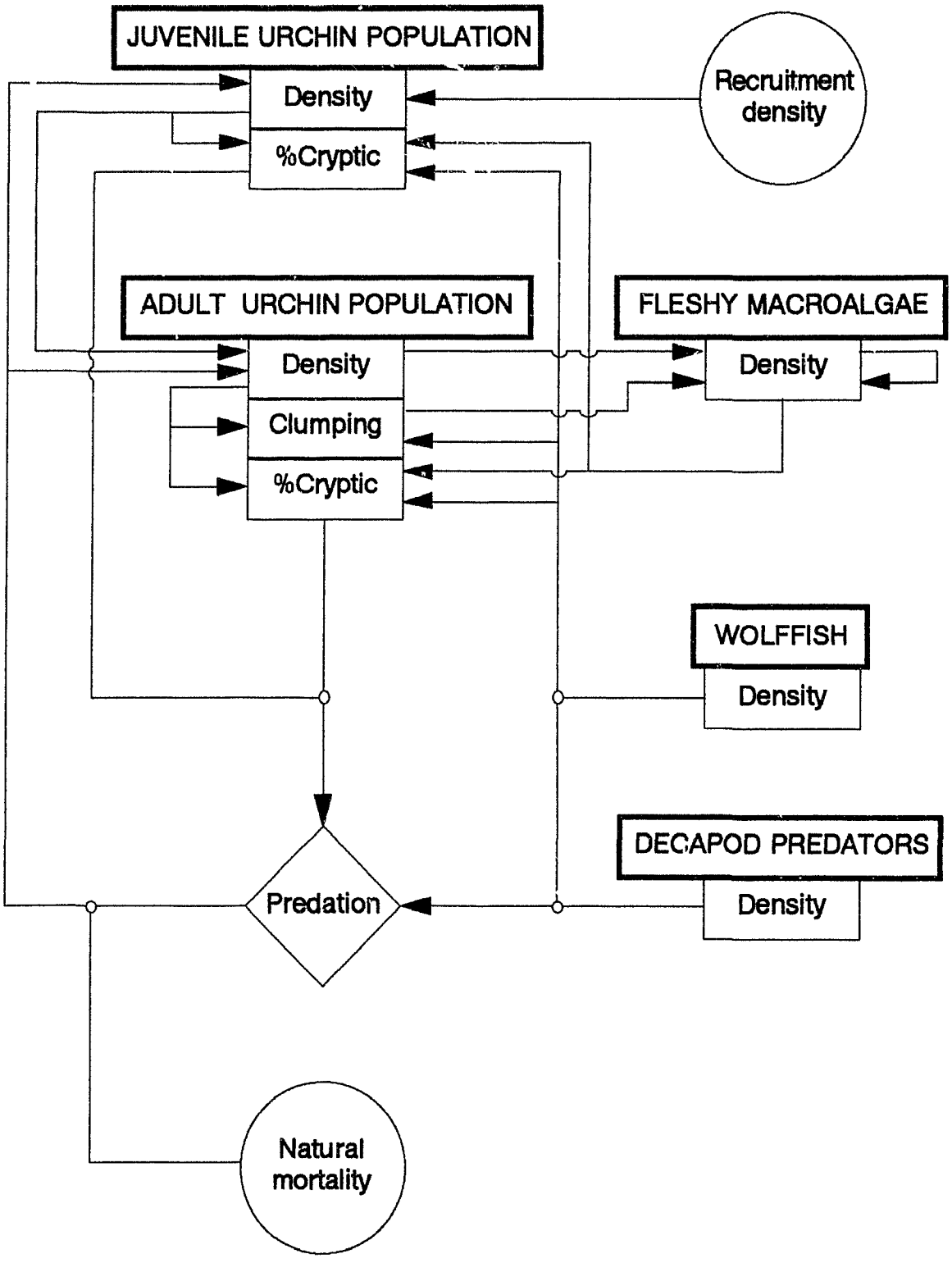

Fig. 8.1 BIOTIC STRUCTURE OF SIMULATION MODEL.

Two different recruitment strategies are implemented in the model. Recruitment is either held constant, *i.e.* steady recruitment of the same number of juvenile urchins every spring throughout the simulated time period, or delivered as a single pulse at time zero. The first strategy was used in Breen's (1974) simulation model. The second strategy corresponds to the hypothesis that urchin outbreaks may be initiated by recruitment of a strong yearclass of sea urchins (Foreman 1977; Hart & Scheibling 1988; Hagen 1983; Ebert 1983; Pringle 1986).

8.2.1.2 Natural mortality

Sea urchins are assumed to suffer age-independent natural mortality at a constant rate (Miller & Mann 1973), λ_U, so that 99 % of a yearclass is eliminated within a predetermined number of years, indicated by the parameter *maxAge* in the model. The actual longevity of *S. droebachiensis* is unknown, but presumably greater than 10 years. Pending more accurate information the value of *maxAge* is arbitrarily set at 12 years (Fig. 8 2). Thus, the constant weekly sea urchin mortality rate λ_U is estimated as follows:

$$U_{t+1} = (1 - \lambda_U) U_t$$

$$U_{52 \cdot maxAge} = \frac{U_0}{100} = (1 - \lambda_U)^{52 \cdot maxAge} U_0$$

$$\lambda_U = 1 - \exp\left(\frac{\ln(100)}{52 \cdot maxAge}\right) = 1 - \exp\left(\frac{-\ln(100)}{52.12}\right) = 0.007353,$$

where t is the number of weeks after recruitment into the model, and U_t is the total size of the sea urchin population at time t.

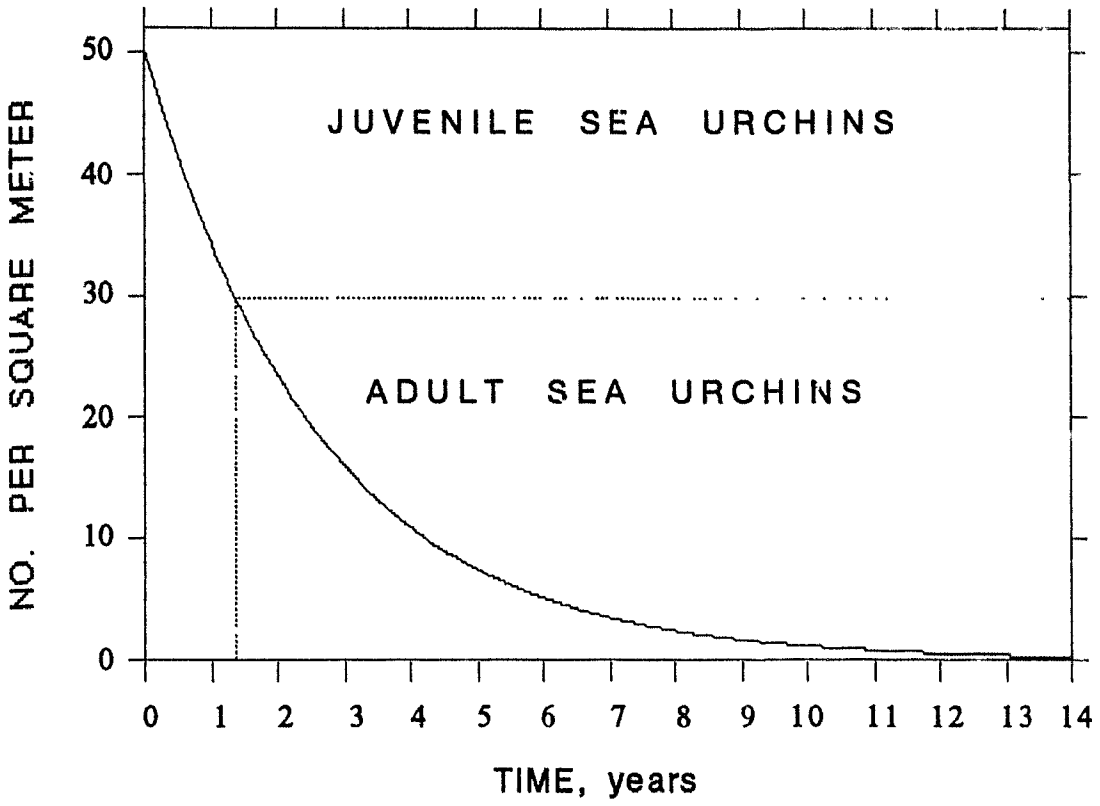

Fig. 8.2 SIMULATION OF AGE-INDEPENDENT NATURAL MORTALITY. The population density of a sea urchin yearclass exposed to a constant rate of natural mortality is plotted against time. Only 1 % of the initial recruitment pulse remains after 12 years. Time zero is the spring of the initial recruitment of juvenile sea urchins into the model. The dotted lines indicate the transition from juveniles to adults, the second fall after recruitment into the model.

8.2.1.3 Predation

The model simulates the effects of two different kinds of predators, decapods and wolffish, corresponding to the two distinct predator treatments in the multifactorial experiment. Decapods are present all year round, whereas wolffish are present only in the summer season (Breen 1974; Bernstein *et al.* 1981; Keats *et al.* 1985a).

The predators select and consume juvenile or adult urchins according to experimentally determined selectivity coefficients and consumption rates. The selectivity coefficients are based on the ratio of juvenile to adult urchins consumed during the entire multifactorial experiment. If the numerical ratio of juveniles to adults in the model is larger than the selection ratio, then the predators eat juvenile urchins, otherwise they eat adult urchins.

Juvenile urchins are consumed in proportion to their abundance according to a Holling type 3 numerical response (Chapter 7). Predation on adult urchins is simulated using both type 2 and type 3 numerical responses. Predation rate estimates are based on diurnal predation rates for the three different sea urchin densities that were used in the multifactorial experiment (Chapter 7).

8.2.1.4 Cryptic behaviour

Cryptic behaviour of sea urchins is simulated using a regression equation based on significant effects and untransformed data from the multifactorial experiment (Chapter 4.3.2). The regression coefficients were calculated using the statistics program "Super ANOVA" from Abacus Incorporated.

The qualitative effects of prefeeding and the presence of kelp are both quantified by multiplying the regression

coefficients for these factor levels by the density of fleshy macroalgae, expressed as a proportion of its ungrazed maximum density (Section 8.2.1.6).

It is assumed that the spatial heterogeneity in a tank with claypipe refuges is more like a natural benthic environment than the smooth interior of a tank without refuges. The effect of refuges is therefore permanently incorporated in the regression equation.

In the cryptic versions of the model the percentage of urchins deemed to be cryptic, based on the above calculations, have absolute refuge from predation. Only the non-cryptic urchins influence the predators' selection and consumption of juvenile or adult sea urchins. In the non-cryptic versions all urchins are equally susceptible to predation.

8.2.1.5 Aggregation

Aggregation behaviour of adult sea urchins is simulated using a regression equation based on significant effects from the multifactorial experiment (Chapter 3). The regression coefficients were calculated, again using the statistics program "Super ANOVA" (Section 8.2.1.4). Aggregation is quantified in terms of the index of mean crowding, $\overset{*}{m}_2$.

The effect of refuges is permanently incorporated in the regression equation (Section 8.2.1.4). The resulting regression equation is a linear function of adult sea urchin density, with added constants corresponding to the three predation factor levels, *i.e.* no predator, decapods or wolffish (Fig. 8.3).

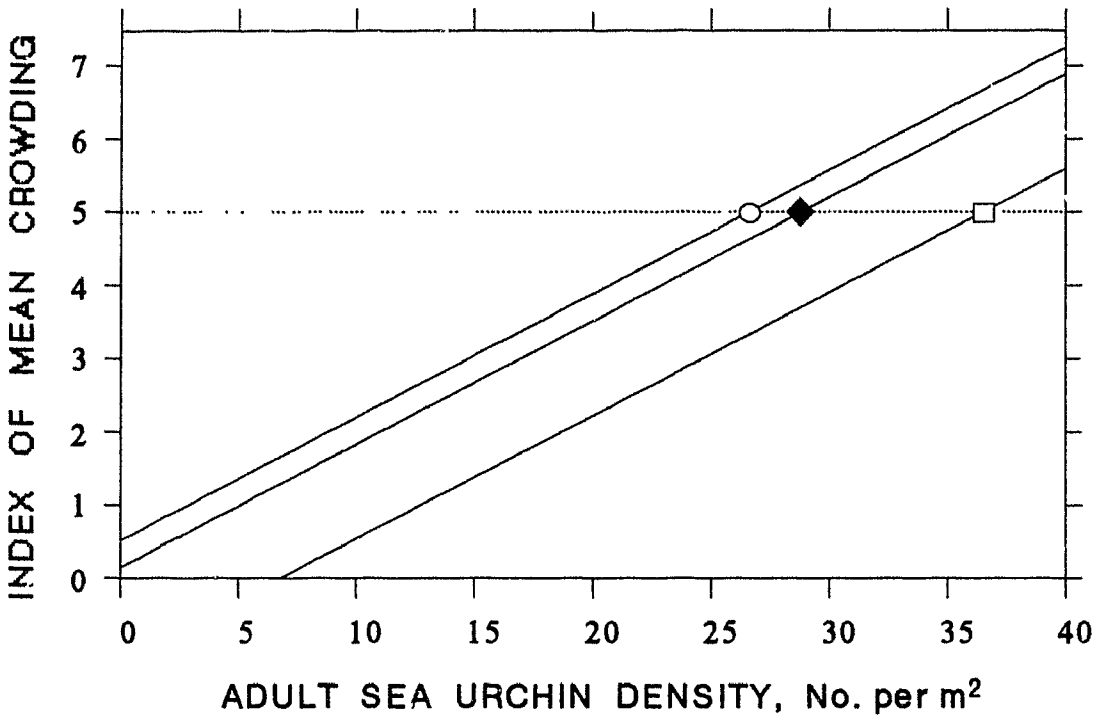

Fig. 8.3 PREDATOR MEDIATED MODIFICATION OF OUTBREAK INITIATION DENSITY. The chosen level for the hypothetical outbreak initiation threshold φ is indicated by the dotted horizontal line. It is expressed as a constant level of adult sea urchin aggregation, and quantified as the index of mean crowding $\overset{*}{m}_2$. The three regressions lines, relating adult sea urchin density and aggregation level, are based on results from the multifactorial experiment. The intersections between the regression lines and the dotted line correspond to the minimum adult sea urchin densities required for destructive grazing of macrophytes. Key to symbols: O decapod predators, ◆ no predators, and □ wolffish.

8.2.1.6 Fleshy macroalgae

In the simulation model the population of fleshy macroalgae, A, is grazed destructively at an exponential rate, λ_A, when the adult urchin populations level of aggregation is greater than or equal to a hypothetical outbreak initiation threshold, φ. The threshold was set at a mean number of 5 aggregation cohabitants per urchin. This value corresponds to adult sea urchin densities of 28.7 individuals per square meter in the absence of predators, 26.5 individuals per square meter in the presence of decapod predators, and 36.6 individuals per square meter in the presence of wolffish (Fig. 8.3). These estimates fall within the range of sea urchin densities actually reported from areas of active kelp bed destruction (Wharton & Mann 1981; Hagen 1983).

It is assumed that a small proportion of the algal population, A_{min}, is inaccessible to urchin grazing (Breen 1980; Himmelman *et al.* 1983). The macroalgae population makes a logistic recovery with a maximum growth rate of, λ_B, when the density of adult sea urchins is less than or equal to a set outbreak termination threshold, ξ. This threshold was set at 5 adult sea urchins per square meter; an approximation derived from estimates by Breen & Mann (1976b) and Chapman (1981). Thus, the dynamics of the algal population are stated as follows:

$$A_{t+1} = (1 - \lambda_A)A_t \qquad \text{if } \overset{*}{m}_{2,t} > \varphi$$

$$A_{t+1} = [1 + \lambda_B(1 - \frac{A_t}{K})]A_t \qquad \text{if } U_{A,t} < \xi$$

$$A_{t+1} = A_{min} \qquad \text{if } A_{t+1} < A_{min}$$

where A_t is the size of the population of fleshy macroalgae at time t, $U_{A,t}$ is the density of adult sea urchins at time t, and $\overset{*}{m}_{2,t}$ is the adult urchin population's level of aggregation. The rates λ_A and λ_B are set so that complete decimation of the macroalgae takes one year of continuous grazing, and recovery takes three years of uninterrupted regrowth. These timeframes are based on actual observations of kelp bed destruction (Breen 1974; Hagen 1983) and recovery (Johnson & Mann 1988). Calculation of λ_A and λ_B follow the same general pattern as the previous calculation of the natural mortality rate, λ_U (Section 8.2.1.2).

8.2.1.7 Time and seasons

Model time progresses in weekly increments. One annual cycle consists of two seasons, a summer of 20 weeks, approximately mid-May to late September, and a winter of 32 weeks. Spring and fall have been reduced to singular points in time, marking the transitions between the two main seasons. This time scheme is a simplified approximation of the natural annual cycles it purports to mimic. It is chosen for its heuristic value and for its similarity to the biseasonal set-up of the multifactorial experiment (Chapter 2).

8.2.1.8 Initial conditions

8.2.1.8.1 Outbreak initiation

8.2.1.8.1.1 Steady recruitment

In the initial phase of this version of the model only the interaction between sea urchins and macrophytes is simulated. Accordingly, the model was started with urchin and predator densities both equal to zero, urchin recruitment density equal to 1 juvenile per square meter, and 100 % macrophyte cover at time zero.

The status of the macrophyte population was checked after 30 years. If more than 10 % of the macrophyte population remained then the model was reinitialized with 100 % macrophyte cover and urchin recruitment density incremented by 1 juvenile per square meter and rerun for another 30

years. This procedure was repeated until less than 10 % of the macrophytes remained. Pertinent model parameters were then recorded, including predator densities and the attained urchin recruitment level.

At this point predators were introduced and the model reinitialized with: the density of one predator type incremented by 0.01 individuals per square meter; the attained urchin recruitment density decremented by 4 individuals per square meter; and macrophyte density reset at 100 %. A new series of 30 year runs with unit increments of urchin recruitment density was then simulated, again until less than 10 % of the macrophytes remained and the model parameters recorded, as described in the preceding paragraph. Successive series of reruns were carried out in this fashion until predator density reached 0.3 individuals per square meter. This procedure was repeated for both predator types and both functional response types, with effects of cryptic behaviour ignored in one set of repetitions and included in the other.

8.2.1.8.1.2 Pulse recruitment

In the initial phase of this version of the model only the interaction between sea urchins and macrophytes is simulated. Accordingly, the model was started with urchin and predator densities both equal to zero, a recruitment pulse of 10 one year old juvenile urchins per square meter, and 100 % macrophyte cover at time zero.

The status of the macrophyte population was checked after 5 years. If more than 10 % of the macrophyte population remained then the model was reinitialized with 100 % macrophyte cover, no urchins, and the density of the urchin recruitment pulse incremented by 1 juvenile per square meter and rerun for another 5 years. This procedure was repeated until less than 10 % of the macrophytes remained. Pertinent model parameters were then recorded, including predator densities and the attained urchin pulse recruitment level.

At this point predators were introduced and the model reinitialized with: the density of one predator type incremented by 0.01 individuals per square meter; the attained urchin recruitment pulse density decremented by 10 individuals per square meter; and macrophyte density reset at 100 %. A new series of 5 year runs with unit increments of urchin recruitment density was then simulated, again until less than 10 % of the macrophytes remained and the model parameters recorded, as described in the preceding paragraph. Successive series of reruns were carried out in this fashion

until predator density reached 0.3 individuals per square meter. This procedure was repeated for both predator types and both functional response types, with effects of cryptic behaviour ignored in one set of repetitions and included in the other.

8.2.1.8.2 Outbreak termination

In the initial phase of this version of the model only the interaction between sea urchins and macrophytes is simulated. The model was started with predator density equal to zero, 30 adult and 10 juvenile urchins per square meter, urchin recruitment density equal to 10 juveniles per square meter, and macrophyte cover equal to A_{min} at time zero.

The status of the macrophyte population was checked after 30 years. If macrophyte cover was less than 90 % of A_{max} then the model was reinitialized with both recruitment density and juvenile urchin density decremented by 1 individual per square meter and rerun for another 30 years. This procedure was repeated until macrophyte density increased to more than 90 % of A_{max}. Pertinent model parameters were then recorded, including predator densities and the attained level of urchin recruitment.

At this point predators were introduced and the model reinitialized with: the density of one predator type incremented by 0.01 individuals per square meter; attained

recruitment and juvenile urchin densities both incremented by 10 individuals per square meter; and macrophyte density reset at A_{min}. A new series of 30 year runs with unit increments of urchin recruitment density was then simulated, again until macrophyte density had increased to more than 90 % of A_{max} and model parameters recorded, as described in the preceding paragraph. Successive series of reruns were carried out in this fashion until predator density reached 0.3 individuals per square meter. This procedure was repeated for both predator types and both functional response types, with effects of cryptic behaviour ignored in one set of repetitions and included in the other.

8.3 Results

8.3.1 Model dynamics

Under steady recruitment conditions the adult sea urchin population density peaks each fall, when the juvenile yearclass makes the transition to adult size. Then, due to a combination of natural mortality and predation, the density gradually decreases until the next fall. Fluctuations in the adult aggregation level, which is a linear function of adult urchin density (Fig. 8.3), follows a similar seasonal pattern. Consequently, adult aggregation levels start rising above the threshold value φ for brief periods annually during early winter when steady recruitment density reaches the level required for outbreak initiation. Destructive grazing takes place as long as the adult level of aggregation is higher than φ, and macrophyte recovery is precluded unless adult sea urchin density drops below the outbreak termination threshold ξ. The resulting pattern of macrophyte destruction is an incremental decline over several years.

Macrophyte destruction caused by pulse recruitment of sea urchins follows a different pattern, since the size of a single yearclass of sea urchins decreases uninterrupted due to a combination of natural mortality and predation (Fig. 8.2), until the simulation run is terminated. Destructive grazing commences when the recruits from a sufficiently strong pulse reach adult size, the second fall after they

have entered the simulation model, and continues as long as the adult level of aggregation remains above the threshold value φ. The result, partial destruction or complete decimation of macroalgae, depends on the length of this time period, which in turn depends on the size of the initial recruitment pulse.

Partially destroyed macrophyte beds will recover rapidly unless adult urchin population density in the created barren area is maintained above the outbreak termination threshold ξ. Such maintenance requires comparatively low levels of sea urchin recruitment. It is therefore suggested that field observations of a persistent, partially destroyed macrophyte bed may be interpreted as evidence of a past recruitment pulse.

8.3.2 Outbreak initiation

8.3.2.1 Steady recruitment

Outbreaks were initiated at a steady recruitment density of 19 juvenile urchins per square meter per year in the absence of predators (Fig. 8.4). The minimum steady recruitment density required for outbreak initiation increased linearly in response to increasing predator density when urchins were non-cryptic. In this case the decapods were slightly more efficient outbreak preventors than the wolffish when predator densities increased beyond 0.05 individuals per square meter.

Simulation of cryptic sea urchin behaviour triggered a qualitative change in the ability of the wolffish to prevent outbreaks, as a small increase in recruitment density rendered the wolffish incapable of outbreak prevention (Fig. 8.3). Cryptic sea urchin behaviour had only minor quantitative effects on the decapod predators ability to prevent outbreaks (Fig. 8.3).

Functional predator response type had no discernible effects on either predator's ability to prevent steady recruitment outbreaks.

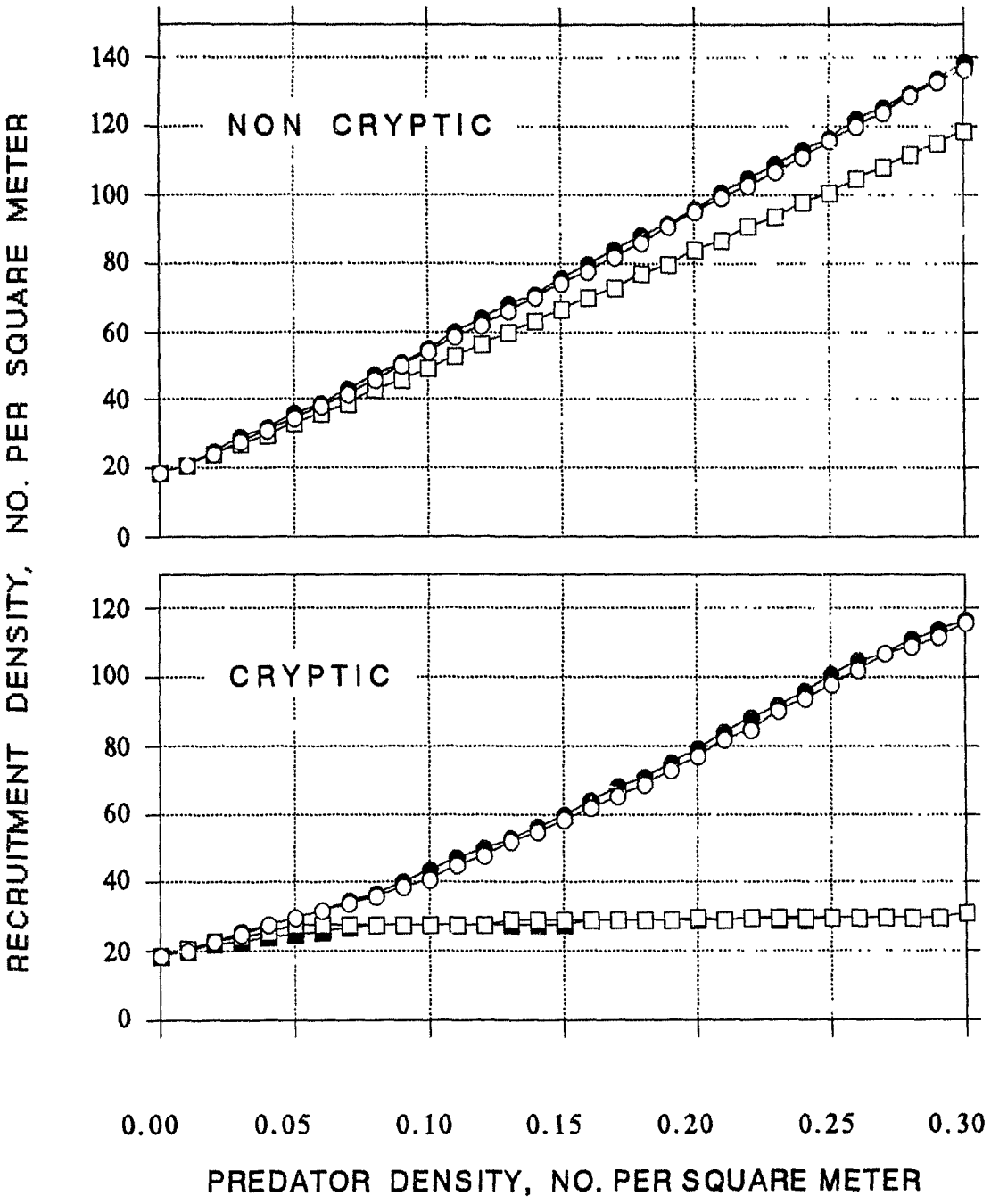

Fig. 8.4 OUTBREAK INITIATION: STEADY RECRUITMENT. Predator density is plotted against the minimum level of urchin recruitment required to initiate an outbreak. Urchins are non-cryptic in the top panel, whereas cryptic urchins are inaccessible to predators in the bottom panel. Key to symbols: O decapods - type 2 predation, ● decapods - type 3 predation, □ wolffish - type 2 predation, ■ wolffish - type 3 predation.

8.3.2.2 Pulse recruitment

Outbreaks were initiated by a pulse of 63 juvenile recruits per square meter in the absence of predators (Fig. 8.5A). The size of the minimum recruitment pulse required for outbreak initiation increased linearly in response to increasing predator density when urchins were non-cryptic. Both predators had similar effects in this case (Fig. 8.5A).

Simulation of cryptic sea urchin behaviour triggered a dramatic change in the ability of the wolffish to prevent outbreaks, as a small increase in recruitment density rendered the wolffish incapable of outbreak prevention. Cryptic sea urchin behaviour had only minor quantitative effects on the decapod predators ability to prevent outbreaks (Fig. 8.5B).

Functional predator response type had little effect on either predator's ability to prevent pulse recruitment outbreaks.

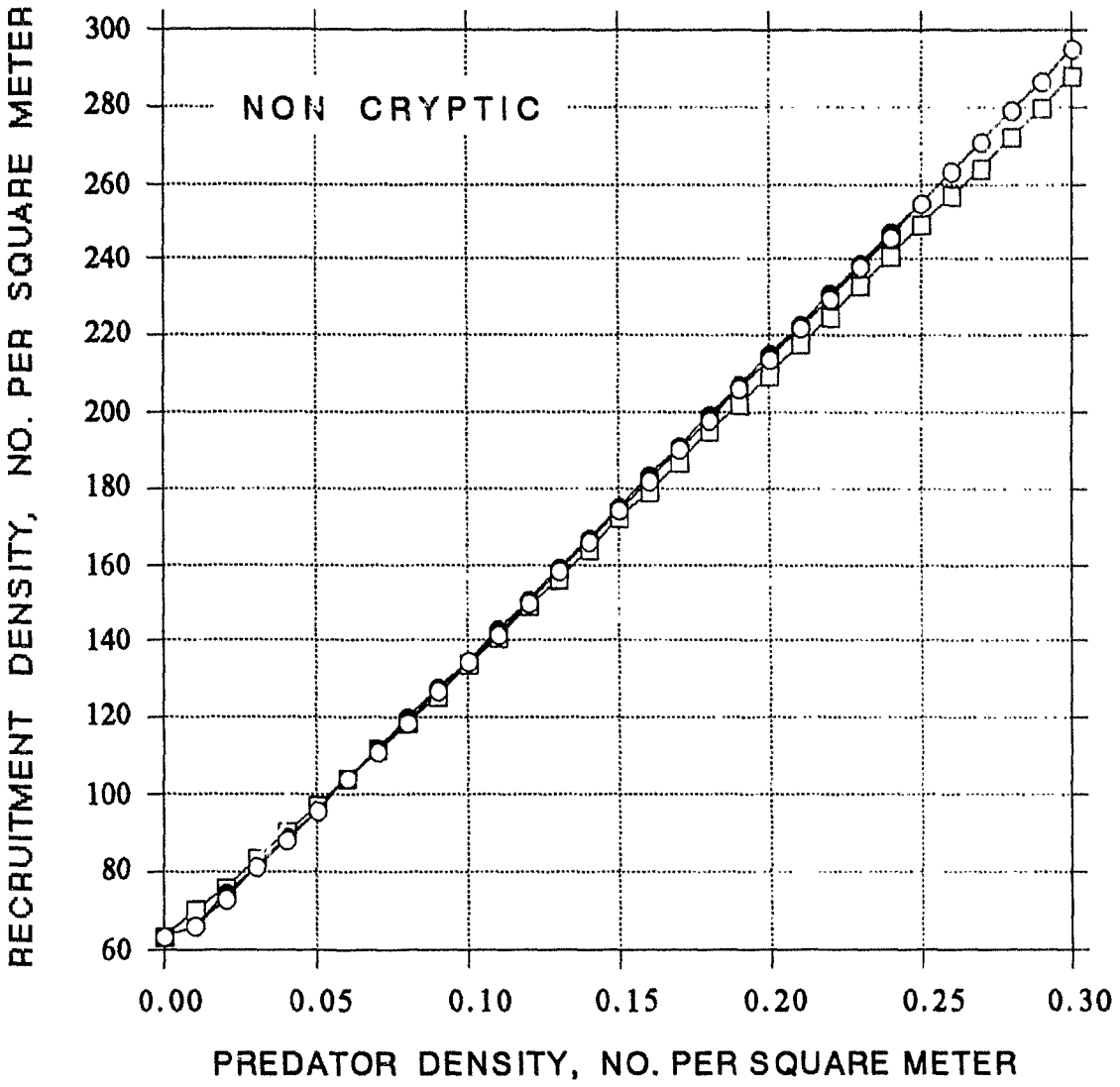

Fig. 8.5A OUTBREAK INITIATION: PULSE RECRUITMENT, URCHINS NON CRYPTIC. Predator density is plotted against the minimum recruitment pulse of juvenile sea urchins required to initiate an outbreak. Key to symbols: O decapods - type 2 predation, ● decapods - type 3 predation, □ wolffish - type 2 predation, ■ wolffish - type 3 predation.

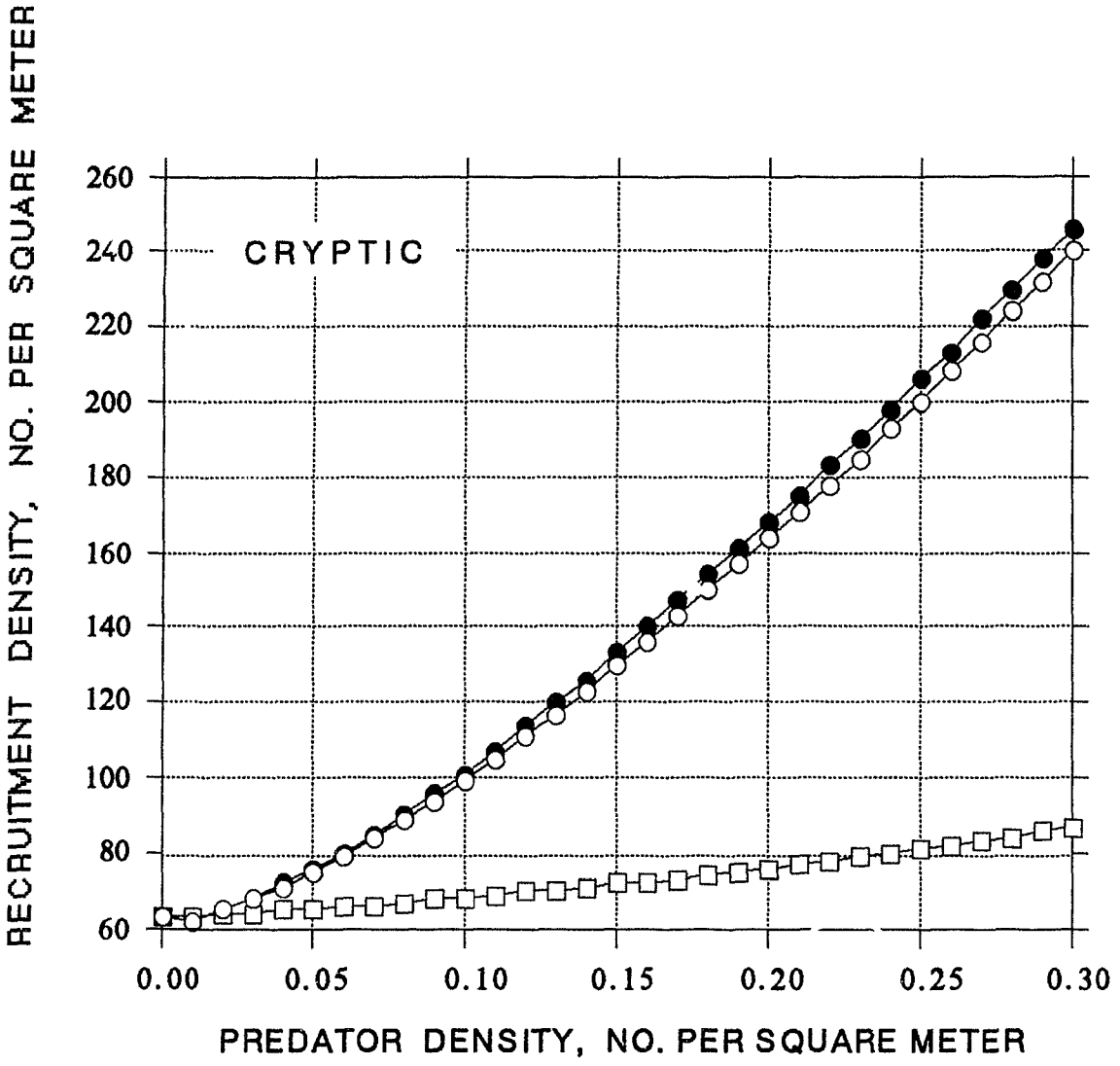

Fig. 8.5B OUTBREAK INITIATION: PULSE RECRUITMENT, URCHINS CRYPTIC. Predator density is plotted against the minimum recruitment pulse of juvenile sea urchins required to initiate an outbreak. Cryptic urchins are inaccessible to predators. Key to symbols: O decapods - type 2 predation, ● decapods - type 3 predation, □ wolffish - type 2 predation, ■ wolffish - type 3 predation.

8.3.3 Outbreak termination

A steady minimum recruitment level of 8 juvenile urchins per square meter per year was required to sustain a sea urchin outbreak in the absence of predators (Fig. 8.6). Decapod predators were shown to be the most effective outbreak terminators. Wolffish had a smaller effect than decapods when urchins were non-cryptic, and practically no effect when urchins were cryptic.

Functional predator response type had no discernible effects on either predator's ability to terminate outbreaks.

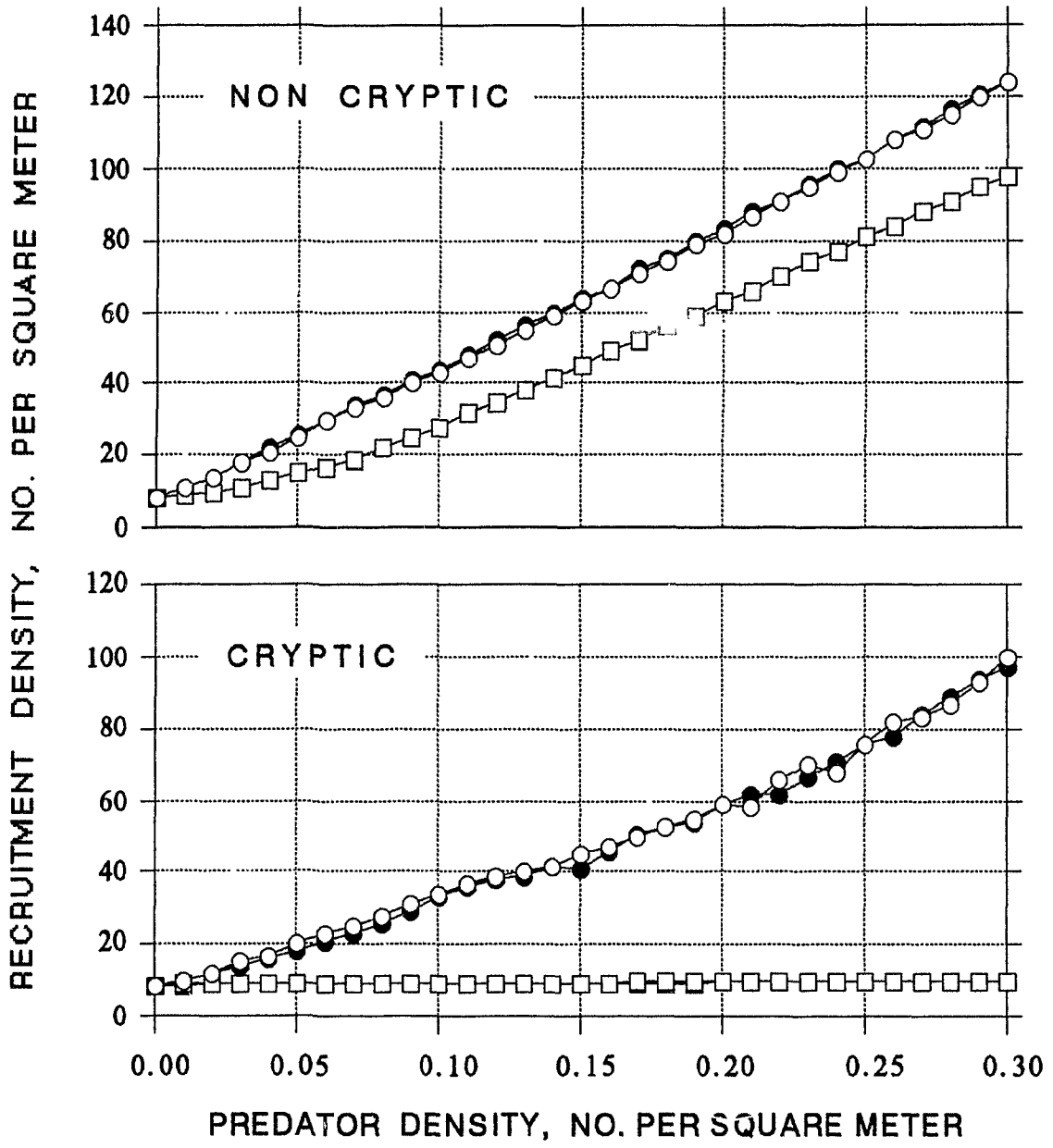

Fig. 8.6 OUTBREAK TERMINATION. Predator density is plotted against minimum level of recruitment of juvenile sea urchins required to sustain a sea urchin outbreak. Urchins are non-cryptic in the top panel, while cryptic urchins are inaccessible to predators in the bottom panel. Key to symbols: O decapods - type 2 predation, ● decapods - type 3 predation, □ wolffish - type 2 predation, ■ wolffish - type 3 predation.

8.4 Discussion

The presence of predators had a general inflatory effect on the recruitment levels required to initiate and sustain sea urchin outbreaks in versions of the model which did not simulate the effect of cryptic sea urchin behaviour. However, in versions of the model which did simulate cryptic behaviour, a qualitative change was triggered in the ability of wolffish to either prevent or terminate outbreaks. Slight increases in urchin recruitment density initiated or sustained outbreaks irrespective of wolffish density when cryptic sea urchins were inaccessible to the wolffish.

The wolffish is a visual predator presumably incapable of exploiting cryptic prey (Keats *et al.* 1986). The simulation results would therefore suggest that the wolffish, despite its acknowledged predatory and behavioural effects on populations of *S. droebachiensis* (Breen 1974; Keats *et al.* 1986; This study), has a limited capacity to prevent or terminate sea urchin outbreaks. The proposed explanation is that juvenile urchins have a cryptic lifestyle and consequently suffer little mortality during two summers of wolffish predation. They reach adult size in the fall when the wolffish migrate offshore and are not preyed upon until the following summer when the wolffish migrate back into shallow waters. Thus, a modest increase in recruitment density would ensure outbreak conditions during the winter

even if the wolffish eliminated all non-cryptic urchins during the summer.

The implication is that a predator either has to be present all year round or capable of exploiting cryptic sea urchins, particularly juveniles, in order to effectively prevent or terminate sea urchin outbreaks. For such predators the question of control of sea urchin populations becomes a quantitative multifactorial hypothesis involving interactions among several members of the benthic community (Breen 1974; Bernstein *et al*. 1983).

As decapod predators are present all year (Witman 1985), they may function as outbreak preventors irrespective of their ability to exploit cryptic sea urchins. Hence, the model results do not negate the original predator hypothesis, that the recent large-scale outbreak of *S. droebachiensis* in Eastern Canada was a result of reduced predation on sea urchins following depletion of local lobster stocks (Mann & Breen 1972; Breen & Mann 1976b).

The model predicts that macrophyte destruction induced by a sufficiently strong steady level of recruitment would take place gradually in annual increments during late fall or early winter, whereas a sufficiently strong recruitment pulse would cause continuous rapid destruction of macrophytes resulting in partial or complete macrophyte destruction. The persistence of the resulting barren area would then depend on

whether subsequent levels of urchin recruitment were adequate to maintain adult urchin densities above a hypothetical outbreak termination threshold ξ.

The model's predictions for the pattern of kelp bed destruction following recruitment pulses is matched by evidence from field observations such as the following: 1) rapid continuous kelp bed destruction observed on a number of occasions (Foreman 1977; Breen & Mann 1976a; Wharton & Mann 1981; Hagen 1983), 2) temporary stalemates between kelp beds and barren grounds following partial kelp bed destruction (Wharton & Mann 1981; Miller 1982), and 3) recruitment patterns of sea urchins characterized by infrequent episodes of high recruitment (Ebert 1983) evoked as the cause of destructive grazing of kelp beds (Foreman 1977).

Predation on adult sea urchins was simulated using both type 2 and type 3 functional predator responses but no noteworthy effects of functional response type were detected. This result is contrary to the qualitative effect of functional response type in current theoretical predator-prey models, where only type 3 responses may influence stability patterns (Hassell *et al.* 1977). This discrepancy is perhaps a result of the static nature of the predator populations in the simulation model, as opposed to the dynamic feedback mechanisms of theoretical predator-prey models. However, a parametric representation of predator density is justified by

observing that at present, there is no evidence to suggest that the dynamics of predator populations are determined, or directly influenced, by fluctuations in sea urchin populations.

The simulation model circumvents the paucity of data on the location of parental sea urchin populations, and the factors which influence survival patterns of planktonic and early benthic stages in the life cycle of the urchins (Fig. 9.2), by taking the recruitment density of one year old juveniles as an input parameter. A self contained model of sea urchin outbreak dynamics should ideally include the complete life cycle of the sea urchin, although this seems like a remote possibility at present.

CHAPTER 9 GENERAL DISCUSSION

9.1 Phenomenological synopsis

Kelp beds and barren grounds are the two principal community configurations in areas where outbreaks of the green sea urchin, *S. droebachiensis*, occur. The basic dichotomy between low density urchin populations with negligible ecological impact, and high density urchin populations with the power to destroy virtually all nonencrusting macroalgae, is well documented from locations throughout the urchin's distributional range (Fig. 9.1; Foreman 1977; Wharton & Mann 1981; Harris 1982; Keats *et al.* 1982; Himmelman *et al.* 1983; Hagen 1987).

Destructive grazing of kelp is the first visible symptom of an outbreak (Breen & Mann 1976a; Hagen 1983), and a barren ground is its chronic manifestation (Lang & Mann 1976; Chapman 1981; Himmelman 1986). Outbreaks are therefore easily diagnosed by the progressive elimination or prolonged exclusion of kelp from suitable substrata, *i.e.* substrata occupied by kelp in the absence of dense urchin populations. Although energetically stable (Chapman 1981), the outbreak state may be terminated in a two-stage process consisting of sea urchin elimination and subsequent macrophyte recovery.

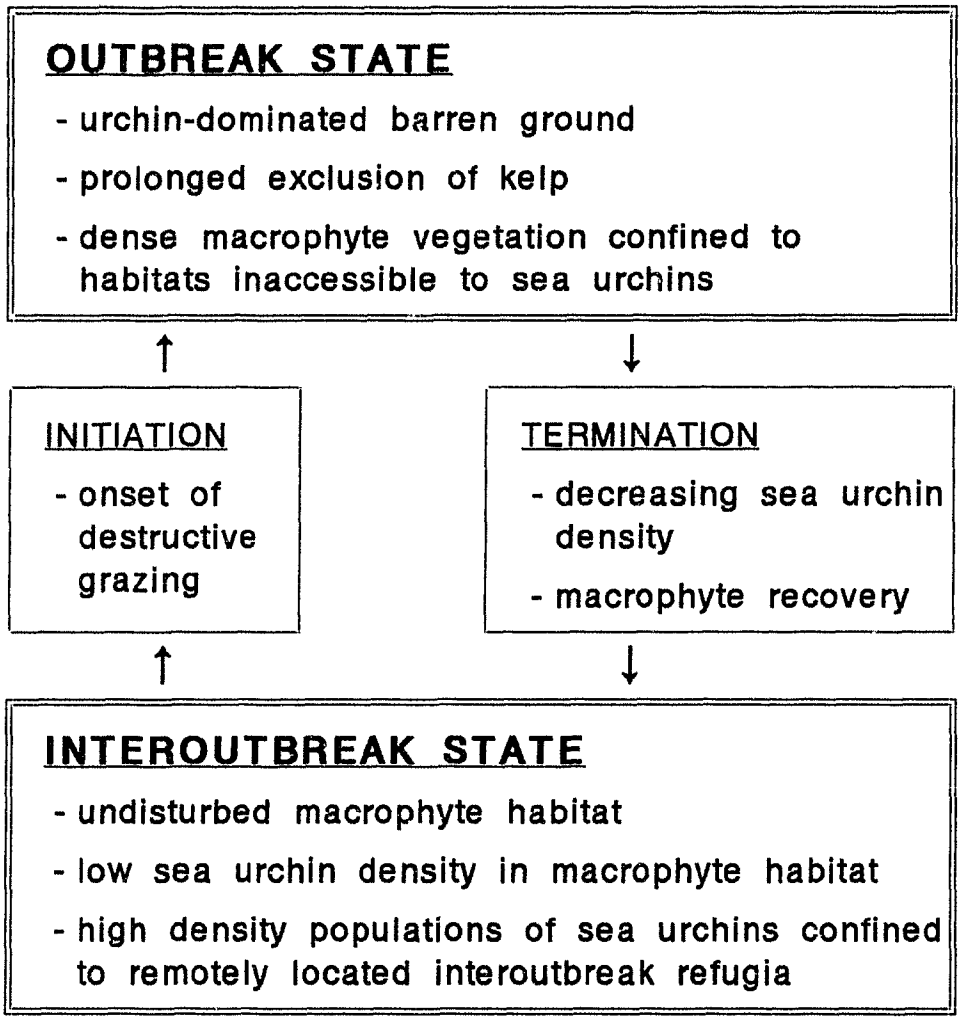

Fig. 9.1 A SIMPLE PHENOMENOLOGICAL MODEL ILLUSTRATING THE BASIC DICHOTOMY OF THE OUTBREAK PHENOMENON. The interoutbreak and outbreak states are connected by the independent, transitory processes of outbreak initiation and termination. Initiation is the least understood aspect of the outbreak phenomenon.

Mechanisms of outbreak termination may include epizootic disease (Miller & Colodey 1983; Scheibling & Stephenson 1984; Hagen 1987), or an insufficient supply of urchin larvae (Foreman 1977). But predation, while important elsewhere for

other species of sea urchin (Duggins 1980; Estes *et al.* 1978, 1982; Breen *et al.* 1982), does not appear to affect the stability of barren grounds dominated by *S. droebachiensis* (Keats *et al.* 1986). In the absence of high density urchin populations, post-outbreak macrophyte recovery is usually a predictable succession process, leading back to an interoutbreak state structurally dominated by large perennial brown algae (Fig. 9.1; Foreman 1977; Miller 1985b; Novaczek & McLachlan 1986; Scheibling 1986; Hagen 1987; Johnson & Mann 1988).

Outbreak initiation is a complex process involving changes in the sea urchins' aggregation behaviour, microhabitat utilization (Part I), and population density (Chapter 8). The mechanisms governing outbreak initiation are, however, largely hypothetical and the etiology of green sea urchin outbreaks is still unknown due to a basic lack of knowledge about the status of sea urchin populations during the interoutbreak state, and about the ecology of early life-history stages (Fig. 9.2).

Outbreak initiation following release from predator control, has been conclusively documented for populations of strongylocentrotid sea urchins in the northeastern Pacific (Dayton & Tegner 1984). However, the hypothesis that sea urchin outbreaks may be caused by diminished predation pressure on adult sea urchins by decapod predators (Mann & Breen 1972; Breen & Mann 1976b), although much debated and

not convincingly negated (Wharton & Mann 1981; Pringle *et al.* 1982), surely has only local applicability (Hagen 1983; Himmelman *et al.* 1983). Therefore, the outbreak phenomenon, although superficially similar in geographically disparate areas, may not yield readily to causal generalizations.

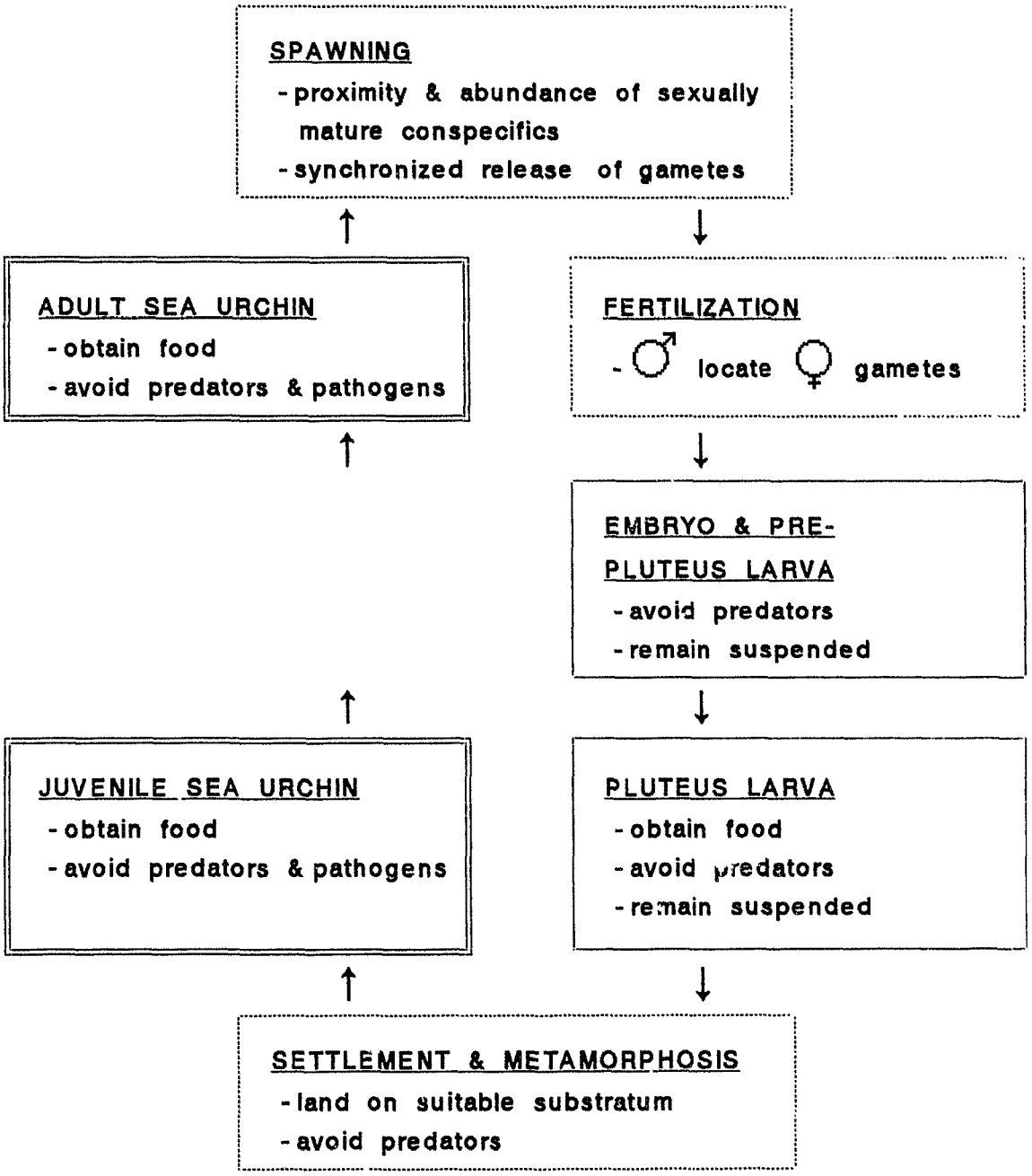

Fig. 9.2 SUMMARY OF SEA URCHIN LIFE HISTORY STAGES. Some of the major requirements for surviving each stage are listed. The relevant time scales, for the duration of each stage, are indicated as follows: dotted lines - hours, solid lines - days, double lines - years. Most studies in sea urchin ecology have been done on adult sea urchins.

9.2 Temporal dynamics

9.2.1 Threshold effects

The results from Part I of this study suggest that the formation of destructive feeding aggregations can be mimicked in the laboratory by increasing the density of large starved urchins beyond a certain density threshold, which corresponds to the density beyond which destructive grazing commences in the field (Wharton & Mann 1981). The laboratory results indicate that this density threshold is not constant but varies in response to altered levels of environmental parameters including food supply, microspatial heterogeneity, and the presence or absence of predators (Fig. 9.3).

The hypothetical outbreak initiation threshold is effectively increased by the presence of wolffish, and by additional spatial heterogeneity, both of which make the urchins less aggregated, more cryptic, and less active feeders, thereby inhibiting the formation of destructive grazing aggregations. A prehistory of a plentiful food supply will also increase the actual value of the hypothetical outbreak initiation threshold by decreasing the feeding activity of large urchins.

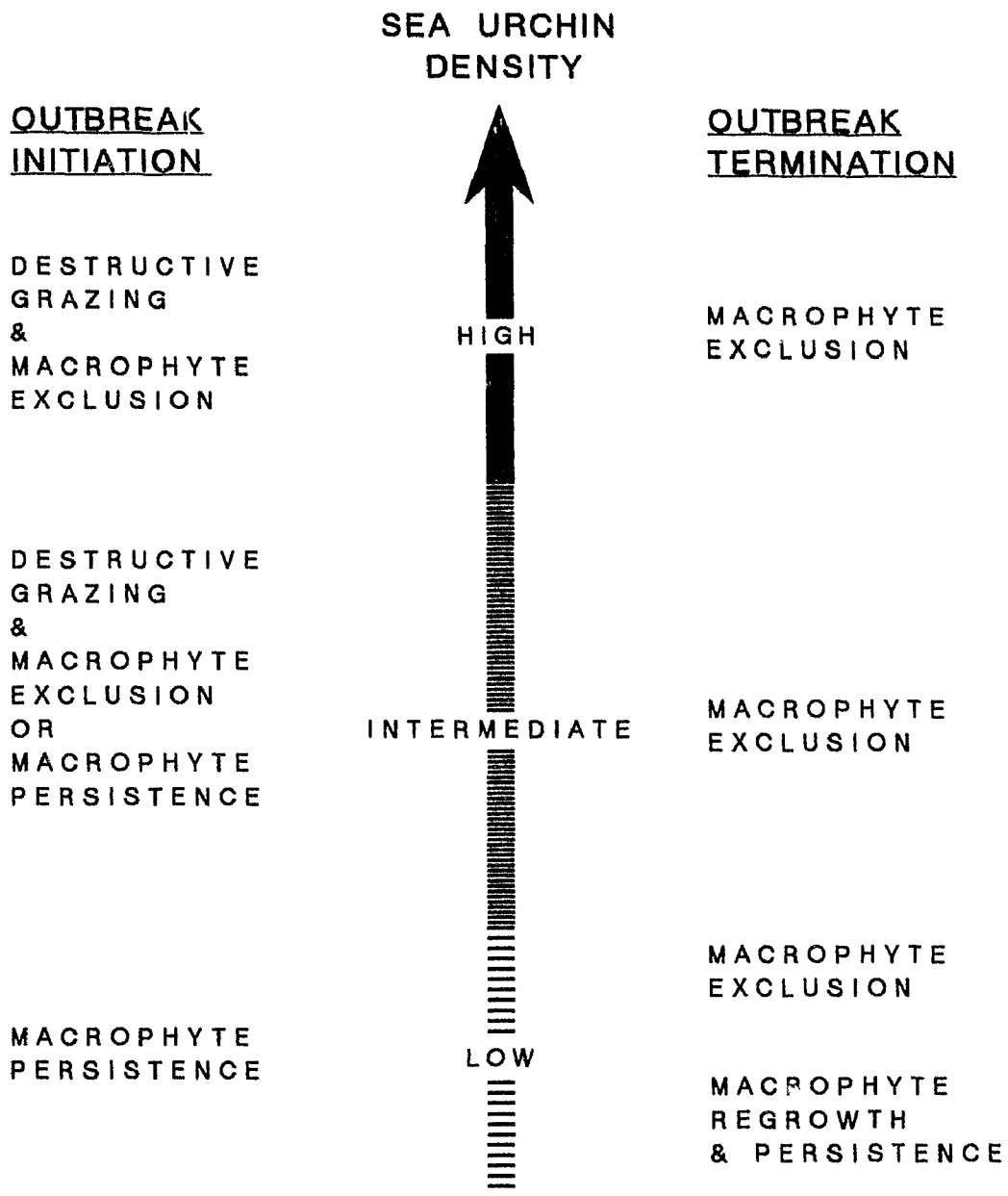

Fig. 9.3 SEA URCHIN DENSITY, AND THE INITIATION AND TERMINATION OF OUTBREAKS. Outbreak initiation, the onset of destructive grazing, is inevitable at high sea urchin densities, environmentally determined at intermediate densities, and impossible at low densities. Outbreak termination, the cessation of macrophyte exclusion, commences at lower urchin densities than the onset of destructive grazing originally required.

This variable outbreak initiation threshold hypothesis predicts that destructive grazing is impossible at low urchin densities, environmentally determined at intermediate densities, and inevitable at high densities (Fig. 9.3). It can be tested by replicated density manipulations in suitable habitats (Section 9.3.2).

Field experiments and natural events have shown that the transition from an urchin-dominated barren ground to a dense algal stand occurs when sea urchin densities are reduced below a certain outbreak termination threshold (Breen & Mann 1976a; Keats *et al.* 1982; Himmelman *et al.* 1983; Miller 1985b; Hagen 1987). This level is probably considerably lower than the outbreak initiation threshold (Bernstein *et al.* 1981), but may be subject to similar variability.

9.2.2 Theoretical models

Most mathematical models of population growth and species interaction incorporate dynamic feedback mechanisms, of a self-regulating, density dependent nature, or in the form of mutually interdependent growth rates. Such models are expressed as a set of differential or difference equations, using respectively a continuous and a discrete time scale.

One of the most fascinating results to date of modern theoretical ecology was the discovery that even the simplest nonlinear difference equations are capable of generating

totally unpredictable chaotic behaviour, which may include irregular outbreaks, when a single growth parameter is increased beyond a certain critical value (May 1974, 1975, 1980; May & Oster 1976). The implication for real world systems is that the population dynamics of any high fecundity species, *e.g. S. droebachiensis*, might prove to be inherently unpredictable.

Aside from the possibility of mathematical chaos, several current models portray scenarios reminiscent of the outbreak phenomenon. For example, May (1977) discusses a deterministic, single species, difference equation model, in which threshold effects and alternate stable states are generated by varying a single parameter representing predation pressure. Abrupt changes in population density may occur spontaneously if this parameter is gradually changed (May 1977), or subjected to low-frequency, red-noise stochastic variation (Steele & Henderson 1984). Other models may generate (Royama 1977), or synchronize (Royama 1984) local outbreaks by adding the effects of weather in the form of white-noise stochastic variation.

The dynamical regimes of May's (1977) alternate stable state model are incorporated and expanded in a cubic differential equation model known as the cusp catastrophe (Jones 1977; Ludwig *et al.* 1978). Sudden population explosions or collapses can be induced in this model by gradually changing two control variables. However, smooth

transitions between high and low population levels are also possible. The cusp catastrophe model has been proposed as a general explanatory metaphor for the population dynamics of taxonomically unrelated outbreak organisms (Rose & Harmsen 1981).

More or less meaningful explanations of the outbreak phenomenon can be given by *a posteriori* elaboration and modification of simple mathematical models such as the above (*e.g.* Mohn & Miller 1987). An alternative approach advocated by Rose & Harmsen (1981), is to first develop a comprehensive simulation model of the outbreak system at hand, and then use sensitivity analysis to identify important variables which may be retained in a simpler explanatory model. The inductive principles underlying the latter approach have great epistemological appeal, but require more detailed ecological knowledge than currently available for *S. droebachiensis*.

9.3 Spatial dynamics

9.3.1 Relevant scales of investigation

The largely unknown factors determining urchin recruitment density fall into three categories: 1) factors affecting the reproductive output of parental sea urchin populations (Keats *et al.* 1984; Thompson 1983, 1984), 2) factors affecting the survival and distribution of planktonic larval stages (Thorson 1950; Ebert 1983; Ebert & Russell 1988; Hart & Scheibling 1988), and 3) factors affecting settlement success and survival of early juvenile stages (Ebert 1983; Andrew & Choat 1985; Pearse & Hines 1987; Raymond & Scheibling 1987; Rowley 1989). In an attempt to delineate the relevant spatial scales required for the investigation of these recruitment factors, I include here a brief, schematic, zoom-out type description of the outbreak phenomenon with reference to the recent outbreak history of *S. droebachiensis* in the North Atlantic.

On a microscopic scale, myriads of urchin larvae settle and survive a critical stage in their life-cycle (cf. Rowley 1989). On a microspatial scale, individual urchins switch from a passive detritivorous lifestyle in cryptic microhabitats, to an aggressive herbivorous lifestyle where they collectively attack intact kelp plants in the openly exposed pursuit of food (Mann 1985). On a local scale, kelp bed destruction progresses through the expansion of urchin-dominated barren patches (Breen & Mann 1976a). On a regional

scale, entire kelp beds are eliminated by the growth and coalescence of several simultaneously appearing barren patches (Mann 1977, 1982). On a larger geographical scale, a wave of destructive grazing proceeds unidirectionally along a coastline (Wharton & Mann 1981), while elsewhere barren areas continue to persist in the outbreak stage (Hooper 1980; Himmelman *et al.* 1983). And finally, on an amphiatlantic scale, outbreaks occur at virtually the same time on both sides of an ocean (Hagen 1983).

Regional, and larger scale patterns of kelp bed destruction involve planktonic processes of a largely unknown status. There is, however, some evidence from California to suggest that regional oceanographic processes associated with coastal upwelling are correlated with areas of low sea urchin recruitment (Ebert & Russell 1988). The persistence of kelp beds in upwelling areas off southern Nova Scotia during the recent sea urchin outbreak (Wharton & Mann 1981) suggests that similar causal mechanisms might be operating on both coasts.

The similarity of patterns of kelp bed destruction by *S. droebachiensis* on both sides of the Atlantic was noted by Hagen (1983). Although events on such a large scale may be purely coincidental, and are difficult to investigate, it should not be overlooked that reduction of commercially important planktivorous fish stocks in the North Atlantic, *e.g.* herring and capelin, may have altered the coastal

ecosystems in ways that could have influenced the dynamics of sea urchin populations, perhaps through reduced predation pressure on urchin embryos and larvae (Rumrill & Chia 1985).

9.3.2 Habitat-related outbreak initiation

Dense populations of kelp and sea urchins appear to be mutually exclusive. High density populations of *S. droebachiensis* do not occur inside kelp beds, but are restricted to narrow transition zones at the edge of kelp beds, where destructive grazing takes place (Breen & Mann 1976a; Breen 1980; Bernstein *et al.* 1981; Hagen 1983). Furthermore, experimental transplantation of up to 400 large urchins to the interior of a Nova Scotian kelp bed failed to induce formation of destructive feeding aggregations (Breen 1974; Breen & Mann 1976a). It was therefore proposed in Chapter 6 that conditions resembling a urchin-dominated barren ground, *i.e.* a habitat patch unsuitable for kelp but with a high density of starved large urchins, must be present in the vicinity, rather than in the interior, of a kelp bed before the initial formation of destructive feeding aggregations can commence (Fig. 9.4). This proposition is consistent with patterns of destructive grazing exhibited by *S. droebachiensis* (Breen & Mann 1976a; Bernstein *et al.* 1981; Hagen 1983), as well as by other species of urchins (Harrold & Pearse 1987). It is also consistent with the behavioural responses documented in Part I of this study (Chapter 6).

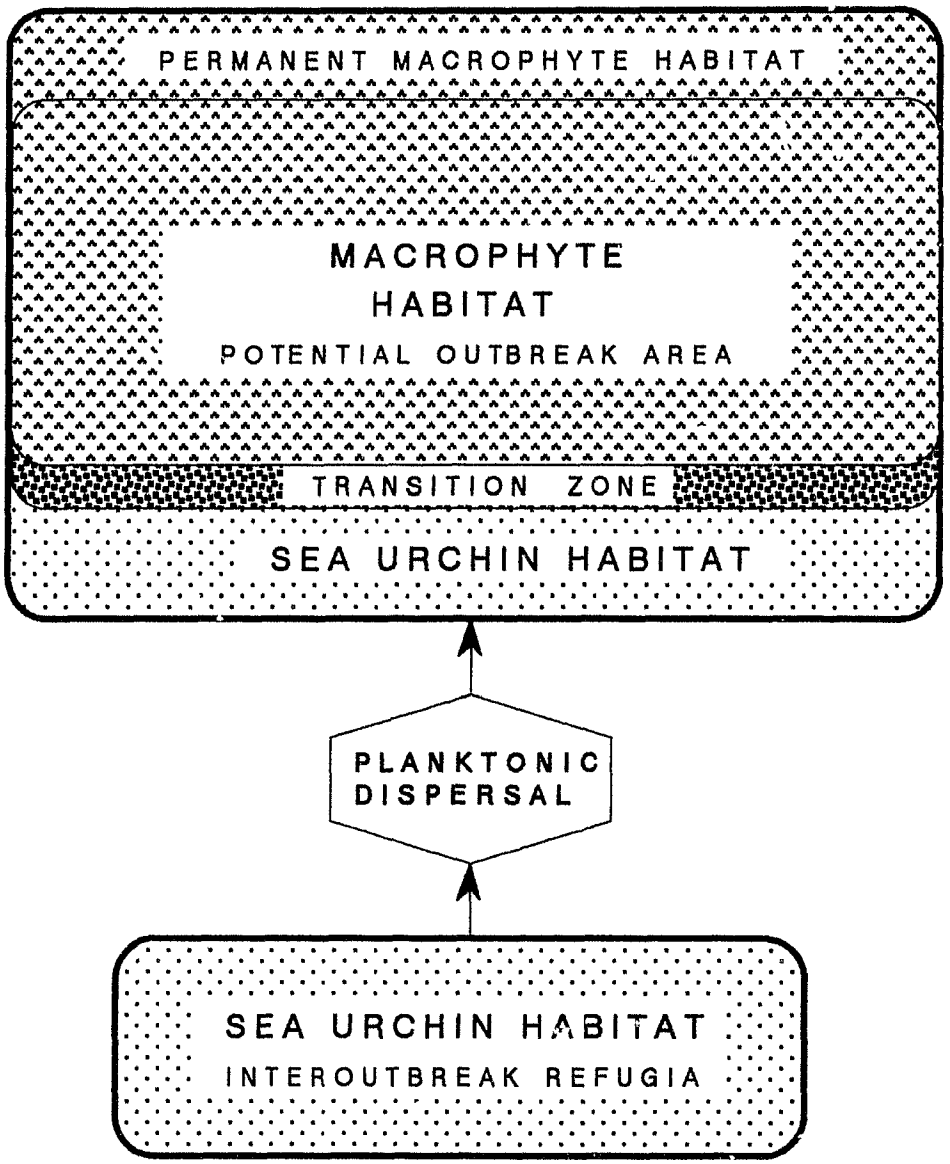

Fig. 9.4 HYPOTHETICAL HABITAT RELATED OUTBREAK DYNAMICS. The macrophyte habitat is divided into a potential outbreak area and a permanent habitat which is inaccessible to sea urchins. The potential outbreak area is also bordered by a sea urchin habitat which is unsuitable for macrophytes. Outbreaks are initiated when urchin densities in this habitat increase beyond a certain threshold value, thus triggering the formation of destructive feeding aggregations in a transition zone on the boundary between the sea urchin habitat and the macrophyte habitat. During the interoutbreak stage, dense sea urchin populations, which may supply larvae to establish outbreak populations, are located in remote refugial habitats.

This dual-habitat hypothesis of outbreak initiation warrants further investigation, and should be tested by experimental density manipulations of sea urchin populations in the field. Experimental outbreak initiation could, for example, be attempted by the replicated release of high numbers of sea urchins both inside kelp beds and in suitable adjacent habitats, *i.e.* habitats unsuitable for kelp growth, such as shallow subtidal boulderfields, red algal communities below the kelp zone, or patches of unstable substrata in the kelp zone.

9.3.3 The outbreak area

Although outbreak populations of *S. droebachiensis* may decimate most of the subtidal vegetation along an entire coastline (Wharton & Mann 1981), a minor portion of the macrophyte habitat appears to be immune to destructive grazing. Such permanent macrophyte habitats include shallow bands of kelp in wave exposed areas (Himmelman & Lavergne 1985), isolated patches of kelp in otherwise barren areas (Bernstein *et al.* 1981; Chapman 1981), and undisturbed kelp beds in districts influenced by coastal upwelling (Wharton & Mann 1981).

Other species of sea urchins establish different patterns of macrophyte exclusion. In Europe, dense populations of *Echinus esculentus* may determine the lower distributional

limit of the kelp *Laminaria hyperborea* (Jorde & Klavestad 1963; Jones & Kain 1967). In New Zealand, *Evechinus chloroticus* maintains barren urchin-dominated areas which are restricted to an intermediate zone, bordered from above and below by dense algal stands (Andrew 1988). In California, the dynamics of variable sized patches dominated by *S. franciscanus* and *S. purpuratus* have been studied for three decades (Schiel & Foster 1986; Harrold & Pearse 1987), and in Australia, localized barren patches are centered on crevices containing *Centrostephanus rodgersii* (Andrew & Underwood 1989).

The evidence would indicate that the extent of macrophyte exclusion by *S. droebachiensis* in the North Atlantic (Wharton & Mann 1983; Hagen 1983; Himmelman *et al.* 1983; Keats *et al.* 1985b), with the possible exception of strongylocentrotid sea urchins in the northernmost Pacific (Simestad *et al.* 1978; Estes *et al.* 1982; Dayton & Tegner 1984), is unrivaled by other sea urchins.

9.3.4 Interoutbreak refugia

Detectable recruitment of juvenile urchins into former barren grounds off Nova Scotia, where adult sea urchins were lacking due to recurrent epizootics (Miller & Colodey 1983; Scheibling & Stephenson 1984), occurred in 3 out of 5 years (Raymond & Scheibling 1987), thus confirming the existence of unidentified interoutbreak refugia harboring parental sea urchin populations (Fig. 9.4). The larvae of *S. droebachiensis* spend 4-12 weeks in the plankton (Strathman 1978; Hart & Scheibling 1988), suggesting that Nova Scotian outbreak populations could be recruited from remote upstream areas where epizootic mass mortality has not occurred, for example from such areas as the persistent barren grounds or rhodolith bottoms off Newfoundland (Himmelman 1980; Keats *et al.* 1984), The Gulf of St. Lawrence (Himmelman *et al.* 1983), or The Canso Strait area (Chapter 2).

9.4 Concluding remarks

Part I of this study demonstrates that the green sea urchins' patterns of feeding (Chapter 5), aggregation (Chapter 3), and microhabitat utilization (Chapter 4), underwent significant changes in response to controlled experimental manipulations in the laboratory. Identification of characteristic patterns, corresponding to different phases in the outbreak sequence, permitted comparison with results from field studies, and reevaluation of hypotheses pertaining to the mechanisms of outbreak initiation (Chapter 6).

Part II of this study demonstrates functional predator responses to increases in urchin density (Chapter 7) and explores the effects of predation and recruitment on the outbreak dynamics of *S. droebachiensis* in a simulation model (Chapter 8). Contrary to indications from Part I, the model suggests that seasonally migratory visual predators (*e.g.* wolffish), which presumably are incapable of exploiting cryptic prey, have little effect on the urchins' overall capacity to destroy seaweed and maintain barren grounds, whereas perpetually present predators (*e.g.* decapods) have a theoretical potential to prevent or terminate outbreaks irrespective of their ability to exploit cryptic prey. The effects of a given level of predation, however, could always be nullified by increasing the recruitment density of the urchins.

These results would suggest that the determinants of urchin recruitment density are also the ultimate determinants of outbreak initiation and termination. The model further suggests that predation on late juvenile and adult stages may influence the interaction between sea urchins and kelp, but only when urchin recruitment density is confined to intervals where outbreaks are possible but not inevitable.

In conclusion, it would appear that further understanding of the outbreak dynamics of S. *droebachiensis* is dependent on coastal ecology research priorities in the two principal outbreak countries, Canada and Norway. The Canadian east coast currently offers excellent opportunities for the study of all aspects of outbreak initiation including, experimental induction of destructive grazing, identification of interoutbreak refugia, and investigation of the dynamics of urchin populations during the interoutbreak state. In Norway, testing the prediction of impending outbreak termination due to a macroparasitic epizootic (Hagen 1987; Jones & Hagen 1987) would appear to be the most urgent focus.

APPENDIX 1. EXAMINATION OF ANOVA-RESIDUALS

Statistical independence, constancy of variance and normality are the three basic assumptions about the distribution of the residuals, or errors, in analysis of variance models. Lack of dependence of the error terms can have serious effects on inferences in the analysis of variance, and is often difficult to correct. Unequal variances and non-normality of the residuals are less problematic because the F tests in the analysis of variance are robust against these deficiencies when fixed effects models are used and sample sizes are approximately equal. Besides, variances can often be stabilized, and lack of normality corrected, by choosing appropriate transformations for the dependent variable (Draper & Smith 1981; Neter *et al.* 1985). Here indices of aggregation were transformed logarithmically; % cryptic and % refuge-usage were transformed using the angular transformation, but % feeding was not transformed (cf. Sokal & Rohlf 1981).

Graphic analysis of residuals is, despite its inherent subjectivity, the standard technique for detecting serious departures from the assumptions of analysis of variance models (Draper & Smith 1981; Neter *et al.* 1985). Here the assumption of independence was evaluated by plotting residuals versus time, temperature and final sea urchin density. Overlap in the data necessitated the use of cellulated sunflower plots. In these plots the number of data

points in the vicinity of the center of a sunflower symbol is illustrated by the number of emanating petals or lines (Cleveland 1985; Feldman *et al.* 1987). A satisfactory plot indicating no dependence among the residuals should give the overall impression of a horizontal band.

Homoscedasticity, or constancy of variance, was evaluated by plotting residuals versus predicted values of the dependent variables, again using cellulated sunflower plots. A satisfactory plot indicating equal variance among the residuals should give the overall impression of a horizontal band.

Normality was evaluated by plotting residuals versus expected values from theoretical normal distributions. A satisfactory normal plot should approximate a straight line. As an additional evaluation of normality theoretical normal curves were superimposed on histograms of the residuals.

Residuals and predicted values were calculated using the Microsoft Excel spreadsheet, sunflower plots were constructed using StatView II, and normal plots were constructed with SYSTAT. All plots were edited in MacDraw II.

A1.1 Mean aggregation size, m_2, Tables 3.4 & 3.5

A1.1.1 Independence

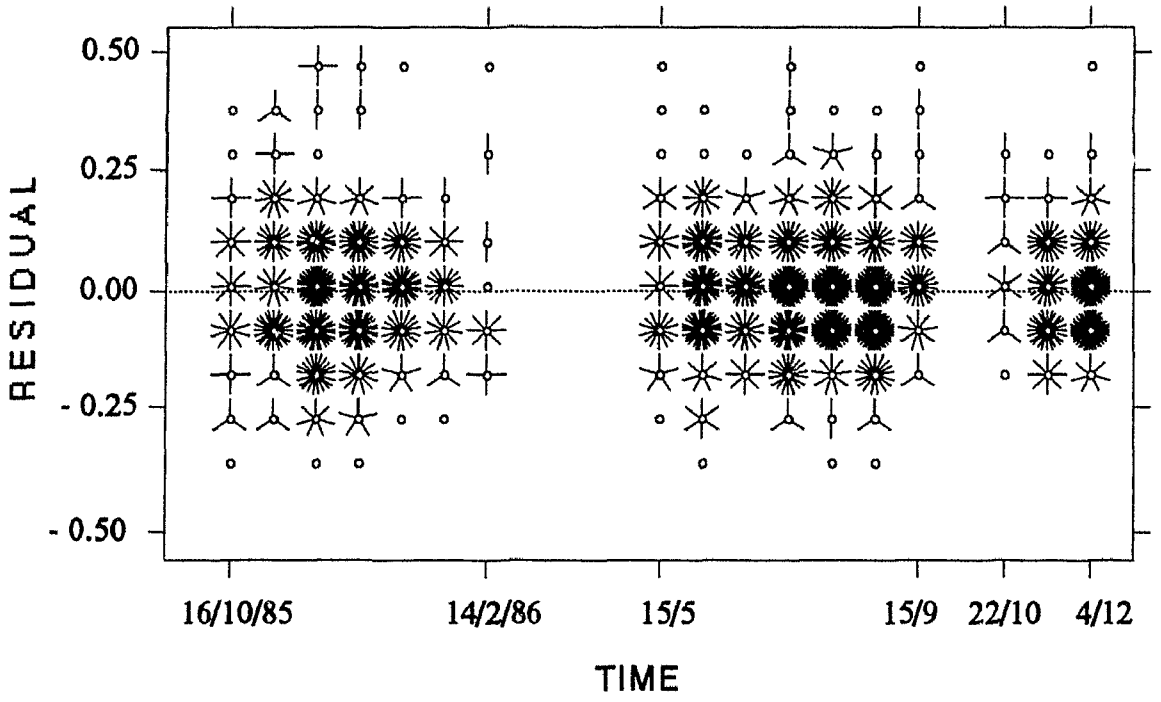

Fig. A1.1 SEQUENTIAL SUNFLOWER PLOT OF $LOG_{10}(m_2)$ RESIDUALS.

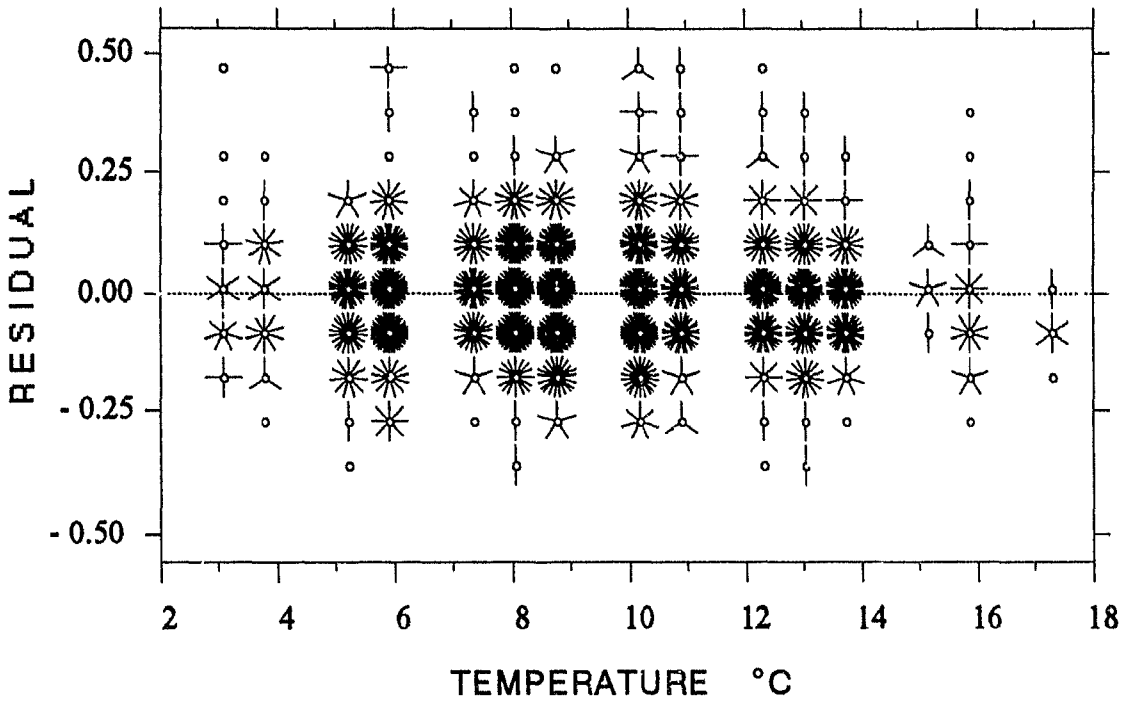

Fig. A1.2 $LOG_{10}(m_2)$ RESIDUALS VERSUS SEAWATER TEMPERATURE.

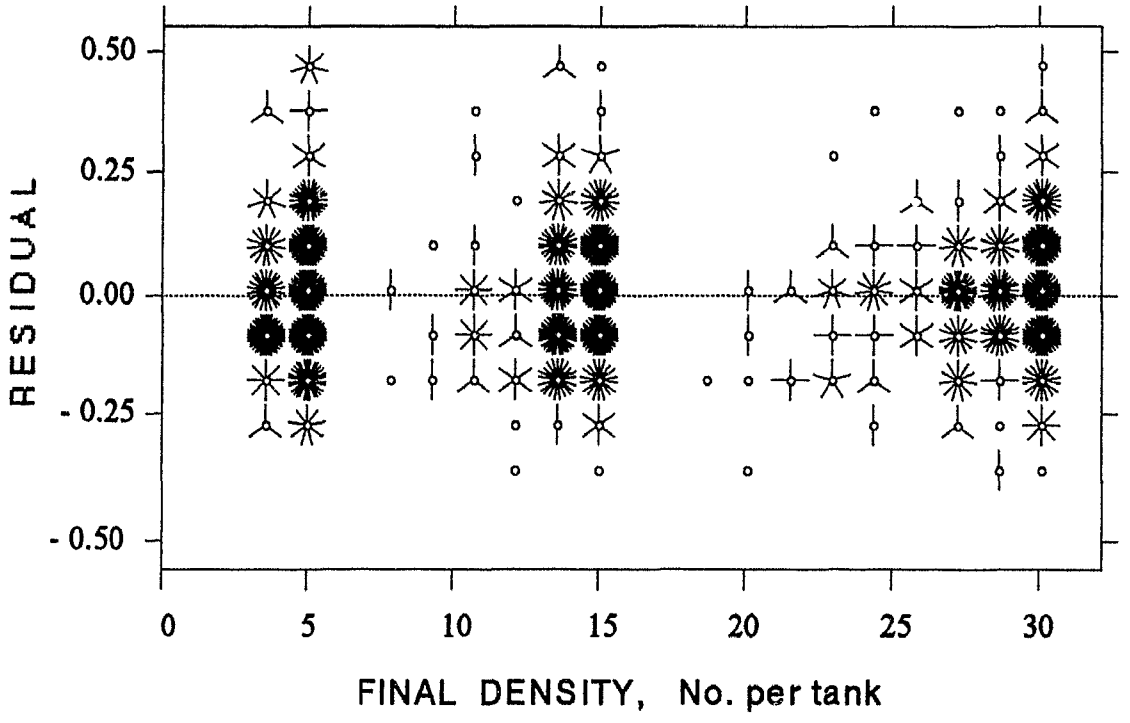

Fig. A1.3 $LOG_{10}(m_2)$ RESIDUALS VERSUS FINAL SEA URCHIN DENSITY.

A1.1.2 Homoscedasticity

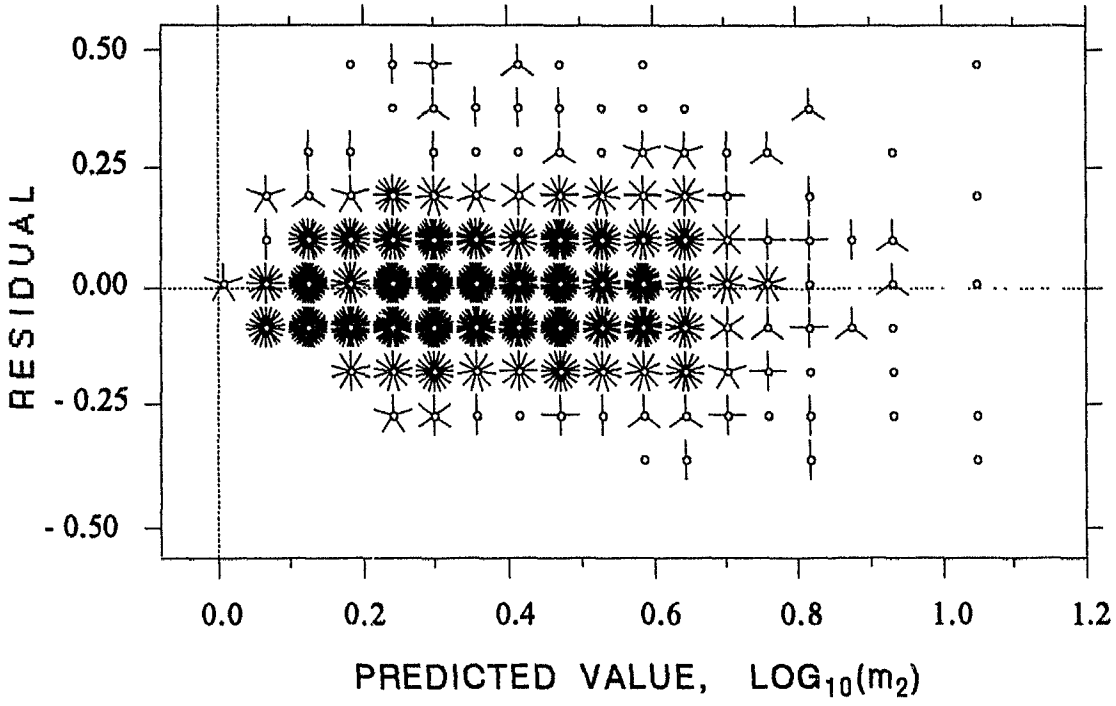

Fig. A1.4 $LOG_{10}(m_2)$ RESIDUALS VERSUS PREDICTED VALUES.

A1.1.3 Normality

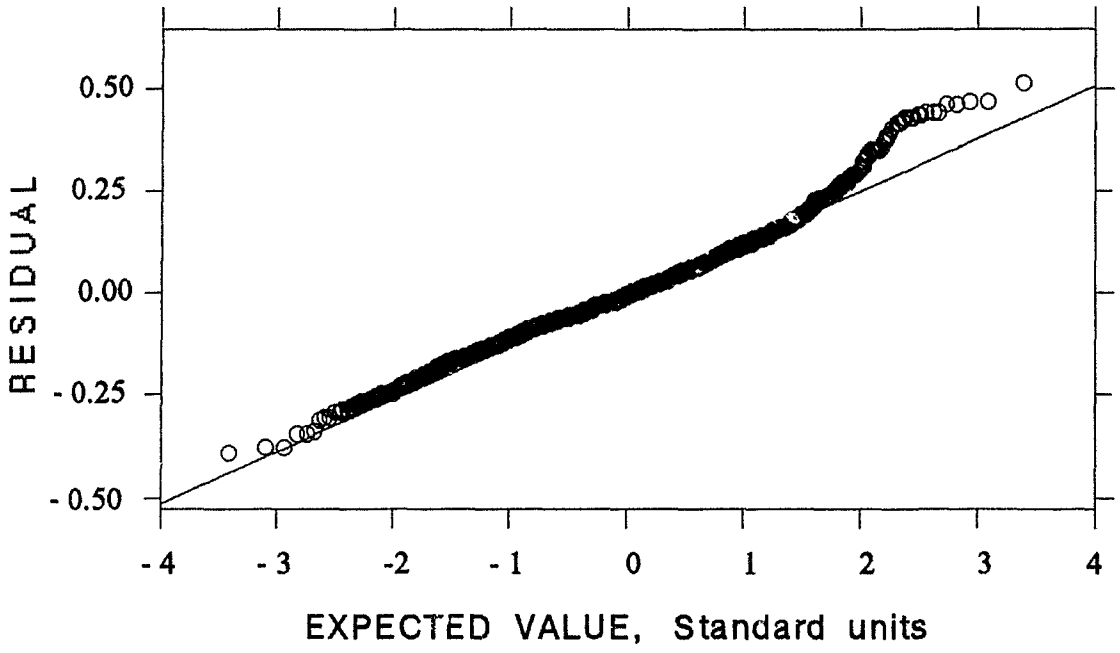

Fig. A1.5 NORMAL PROBABILITY PLOT OF $LOG_{10}(m_2)$ RESIDUALS. The residuals of are plotted against corresponding values from a theoretical normal distribution.

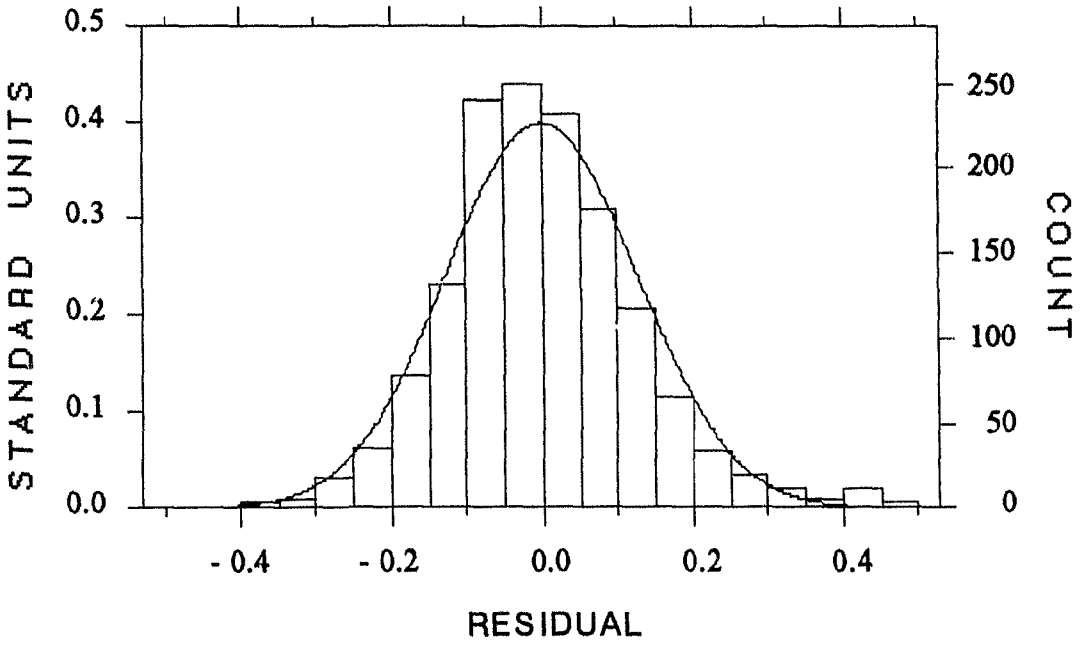

Fig. A1.6 HISTOGRAM OF $LOG_{10}(m_2)$ RESIDUALS WITH FITTED NORMAL CURVE.

A1.2 Mean crowding within aggregations, $\overset{*}{m}_2$, Tables 3.4 & 3.5

A1.2.1 Independence

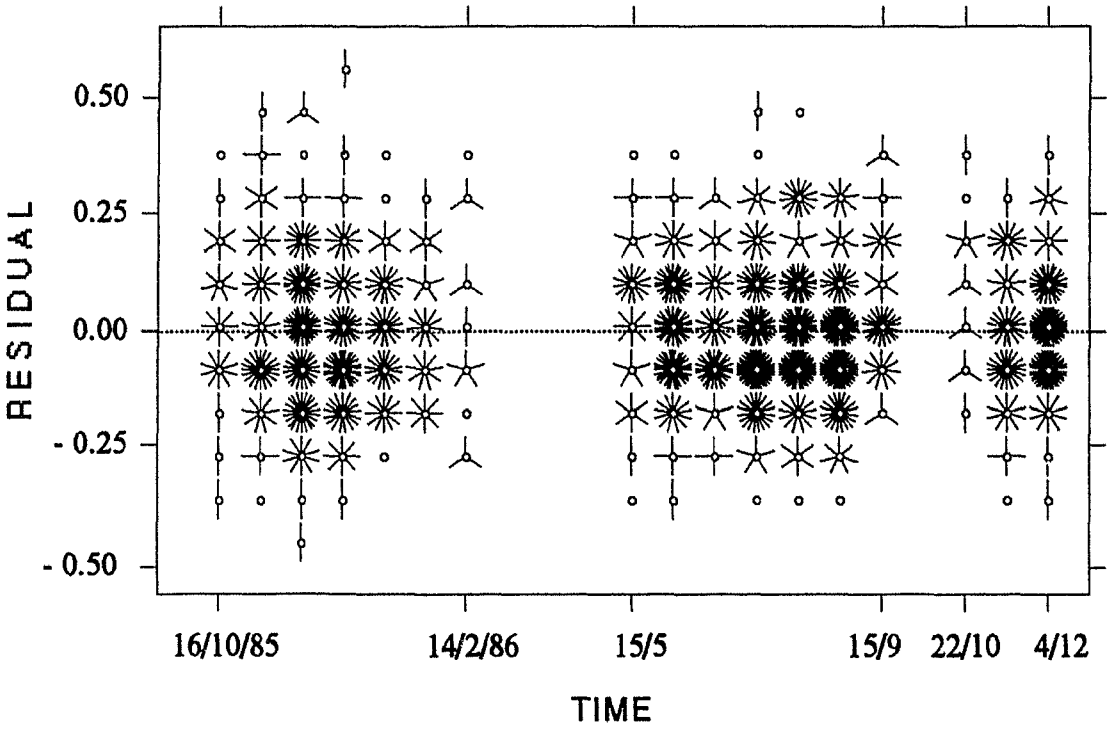

Fig. A1.7 SEQUENTIAL SUNFLOWER PLOT OF $LOG_{10}(1 + \overset{*}{m}_2)$ RESIDUALS.

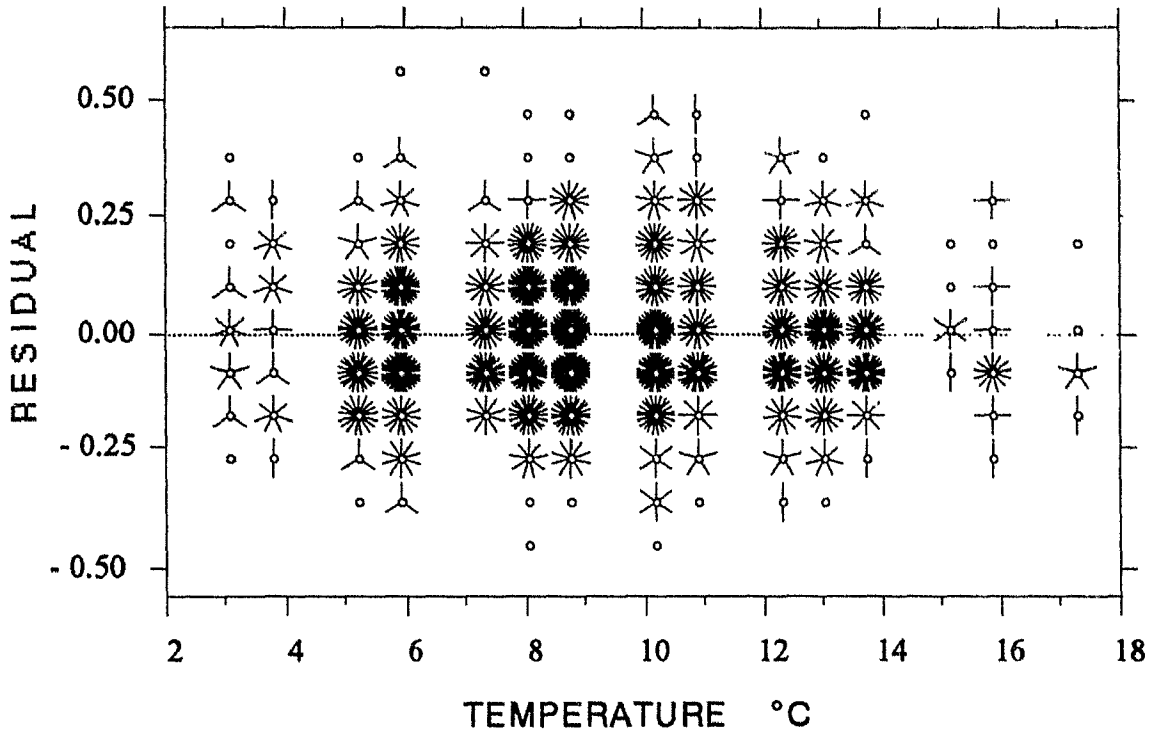

Fig. A1.8 $LOG_{10}(1 + \overset{*}{m}_2)$ RESIDUALS VERSUS SEAWATER TEMPERATURE.

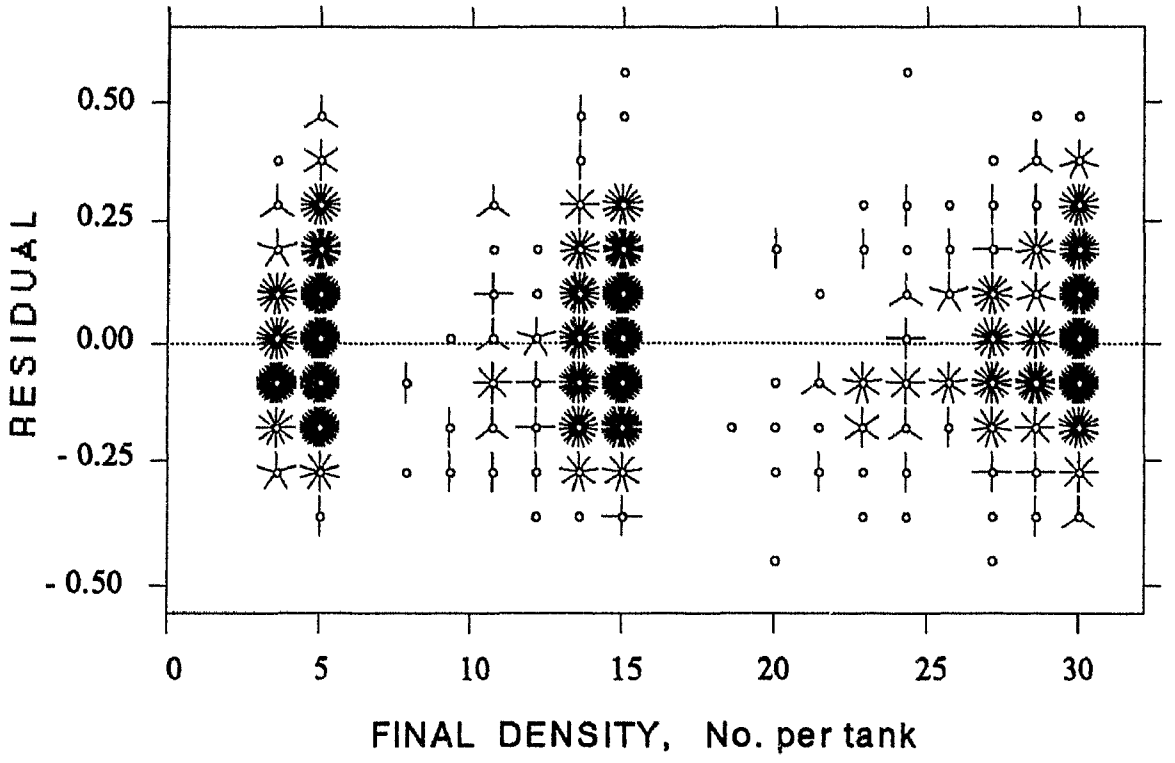

Fig. A1.9 $LOG_{10}(1 + \overset{*}{m}_2)$ RESIDUALS VERSUS FINAL URCHIN DENSITY.

A1.2.2 Homoscedasticity

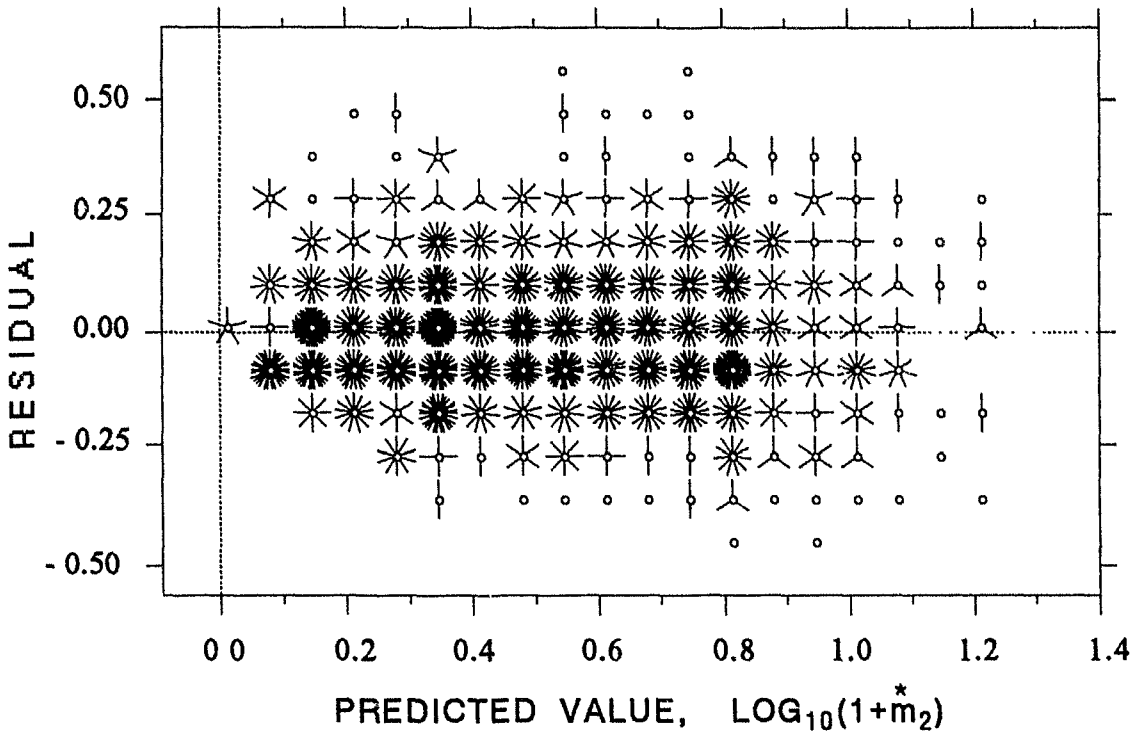

Fig. A1.10 $LOG_{10}(1+\overset{*}{m}_2)$ RESIDUALS VERSUS PREDICTED VALUES.

A1.2.3 Normality

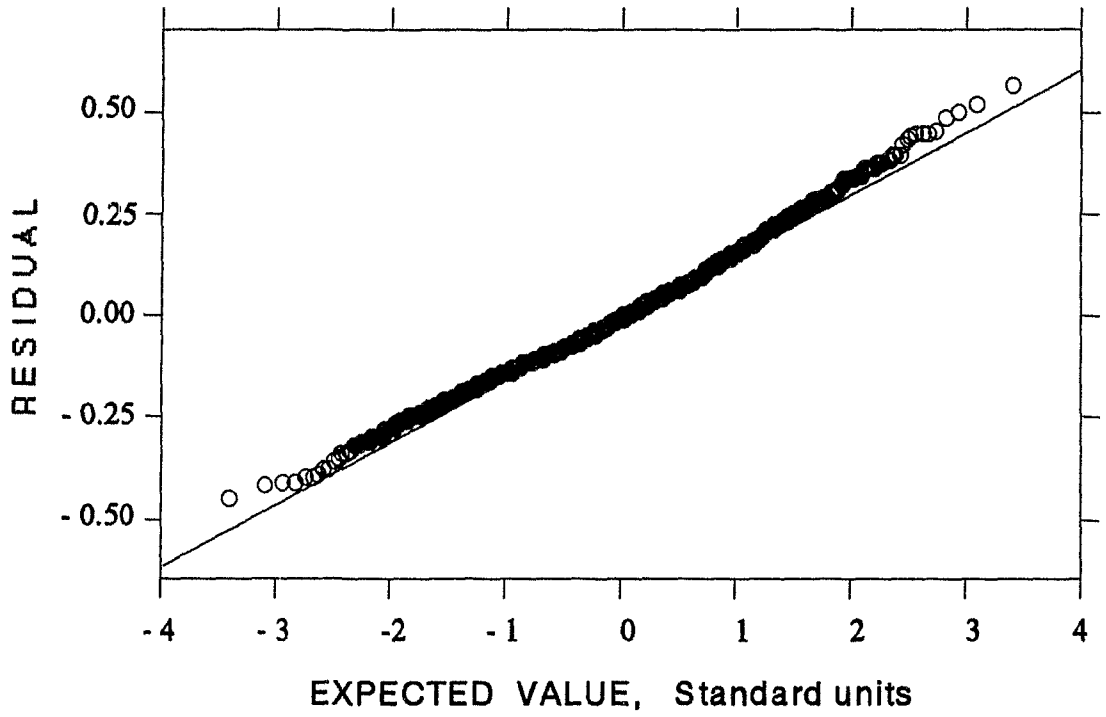

Fig. A1.11 NORMAL PROBABILITY PLOT OF $LOG_{10}(1 + \tilde{m}_2^*)$ RESIDUALS.

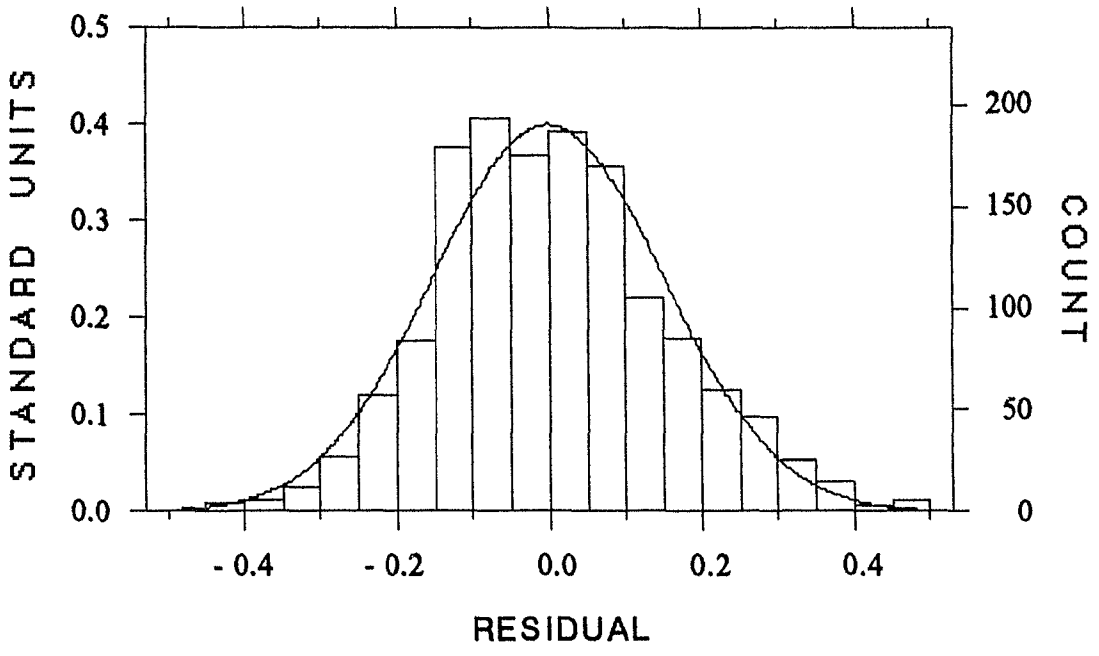

Fig. A1.12 HISTOGRAM OF $LOG_{10}(1 + \tilde{m}^{*}_{2})$ RESIDUALS WITH FITTED NORMAL CURVE.

A1.3 Patchiness, $\frac{\overset{*}{m}_2}{m_2}$, Table 3.5

A1.3.1 Independence

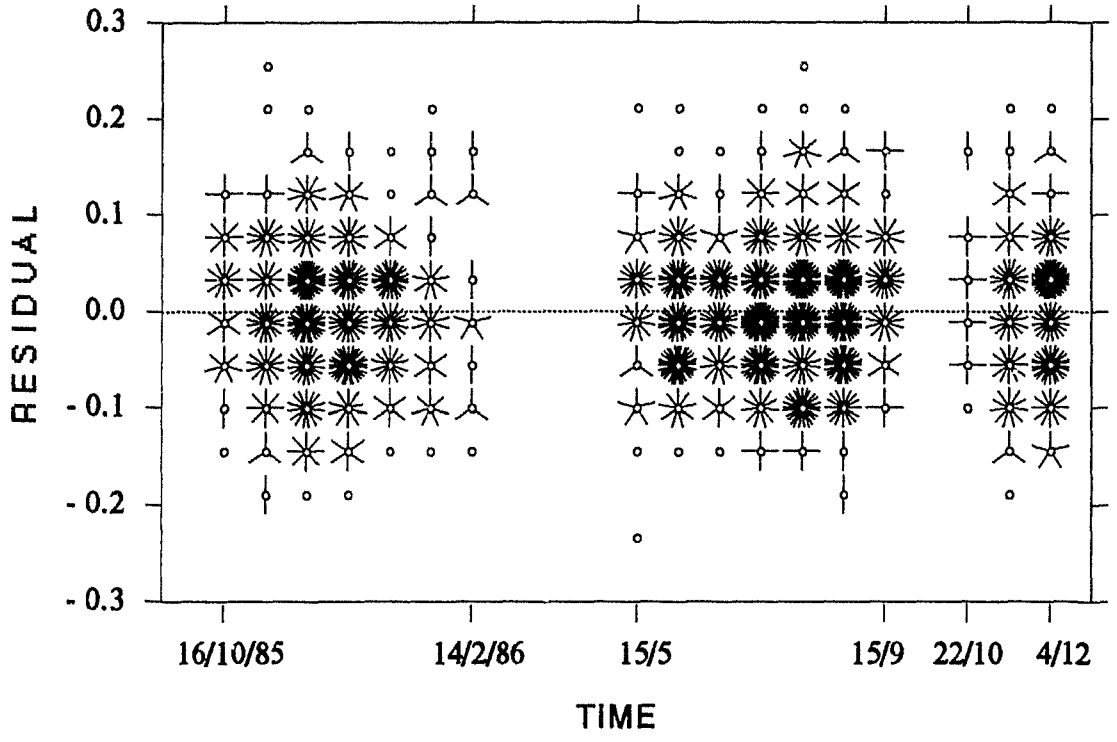

Fig. A1.13 SEQUENTIAL SUNFLOWER PLOT OF $LOG_{10}(1 + \frac{\overset{*}{m}_2}{m_2})$ RESIDUALS.

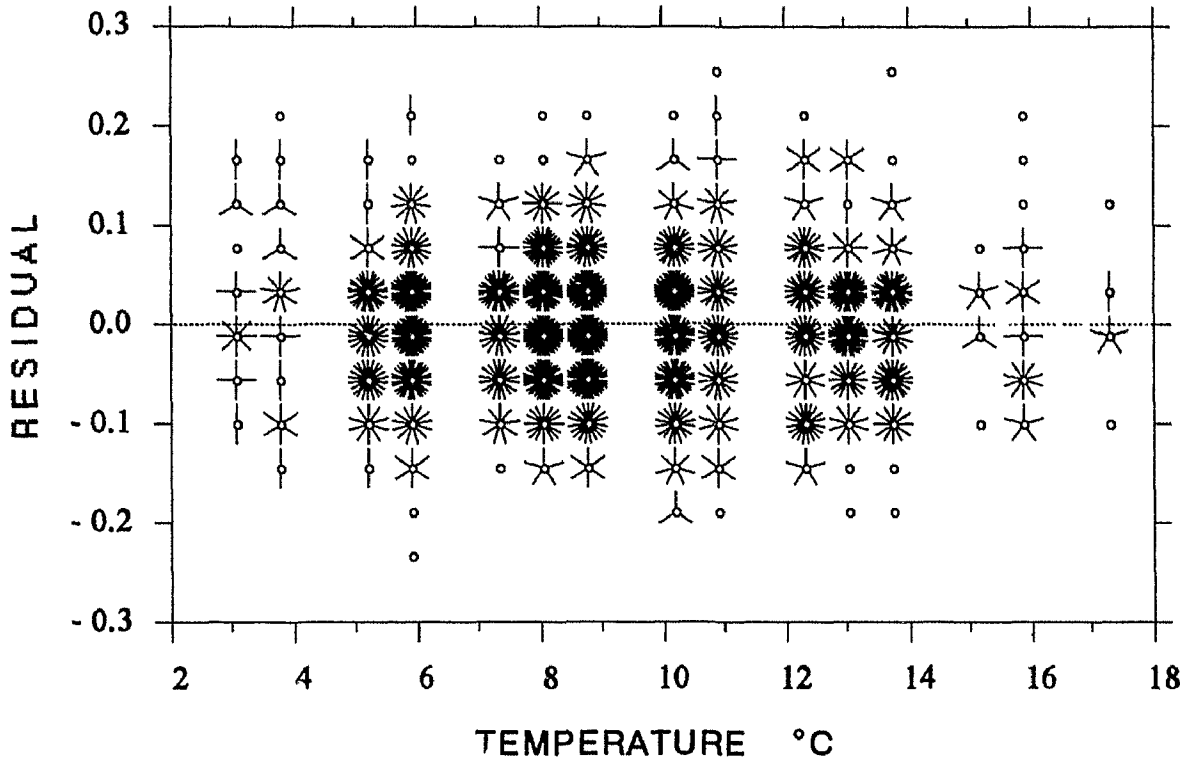

Fig. A1.14 $LOG_{10}(1 + \frac{\overset{*}{m}_2}{m_2})$ RESIDUALS VERSUS SEAWATER TEMPERATURE.

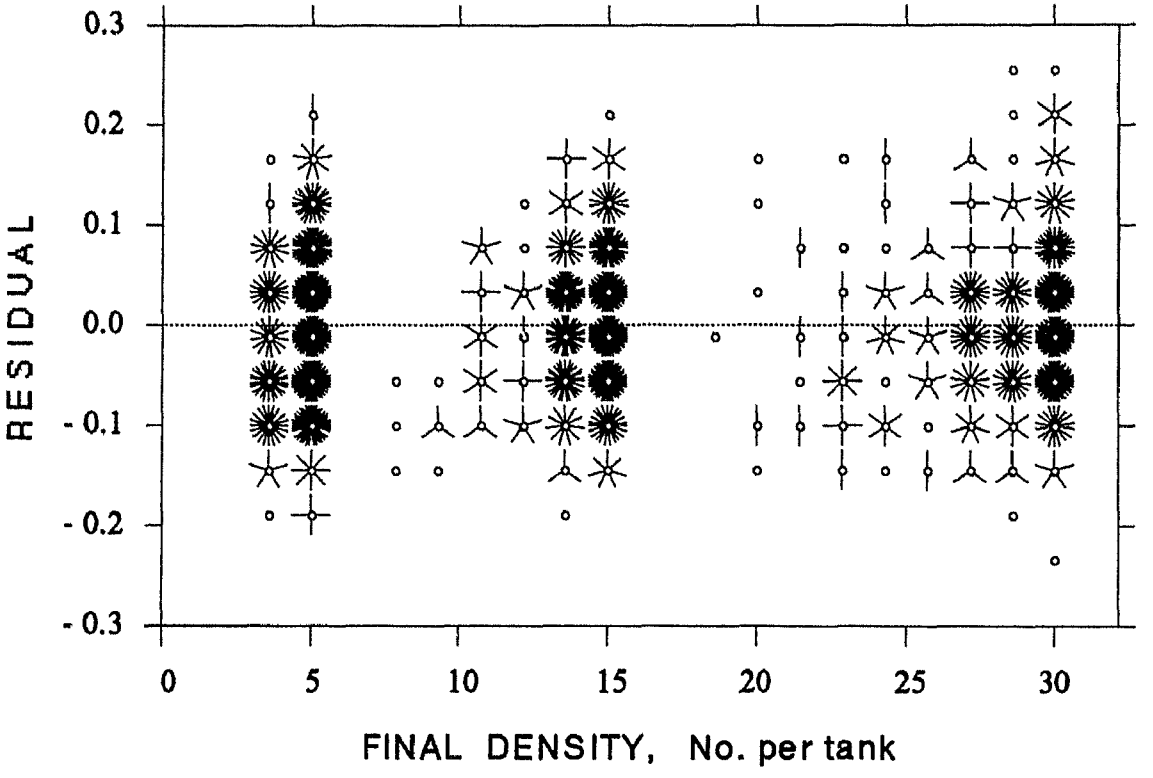

Fig. A1.15 $LOG_{10}(1 + \frac{\overset{*}{m}_2}{m_2})$ RESIDUALS VERSUS FINAL URCHIN DENSITY.

A1.3.2 Homoscedasticity

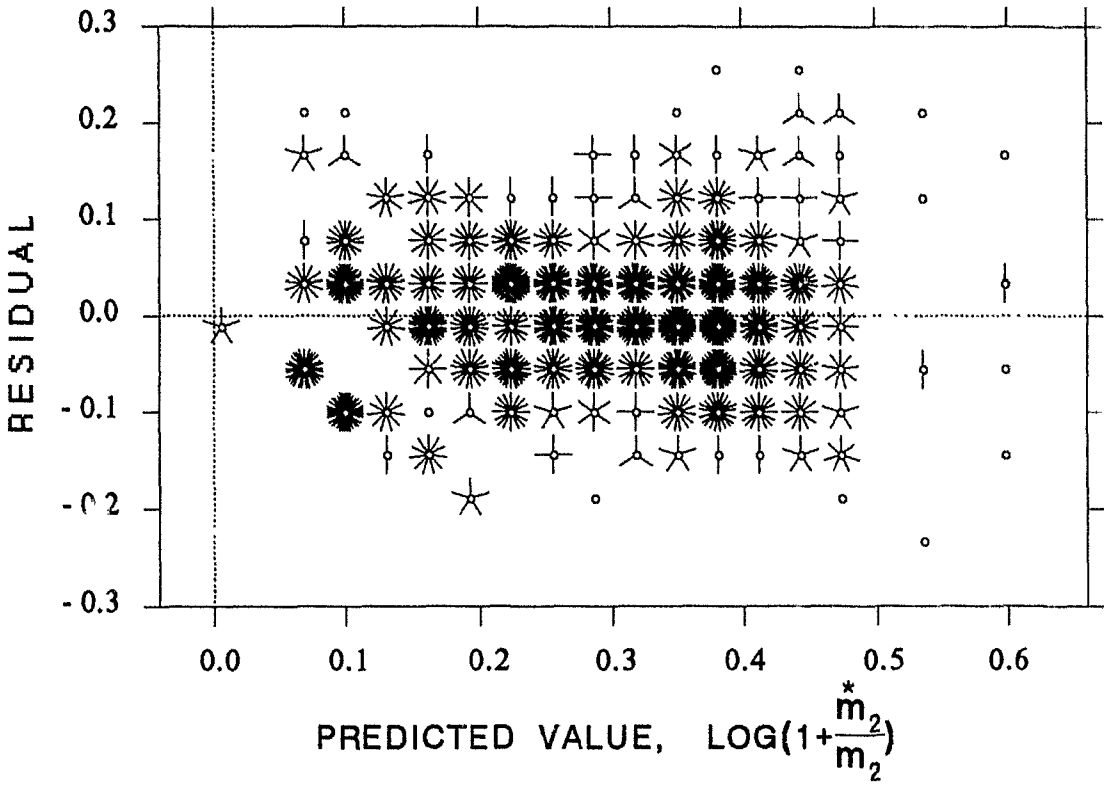

Fig. A1.16 $LOG_{10}(1+\frac{m^*_2}{m_2})$ RESIDUALS VERSUS PREDICTED VALUES.

A1.3.3 Normality

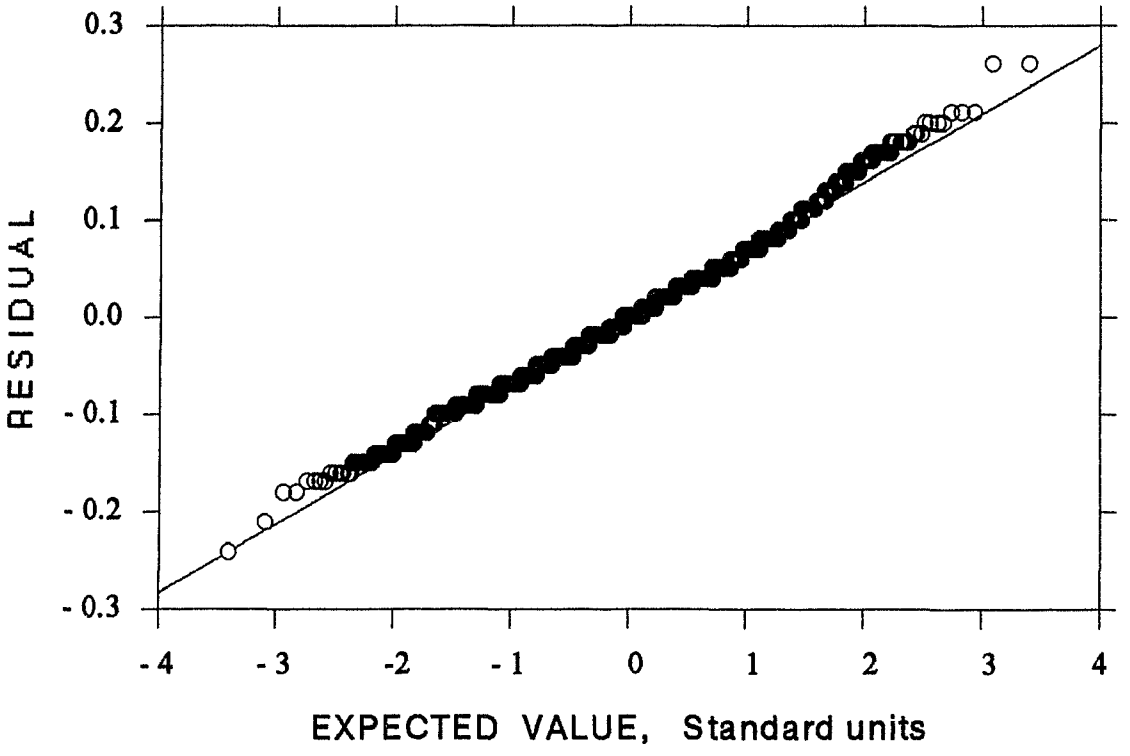

Fig. A1.17 NORMAL PROBABILITY PLOT OF $LOG_{10}(1 + \frac{\overset{*}{m}_2}{m_2})$ RESIDUALS.

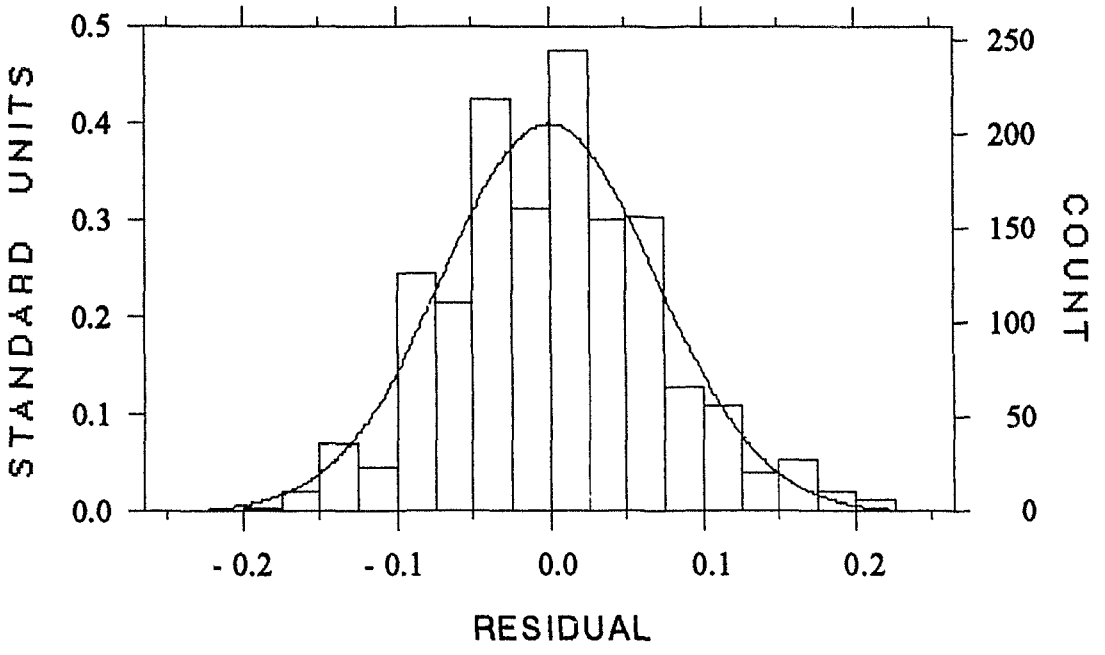

Fig. A1.18 HISTOGRAM OF $LOG_{10}(1 + \tilde{m}_2^*)$ RESIDUALS WITH FITTED NORMAL CURVE.

A1.4 Mean % cryptic, Table 4.5

A1.4.1 Independence

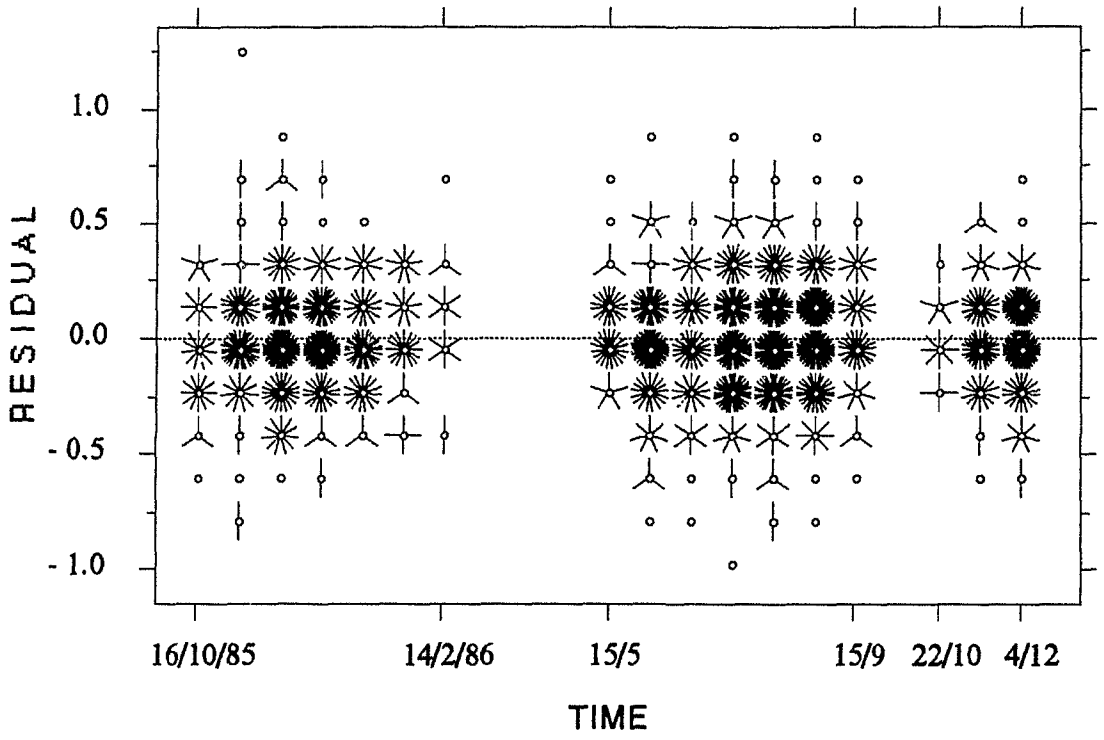

Fig. A1.19 SEQUENTIAL SUNFLOWER PLOT OF ASIN($\sqrt{\%\ \text{CRYPTIC}}$) RESIDUALS.

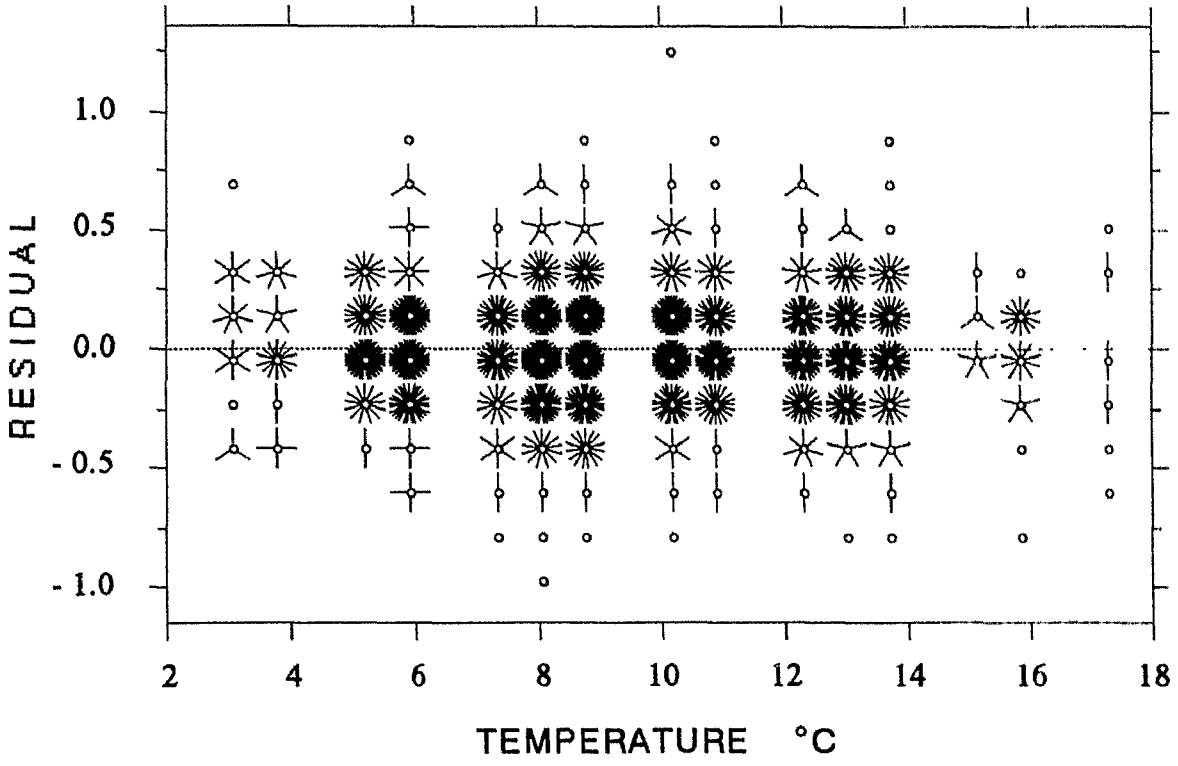

Fig. A1.20 ASIN($\sqrt{\%}$ CRYPTIC) RESIDUALS VERSUS SEAWATER TEMPERATURE.

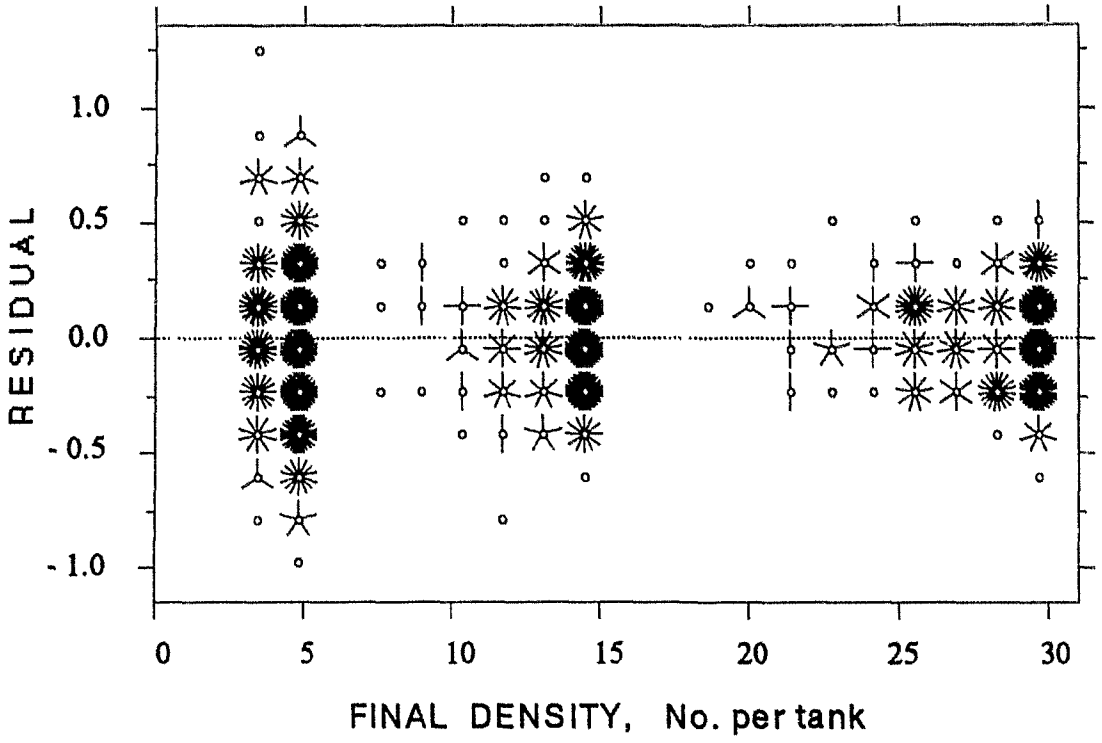

Fig. A1.21 ASIN($\sqrt{\%}$ CRYPTIC) RESIDUALS VERSUS FINAL SEA URCHIN DENSITY.

A1.4.3 Homoscedasticity

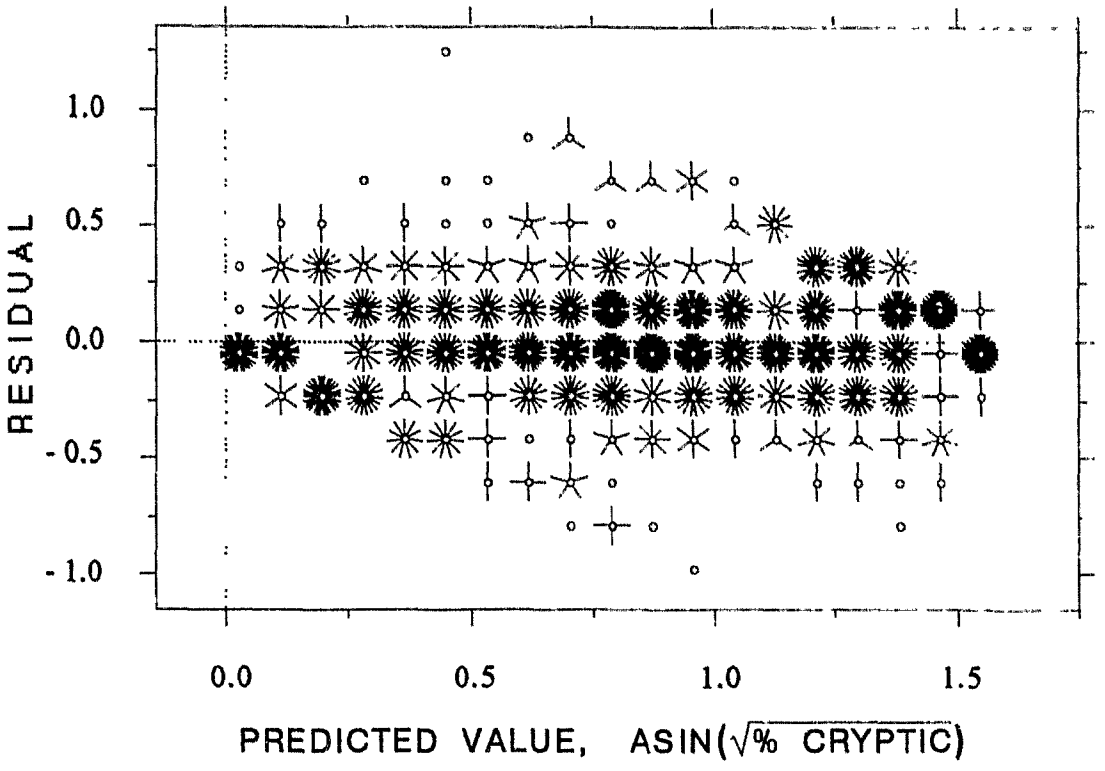

Fig. A1.22 ASIN($\sqrt{\%\ \text{CRYPTIC}}$) RESIDUALS VERSUS PREDICTED VALUES.

A1,4,3 Normality

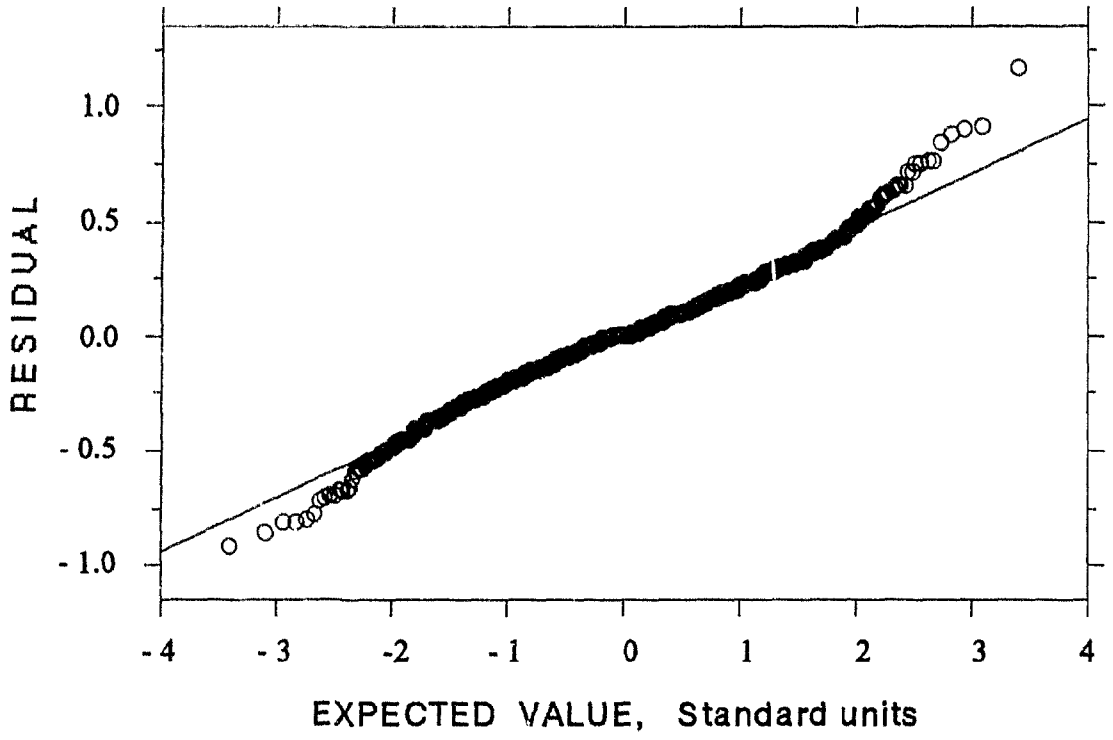

Fig. A1.23 NORMAL PROBABILITY PLOT OF ASIN($\sqrt{\%\ \text{CRYPTIC}}$) RESIDUALS.

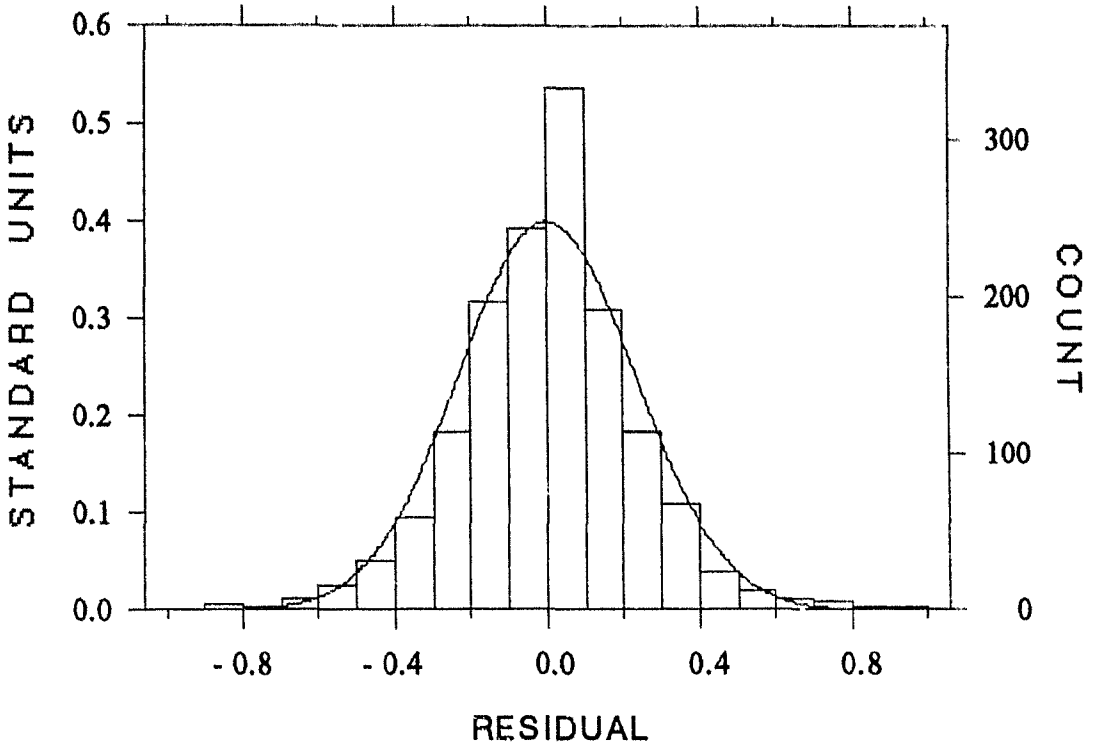

Fig. A1.24 HISTOGRAM OF ASIN($\sqrt{\%\ \text{CRYPTIC}}$) RESIDUALS WITH FITTED NORMAL CURVE.

A1.5 Mean % refuge usage, Table 4.8

A1.5.1 Independence

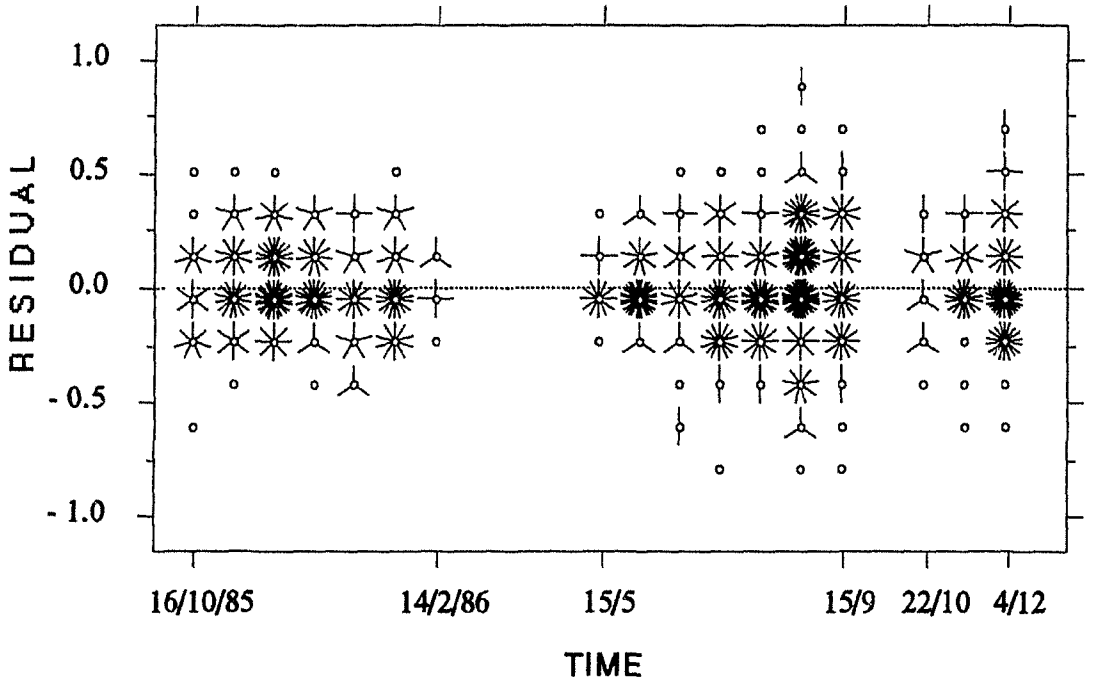

Fig. A1.25 SEQUENTIAL SUNFLOWER PLOT OF ASIN($\sqrt{\%}$ REFUGE USAGE) RESIDUALS.

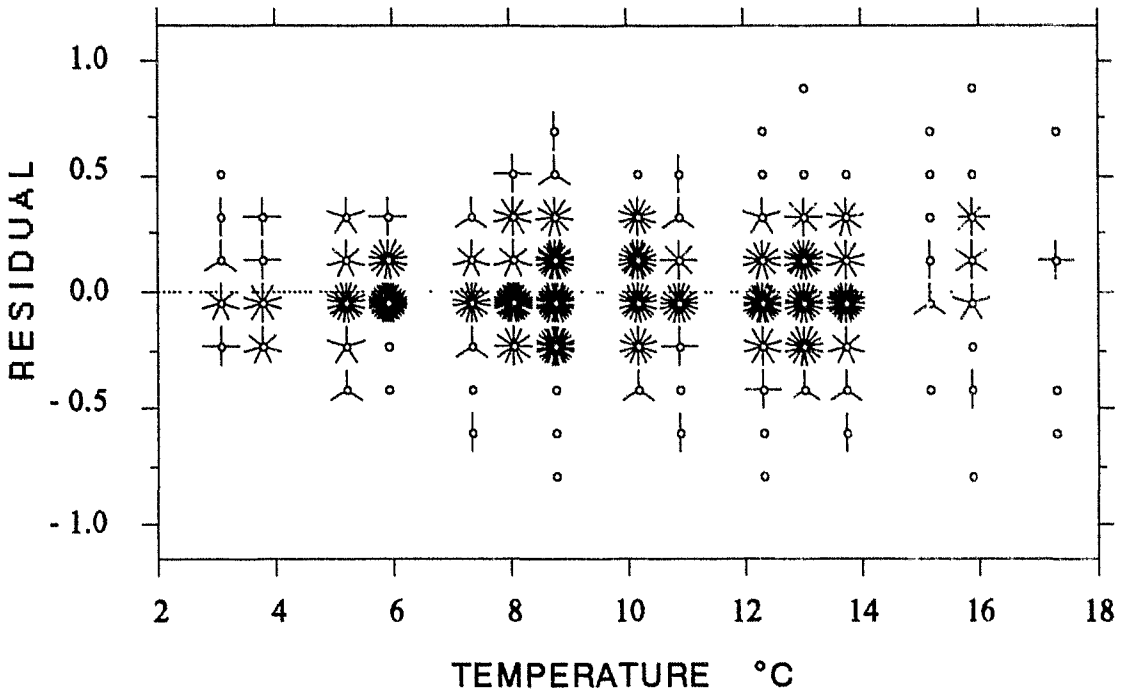

Fig. A1.26 ASIN($\sqrt{\%}$ REFUGE USAGE) RESIDUALS VERSUS SEAWATER TEMPERATURE.

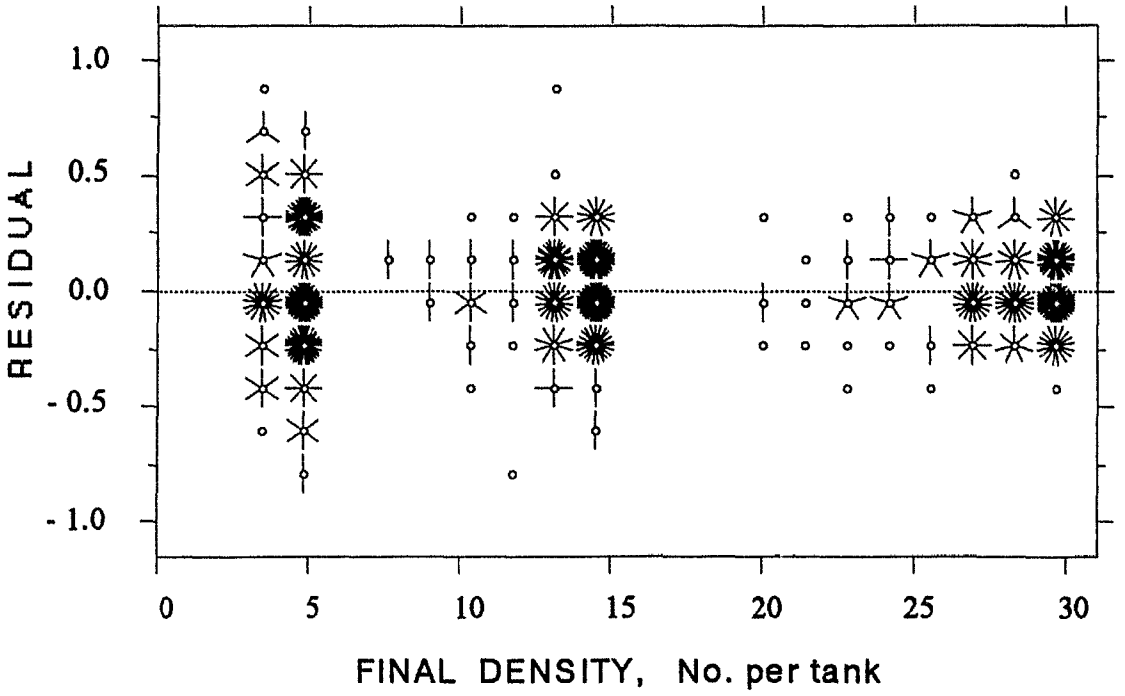

Fig. A1.27 ASIN($\sqrt{\%}$ REFUGE USAGE) RESIDUALS VERSUS FINAL SEA URCHIN DENSITY.

A1.5.2 Homoscedasticity

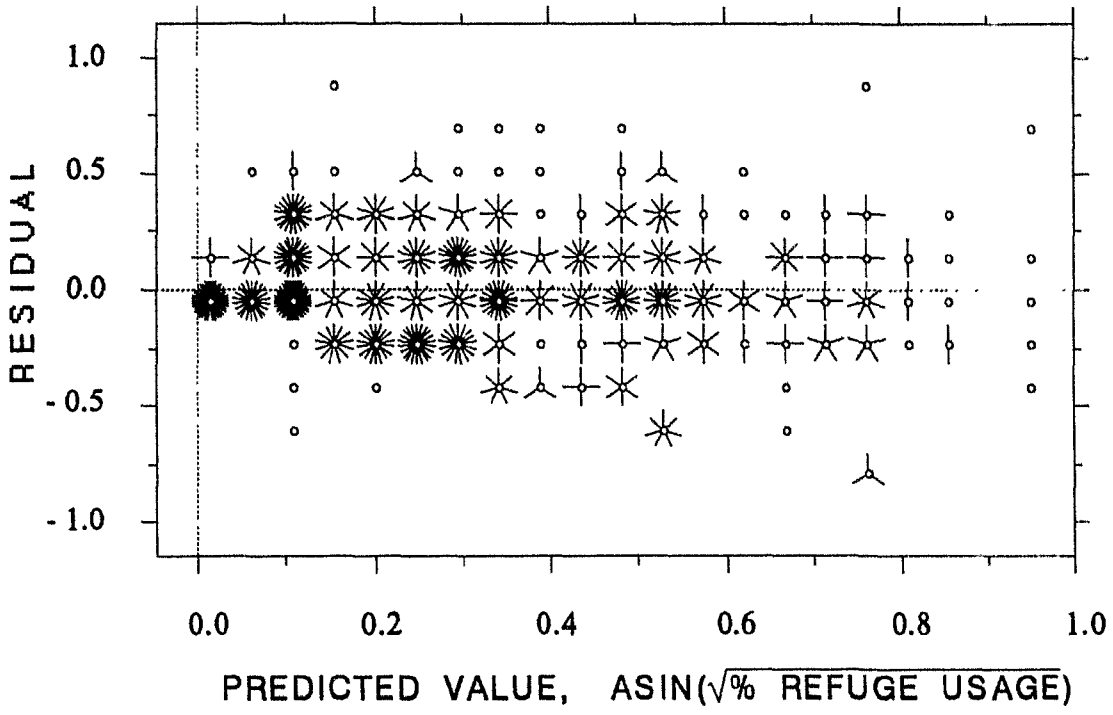

Fig. A1.28 ASIN(√% REFUGE USAGE) RESIDUALS VERSUS PREDICTED VALUES.

A1.5.3 Normality

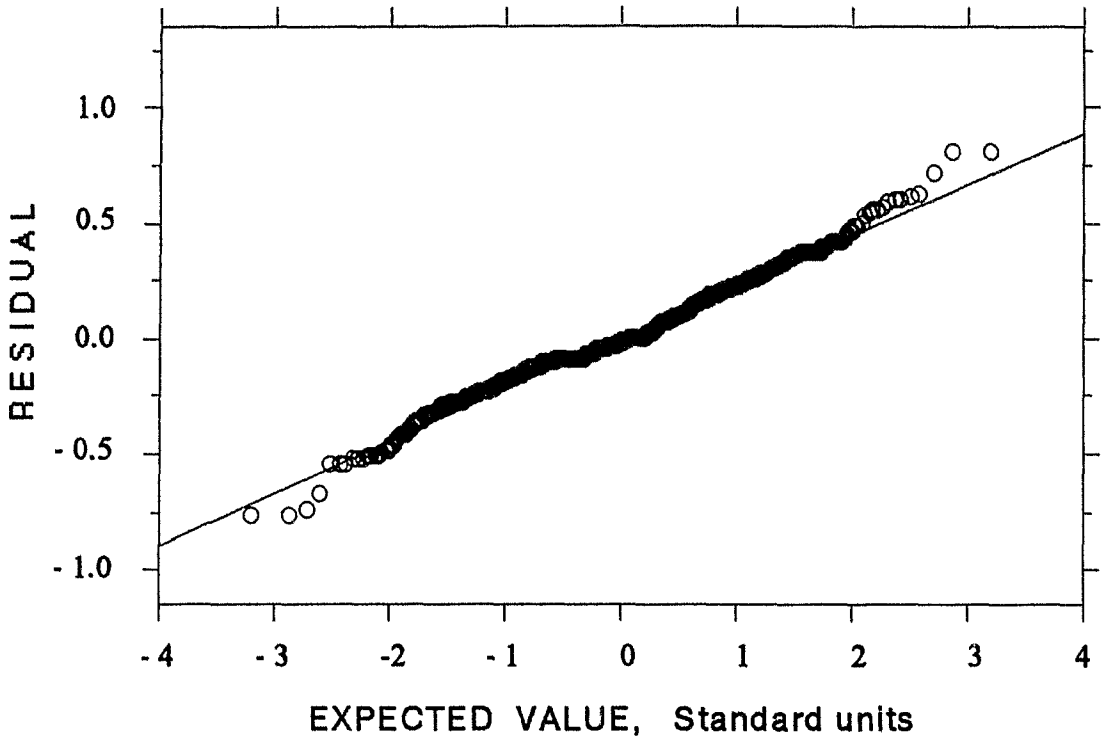

Fig. A1.29 NORMAL PROBABILITY PLOT OF ASIN($\sqrt{\%}$ REFUGE USAGE) RESIDUALS.

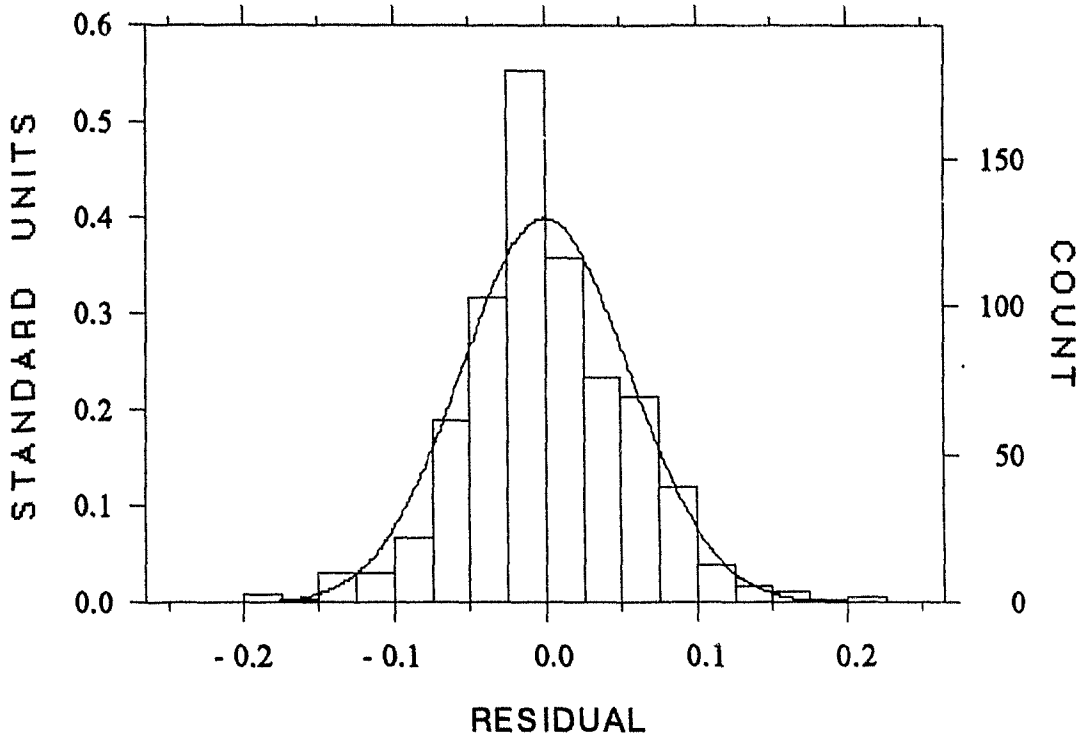

Fig. A1.30 HISTOGRAM OF ASIN($\sqrt{\%\ \text{REFUGE USAGE}}$) RESIDUALS WITH FITTED NORMAL CURVE.

A1.6 Mean % feeding, Table 5.1

A1.6.1 Independence

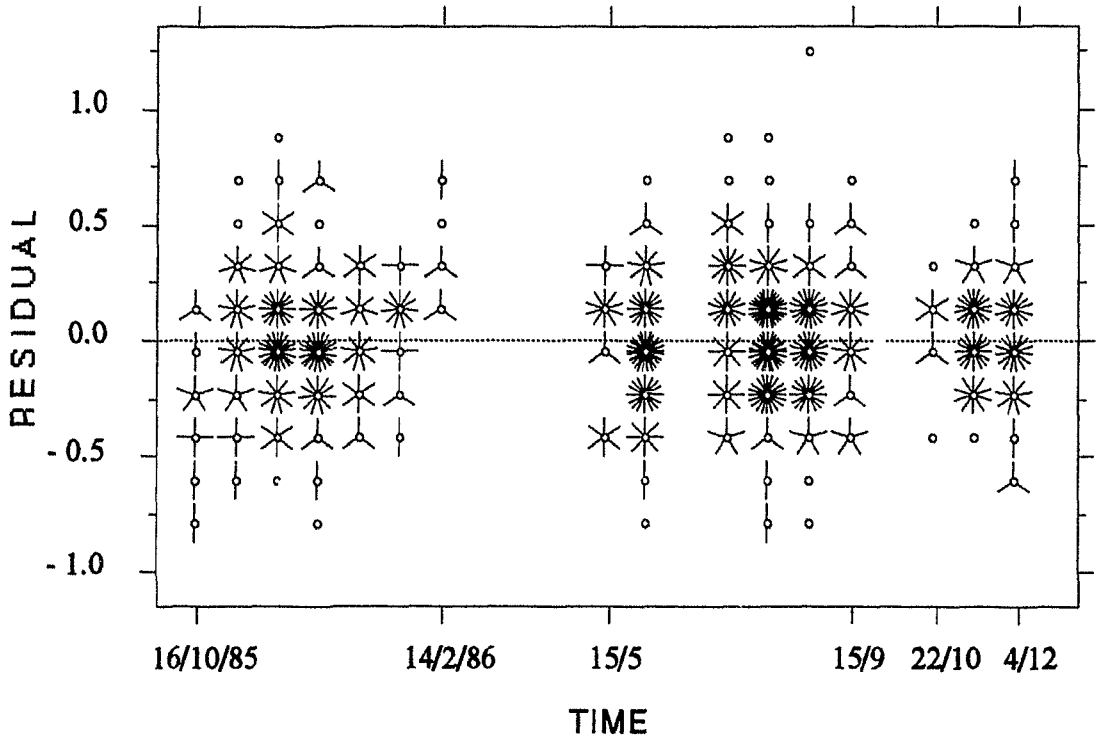

Fig. A1.31 SEQUENTIAL SUNFLOWER PLOT OF % FEEDING RESIDUALS.

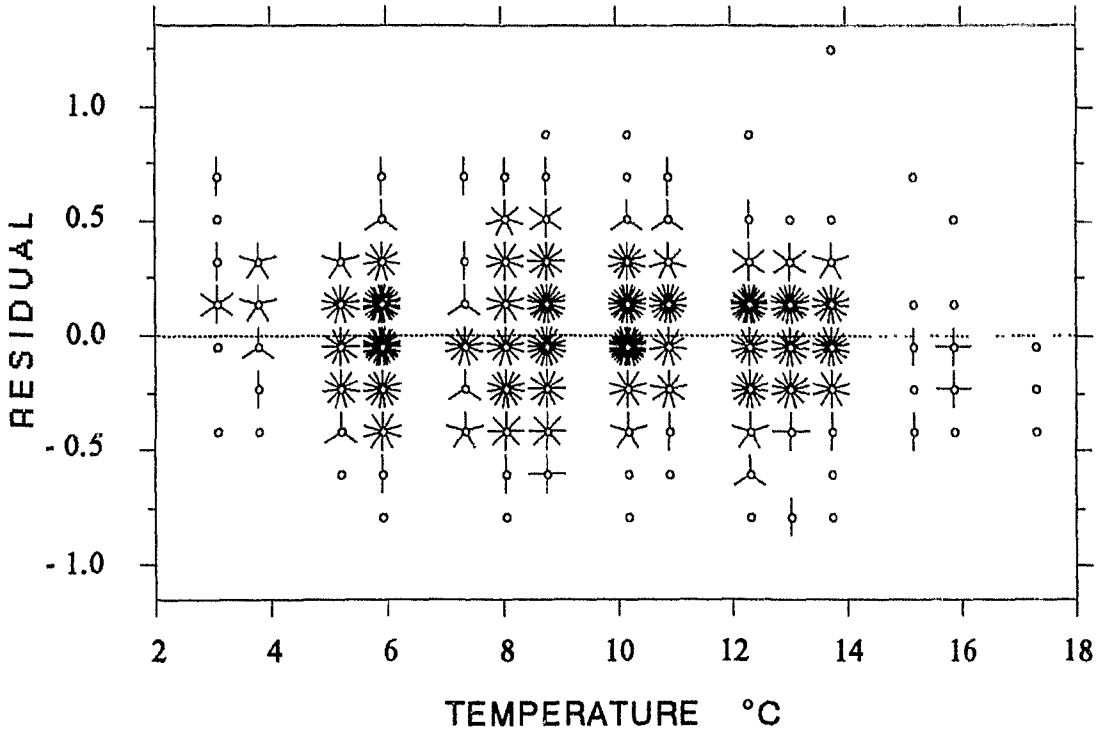

Fig. A1.32 SEAWATER TEMPERATURE VERSUS % FEEDING RESIDUALS.

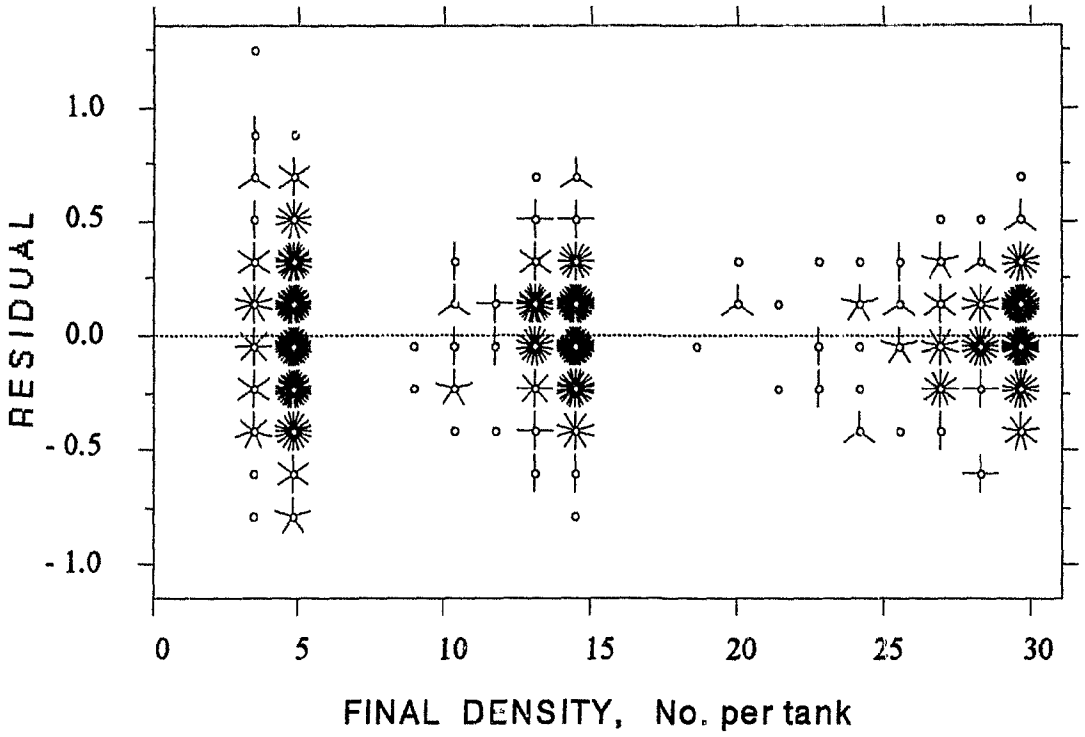

Fig. A1.33 FINAL SEA URCHIN DENSITY RESIDUALS VERSUS % FEEDING.

A1.6.2 Homoscedasticity

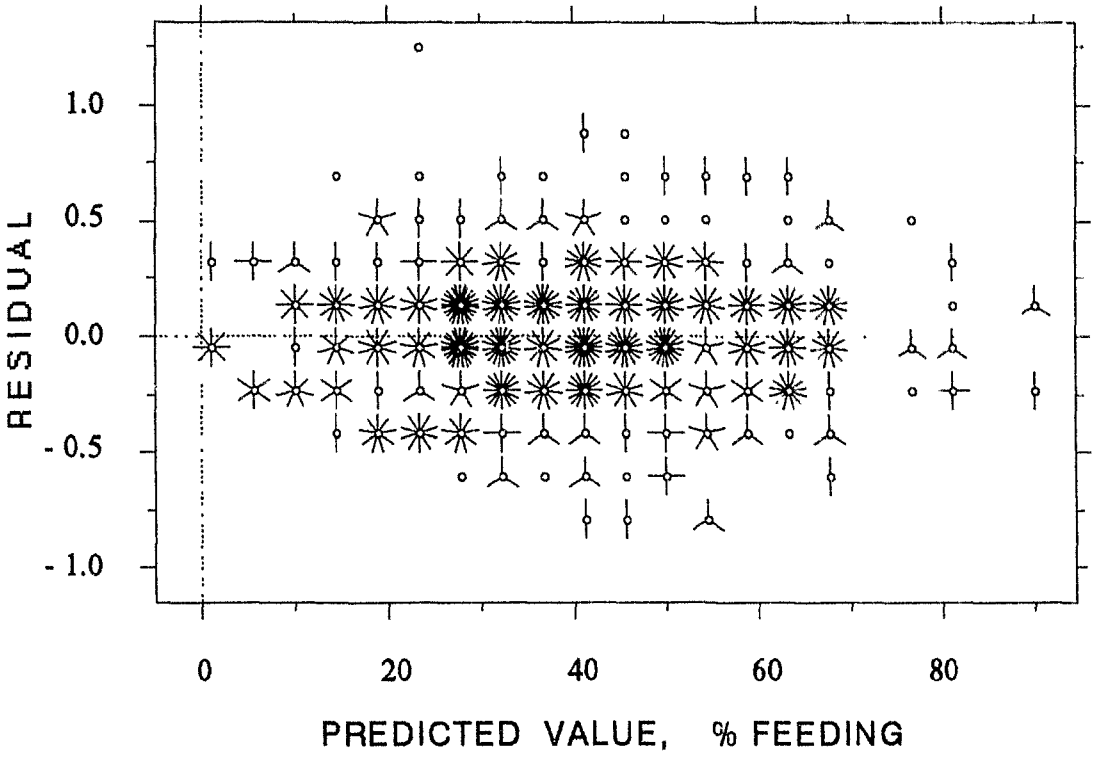

Fig. A1.34 PREDICTED VALUES VERSUS % FEEDING RESIDUALS.

A1,6,3 Normality

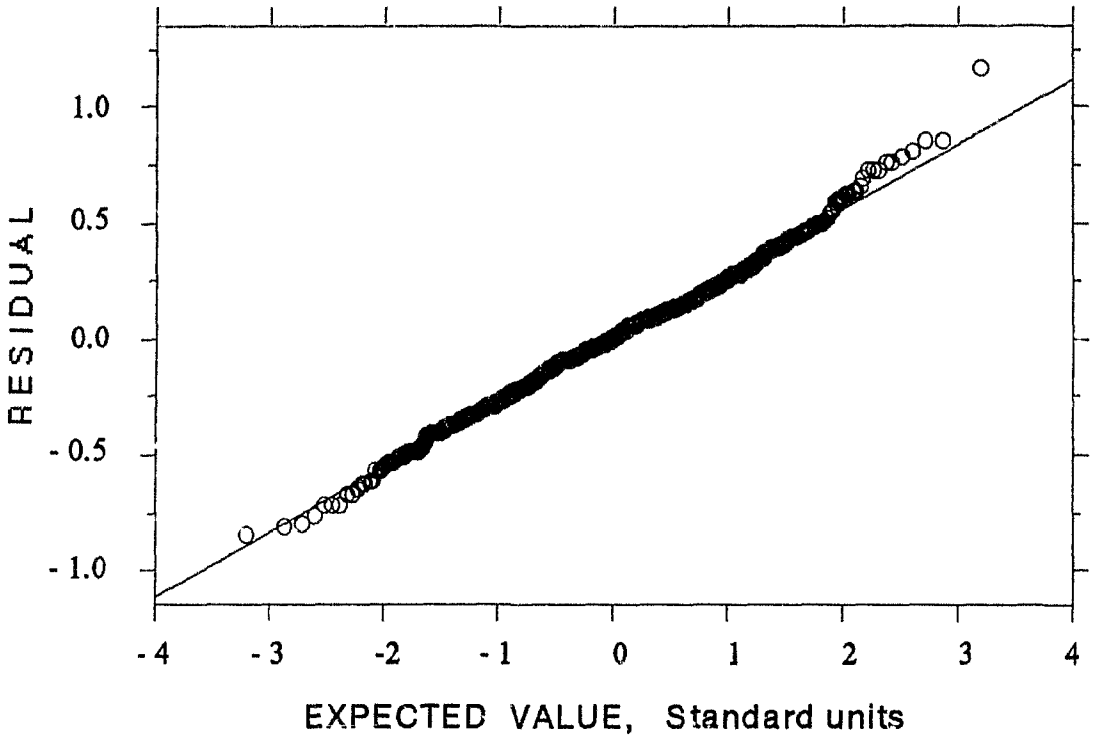

Fig. A1.35 NORMAL PROBABILITY PLOT OF % FEEDING RESIDUALS.

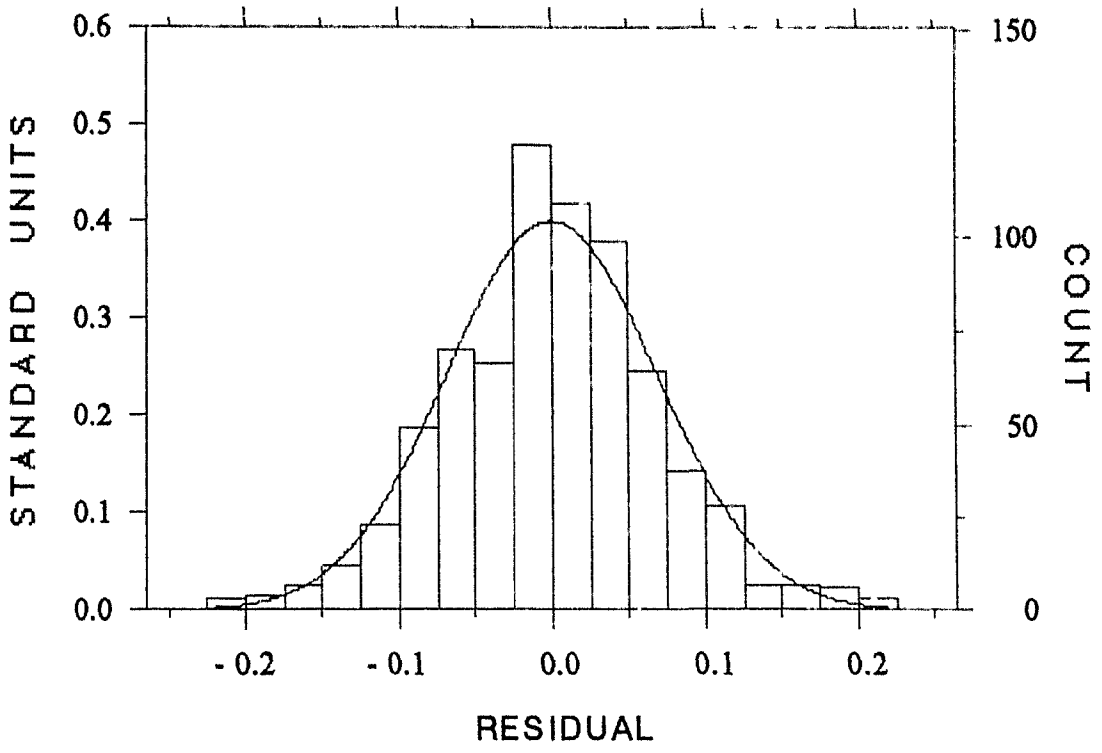

Fig. A1.36 HISTOGRAM OF % FEEDING RESIDUALS WITH FITTED NORMAL CURVE.

APPENDIX 2 SOURCES OF PREDATION RATE ESTIMATES

All available quantitative estimates of lobster predation on *Strongylocentrotus droebachiensis* have been converted to number of urchins eaten per predator per day in order to facilitate comparative and functional response analyses (Tables A2.1, A2.2). Assumptions and pertinent details are elaborated in "Comments to Table A2.1" and "Comments to Table A2.2".

Table A2.1 Relationship between two different measurements of lobster predation on *S. droebachiensis*. Estimates above the dotted line have been converted directly to the indicated units. Estimates below the dotted line indicated by asterisks (*) have been calculated by extrapolation from a regression line based on the datapoints above the dotted line.

Quantities consumed		
#urchins per predator day	% of predator body weight per day	Source
0.18	0.6	[a] Elner (1980, table 1)
1.33	3.2	[b] Elner (1980, fig. 3)
0.54	2.5	[c] Breen (1974, section 2, tables 3, 4)
0.3	1.2	[d] Himmelman & Steele (1971)
0.24	0.7	[e] Evans & Mann (1977, table 1)
2.69*	8.2	[f] Breen (1974, section 2, table 8)
3.79*	11.5	[f] Breen (1974, section 2, table 8)
5.23*	15.9	[f] Breen (1974, section 2, table 8)

* Mean feeding rates expressed as #urchins/predator per day has been estimated using a linear regression through the origin with slope 0.329 (standard error 0.048). The regression was calculated using the first five datapoints in Table A2.1 (Fig. A2.1).

COMMENTS TO TABLE A2.1

(a) Mean body weight for sea urchins in the size range 30 - 39 mm diameter is approximately 21 g (based on Breen 1974, section 2, table 6), and mean body weight for lobsters 85-95 mm carapace length is approximately 613 g (based on Breen 1974, table A2). Thus, 0.18 urchins/predator per day is equivalent to (0.18 × 21 × 100)/613 = 0.6 % of predator body weight per day

(b) Mean body weight for sea urchins in the size range 10 - 69 mm diameter is approximately 27 g (based on Breen 1974, table 6), and mean body weight for the three size classes of lobsters, 55-65 mm, 85-95 mm and 145-155 mm carapace length is approximately 1113 g (based on Breen 1974, table A2). Thus, 1.33 urchins/predator per day (cf. Table A2.2 below) is equivalent to (1.33 × 27 × 100)/1113 = 3.2 % of predator body weight per day.

(c) Mean feeding rate was 75 urchins/20 predator weeks = 0.54 urchins/predator per day (Breen 1974, section 2, table 4), or 0.1781 g urchin/g predator per week (Breen 1974, table 2) which is equivalent to (0.1781 × 100)/7 = 2.5 % of predator body weight per day.

(d) Mean feeding rate was 7 g urchin/predator per day for two lobsters of 88 and 95 mm carapace lengtn. The mean body weight for the these lobsters was approximately 610 g (based on Breen 1974, table A2). Thus, the mean feeding rate is

approximately (7 × 100)/610 = 1.2 % of predator body weight per day.

(e) Mean feeding rate for all urchin densities weighted for the number of replicates is 6.73 urchins/4 lobsters per week = 0.24 urchins/lobster per day. Assuming a mean body weight of approximately 1 kg for lobsters of 92 115 mm carapace length, and approximately 30 g for sea urchins, gives a mean feeding rate of approximately (0.24 × 30 × 100)/1000 = 0.7 % of predator body weight per day. [cf. Miller (1985a), who arrived at a slightly lower figure of 0.5 % of predator body weight per day].

(f) Mean feeding rates were 0.572 g urchin/g lobster per week or (0.572 × 100)/7 = 8.2 % of predator body weight per day at 212 g/m^2 urchin biomass; 1.112 g urchin/g lobster per week or (1.112 × 100)/7 = 15.9 % of predator body weight per day at 1270 g/m^2 urchin biomass; and averaged (1.869 + 0.534 + 0.267 + 0.538)/4 = 0.806 g urchin/g lobster per week or (0.806 × 100)/7 = 11.5 % of predator body weight per day at [(635 × 3) + 583]/4 = 622 g/m^2 urchin biomass. The effect of temperature is not considered in these calculations.

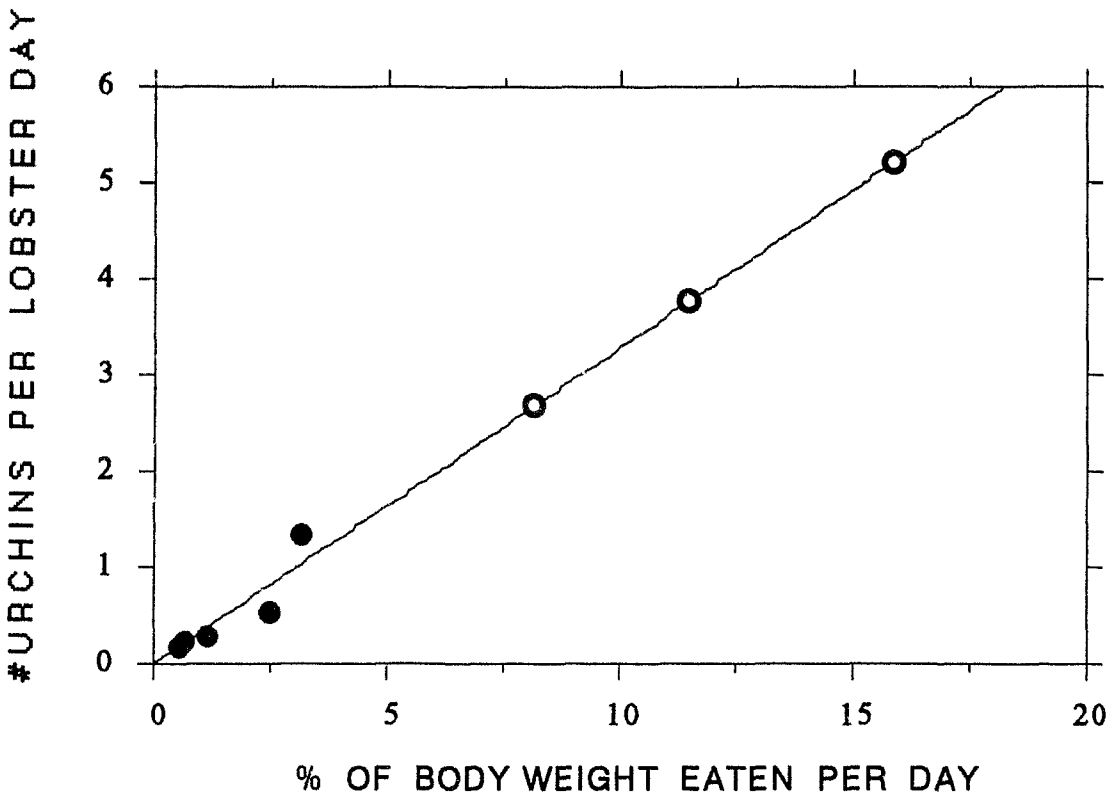

Fig. A2.1 RELATIONSHIP BETWEEN TWO DIFFERENT MEASUREMENTS OF LOBSTER PREDATION ON *STRONGYLOCENTROTUS DROEBACHIENSIS*. ● Data from the literature (Evans & Mann 1977; Breen 1974, Experiment 1; Elner 1980; Himmelman & Steele 1971). ○ % of body weight eaten per day estimates from Breen (1974, Experiment 3, Table 8) converted to # of urchins eaten per lobster per day using a linear regression through the origin (slope 0.329, standard error 0.048).

Table A2.2 Relationship between sea urchin density and lobster predation.

Density # of urchins per m^2	Predation # of urchins eaten per lobster per day	Source
40.5844	0.07 - 0.18	(1) Elner (1980, table 1)
73.052	0.52 - 1.33	(2) Elner (1980, fig. 3)
9.2593	0.3542	(3) This study, large urchins
27.7778	0.6914	(3) This study, large urchins
55.5556	0.9651	(3) This study, large urchins
9.2593	0.3855	(3) This study, small urchins
27.7778	0.7857	(3) This study, small urchins
55.5556	1.8452	(3) This study, small urchins
15 - 30	0.3	(4) Himmelman & Steele (1971)
7	2.69	(5) Breen (1974; c.f. Table A2.1)
20.5	3.79	(5) Breen (1974; c.f. Table A2.1)
42	5.23	(5) Breen (1974; c.f. Table A2.1)
10	0.54	(6) Breen (1974, section 2, table 4)
4	0.027	(7) Evans & Mann (1977)
4	0.068	(7) Evans & Mann (1977)
6	0.057	(7) Evans & Mann (1977)
8	0.264	(7) Evans & Mann (1977)
16	0.339	(7) Evans & Mann (1977)
32	0.468	(7) Evans & Mann (1977)
96	0.357	(7) Evans & Mann (1977)
100	0.411	(7) Evans & Mann (1977)

COMMENTS TO TABLE A2.2

(1) Includes data for 4 lobsters offered a mixed diet of mussels and large sea urchins (30-39 mm test diameter) over an 11 day period. The experimental lobsters were selected from a group of animals (39 % of total) which had successfully consumed sea urchins during a six day preliminary trial. Assuming that the lobsters which did not eat urchins during the preliminary trial would not have eaten any urchins during the experiment, the feeding rate estimate may be reduced to 0.18 × 0.39 = 0.07 urchins/predator per day [cf. Miller (1985a), Table 1]. Urchin density was 10 individuals/(77 × 32) cm^2 = 40.5844 individuals/m^2.

(2) Includes data for 15 lobsters offered sea urchins ranging from 10-69 mm test diameter over an 11 day period. Mean individual feeding rates were read from the abscissa of Fig. 3 (in Elner 1980) and divided by the number of lobsters to obtain an average feeding rate of approximately 1.33 urchins/predator per day. Assuming that the lobsters which did not eat urchins during the preliminary trial would not have eaten any urchins during the experiment, the feeding rate estimate may be reduced to 1.33 × 0.39 = 0.52 urchins/predator per day [see (1) above; cf. Miller (1985a), Table 1]. Urchin density was 18 individuals/(77 × 32) cm^2 = 73.052 individuals/m^2.

(3) Based on data from Table 7.4, assuming that sea urchin densities of 5, 15 and 30 individuals per tank corresponds to

5/(0.6 × 0.9) = 9.2593 urchins/m^2, 15/(0.6 × 0.9) = 27.7778 urchins/m^2 and 30/(0.6 × 0.9) = 55.5556 urchins/m^2. It is also assumed that all predation can be attributed to the lobsters (see Section 7.4.2).

(4) Sea urchin density ranged from 10 to 20 individuals per tank. Tank size and mean urchin density were not indicated in the original publication. Therefore sea urchin density is tentatively indicated here as somewhere between 15 and 30 individuals/m^2.

(5) Urchin biomasses in the experiment were 212 g/m^2, 1270 g/m^2, and [(635 × 3) + 583]/4 = 622 g/m^2 (cf. Table 7.9) composed of equal numbers of individuals from each 5 mm size class between 20 and 55 mm. These figures correspond to urchin densities of 7 individuals/m^2, 6 × 7 = 42 individuals/m^2, and [(3 × 7 × 3) + (7 × 3 - 2)]/4 = 20.5 individuals/m^2, respectively (based on Breen 1974, section 2, tables 6, 8).

(6) Total consumption of sea urchins was 75 individuals/20 lobster weeks = [(3 × 7 × 3) + (7 × 3 - 2)]/4 = 0.54 individuals/lobster per day (Breen 1974, table 4). Urchin density was 20 individuals/2 m^2 = 10 individuals/m^2 (Breen 1974, section 2, table 1).

(7) Feeding rates were tabulated as the mean number of urchins eaten per week by 4 lobsters. Data from the original

publication were multiplied by $\frac{1}{(7 \times 4)} = \frac{1}{28}$ in order to obtain the mean number of urchins eaten per lobster per day.

APPENDIX 3 DATA TABLES

A3.1 Tables from Chapter 3

Table A3.1 Mean aggregation size, m_2, and mean crowding, $\overset{*}{m}_2$, for small and large *S. droebachiensis* at different densities.

Density	$m_{2,small}$	$m_{2,large}$	$\overset{*}{m}_{2,small}$	$\overset{*}{m}_{2,large}$
low	1.41	1.836	0.579	1.119
medium	2.119	3.093	1.993	3.037
high	2.944	4.919	4.146	8.296

Table A3.2 Mean aggregation size, m_2, and mean crowding, $\overset{*}{m}_2$, for small and large *S. droebachiensis* in the presence and absence of predators.

Predators	$m_{2,small}$	$m_{2,large}$	$\overset{*}{m}_{2,small}$	$\overset{*}{m}_{2,large}$
None	2.21	3.638	2.395	5.000
Crab&lobster	2.436	3.732	2.571	5.231
Wolffish	2.158	3.283	1.752	3.021

Table A3.3 Mean crowding, $\overset{*}{m}_2$, and patchiness, $\frac{\overset{*}{m}_2}{m_2}$, for small and large *S. droebachiensis* in the presence and absence of food.

Food	$\overset{*}{m}_{2,small}$	$\overset{*}{m}_{2,large}$	$\left(\frac{\overset{*}{m}_2}{m_2}\right)_{small}$	$\left(\frac{\overset{*}{m}_2}{m_2}\right)_{large}$
none	2,422	4,341	,898	1,064
kelp	2,057	4,494	,822	1,175

A3.2 Tables from Chapter 4

Table A3.4 Effects of density on the cryptic behaviour of small and large sea urchins. The tabulated figures are treatment means. n = 240 tankdays per treatment.

Size	Small sea urchins	Large sea urchins
	% cryptic	% cryptic
Low density	81.2	33.4
Medium density	76.7	33.3
High density	70.0	29.4
Total	75.9	32.1

Table A3.5 Effects of refuges and food on the cryptic behaviour of small and large sea urchins. The tabulated figures are treatment means. **n** = 180 tankdays per treatment.

Size	Small sea urchins		Large sea urchins	
Food	No kelp	Kelp	No kelp	Kelp
	% cryptic	% cryptic	% cryptic	% cryptic
Refuges absent	70.3	79.7	8.4	43.0
Refuges present	72.8	81.0	28.4	48.4

Table A3.6 Effects of season, prefeeding and predators on the cryptic behaviour of small and large sea urchins. The tabulated figures are treatment means. **n** = 60 tankdays per treatment.

Season	Summer		Winter	
Prefeeding	Starved	Well fed	Starved	Well fed
	% cryptic	% cryptic	% cryptic	% cryptic
Small sea urchins				
No predators	70.7	91.3	38.0	64.4
Crab & lobster	81.1	89.3	55.0	73.7
Wolffish	79.5	90.4	83.9	94.0
Large sea urchins				
No predators	20.5	21.9	18.1	18.2
Crab & lobster	39.9	29.7	20.1	23.0
Wolffish	56.5	44.9	49.7	42.0

Table A3.7 Effects of season and prefeeding on the refuge usage of *S. droebachiensis*. The tabulated figures are treatment means. n = 180 tankdays per treatment.

Season	Summer	Winter
	% refuge usage	% refuge usage
Starved	13.0	11.6
Well fed	25.9	14.0

Table A3.8 Effects of urchin size and predators on the refuge usage of *S. droebachiensis*. The tabulated figures are treatment means. n = 120 tankdays per treatment.

Size	Small	Large
	% refuge usage	% refuge usage
No predator	11.9	7.9
Crab & lobster	8.1	12.0
Wolffish	19.3	37.7

A3.3 Tables from Chapter 5

Table A3.9 Effects of season, size and prefeeding on the feeding behaviour of *S. droebachiensis*. The tabulated figures are treatment means. **n** = 90 tankdays per treatment.

Season	Summer		Winter	
Prefeeding	Starved	Well fed	Starved	Well fed
	% feeding	% feeding	% feeding	% feeding
Small sea urchins	37.02	34.41	44.98	28.83
Large sea urchins	60.33	31.96	53.72	36.02

Table A3.10 Effects of predators and prefeeding on the feeding behaviour of *S. droebachiensis*. The tabulated figures are treatment means. **n** = 120 tankdays per treatment.

Size	Starved	Well fed
	% feeding	% feeding
No predators	53.2	25.27
Crab & lobster	38.88	31.9
Wolffish	54.96	41.24

APPENDIX 4 MODEL PROGRAM

```
program MODEL;
(* Simulation model of sea urchins,  predators and kelp  *)

     uses
          Globals, Plotting, Regression, Predation;
     var
          i, j: integer;

begin                          { Model program }
     InitializeFiles;
     urchin.maxDisp := 50;
     maxTime := 30;

     testWritingYes := FALSE;
     urchin.adultPlot := FALSE;
     urchin.juvenilePlot := FALSE;
     kelp.plot := FALSE;

     crypticYes := TRUE;
     holling := 2;
     crabLobster.activePredator := FALSE;
     wolffish.activePredator := TRUE;
{ NB ONLY ONE OF THE PREDATORS CAN BE THE ACTIVE PREDATOR }

     Initialize;
     Clear;
     SteadyOutbreakInitiation;

     Initialize;
     Clear;
     PulseOutbreakInitiation;

     Initialize;
     Clear;
     OutbreakTermination;
```

```
end.                          { Model program }

unit Globals;

interface

     const
          EPSILON = 0.000000000001;
          SUMMER = 1;
          WINTER = 0;
          SMALL = 1;
          LARGE = 0;
          ABSENT = 1;
          PRESENT = 0;

     var
          pulse: boolean;
          cryptic: boolean;
          crypticYes: boolean;
          testWriting: boolean;
          testWritingYes: boolean;

          holling: integer;
          maxTime: integer;

          time: real;
          outbreakInitiationThreshold: real;
          outbreakTerminationThreshold: real;
          naturalMortalityRate: real;
          maxAge: real;
          season: real;
          size: real;
          refuges: real;
          prefed: real;
          food: real;
          noPredator: real;
          decapods: real;
          xMaxDisp: real;
```

```
        kelp: laminaria;
        urchin: echinoid;
        crabLobster: predator;
        wolffish: predator;

        steadyFile: text;
        steadyData: string:
        pulseFile: text;
        pulseData: string;
        terminationFile: text;
        terminationData: string;

type
        laminaria = record    { Laminaria declaration }

                plot: boolean;

                maxDensity, minDensity: real;
                density, oldDensity: real;
                overgrazingRate, recoveryRate: real;
            end;              { Laminaria declaration }

        echinoid = record     { Echinoid declaration }

                juvenilePlot, adultPlot: boolean;

                maxDisp: integer;

                aggregation: real;
                recruitment, pulseDensity: real;
                juvenileDensity, adultDensity: real;
                oldJuvenileDensity: real;
                oldAdultDensity: real;
                %crypticJuveniles, %crypticAdults: real;
            end;              { Echinoid declaration }

        predator = record     { Predator declaration }

                activePredator: boolean;
```

```
                    k2Adult, d2Adult: real;
                    k3Adult, d3Adult: real;
                    k3Juvenile, d3Juvenile: real;
                    density: real;
                end;            { Predator declaration }

    procedure SetKelpRecoveryRate;
    procedure SetKelpOvergrazingRate;
    procedure InitializeFiles;
    procedure Initialize;


implementation

    procedure SetKelpRecoveryRate;
(* Exponential kelp recovery in 3 years *)
    begin
        kelp.recoveryRate := Exp(ln(1 / kelp.minDensity) /
        (52 * 3)) - 1;
    end; { SetKelpRecoveryRate }


    procedure SetKelpOvergrazingRate;
(* Exponential kelp destruction in 1 year *)
    begin
        kelp.overgrazingRate := Exp(ln(kelp.minDensity) /
        (52 + 1)) - 1;
    end; { SetKelpOvergrazingRate }


    procedure InitializeFiles;
    begin
        steadyData := 'SteadyData';
        Rewrite(steadyFile, steadyData);
        pulseData := 'PulseData';
        Rewrite(pulseFile, pulseData);
        terminationData := 'TerminationData';
```

```
        Rewrite(terminationFile, terminationData);
end;

procedure Initialize;
begin
        time := 0;
        maxAge := 12;

        urchin.pulseDensity := 0;
        urchin.%crypticAdults := 0;
        urchin.%crypticJuveniles := 0;
        urchin.recruitment := 0;
        urchin.aggregation := 0;
        urchin.adultDensity := 0;
        urchin.oldAdultDensity := 0;
        urchin.juvenileDensity := 0;
        urchin.oldJuvenileDensity := 0;

        kelp.maxDensity := 1;
        kelp.minDensity := 0.0001;
        kelp.density := kelp.maxDensity;
        kelp.oldDensity := kelp.density;
        SetKelpOvergrazingRate;
        SetKelpRecoveryRate;

        crabLobster.k2adult := 1.527;
        crabLobster.d2adult := 32.720;
        crabLobster.k3adult := 0.968;
        crabLobster.d3adult := 13.903;
        crabLobster.k3juvenile := 0.968;
        crabLobster.d3juvenile := 13.903;
        crabLobster.density := 0.0;

        wolffish.k2adult := 7.597;
        wolffish.d2adult := 65.586;
        wolffish.k3adult := 3.782;
        wolffish.d3adult := 20.070;
```

```
            wolffish.k3juvenile := 2.147;
            wolffish.d3juvenile := 22.226;
            wolffish.density := 0.0;

            outbreakInitiationThreshold := 5;
            outbreakTerminationThreshold := 10;

            refuges := PRESENT;
            size := SMALL;
            season := SUMMER;
            noPredator := 0;
            decapods := 1;
            prefed := 1;
            food := 1;

            pulse := FALSE;
            testWriting := FALSE;

            xMaxDisp := 52.0 * maxTime;

            naturalMortalityRate := 1 - (exp(-ln(100) / (52 *
            maxAge))); { Assumes 99% mortality after maxAge
                         years }

      end; { Initialize procedure }


end.        { Globals unit }



unit Plotting;

interface

      uses
            Globals;

      procedure DrawXYaxes;
```

```
     procedure Clear;
     procedure Plot;

     const
          MAXX = 450;
          MAXY = 260;

     var
          origo: point;


implementation

     procedure DrawXYaxes;
(* Draws XY-axes *)
     begin
          MoveTo(origo.h + MAXX, origo.v);
          LineTo(origo.h, origo.v);
          MoveTo(origo.h, origo.v - MAXY);
          LineTo(origo.h, origo.v);
     end; { DrawXYaxes }


     procedure LabelXYaxes;
     (* Labels XY-axes *)
          var
               i: integer;
     begin
          for i := 0 to maxTime do
               begin
                    MoveTo(trunc(origo.h + i * (MAXX /
                    maxTime)), origo.v);
                    LineTo(trunc(origo.h + i * (MAXX /
                    maxTime)), origo.v + 5);
               end;
          for i := 0 to urchin.maxDisp do
               begin
```

```
                    MoveTo(origo.h, trunc(origo.v - i * 10 *
                    (MAXY / urchin.maxDisp)));
                    LineTo(origo.h - 5, trunc(origo.v - i *
                    10 * (MAXY / urchin.maxDisp)));
               end;
     end; { LabelXYaxes }


     procedure Clear;
(* Activates and expands Drawing Window *)
(* Positions origo in lower left corner *)
(* Draws & Labels XY-axes *)
          var
               writeRect: rect;
               drawRect: rect;
     begin
          HideAll;
          SetRect(writeRect, 2, 385, 532, 475);
          SetTextRect(writeRect);
          ShowText;
          SetRect(drawRect, 2, 35, 532, 362);
          SetDrawingRect(drawRect);
          ShowDrawing;
          origo.v := MAXY + 20;{ Vertical displacement of
          origo from upper left corner }
          origo.h := 40;       { Horisontal displacement of
          origo from upper leit corner }
          DrawXYaxes;
          LabelXYaxes;
     end; { Clear }


     procedure PlotDensity (oldDensity, newDensity: real);
     begin
```

```
            MoveTo(origo.h + trunc(time * MAXX / xMaxDisp),
            origo.v - trunc((oldDensity * MAXY) /
            urchin.maxDisp));
            LineTo(origo.h + trunc(time * MAXX / xMaxDisp),
            origo.v - trunc((newDensity * MAXY) /
            urchin.maxDisp));
      end; { PlotUrchin }


      procedure Plot;
(* Conditional plotting *)
      begin
            if urchin.adultPlot then
                  PlotDensity(urchin.oldAdultDensity,
                  urchin.adultDensity);
            if urchin.juvenilePlot then
                  PlotDensity(urchin.oldJuvenileDensity,
                  urchin.juvenileDensity);
            if kelp.plot then
                  PlotDensity(kelp.oldDensity * urchin.maxDisp,
                  kelp.density * urchin.maxDisp);
      end; { Plot }

end.        { Plotting unit }

unit Regression;

interface

      uses
            Globals, Plotting;

      procedure CrypticRegression;
      procedure AggregationRegression;

implementation

      var
```

```
     procedure Clear;
     procedure Plot;

     const
          MAXX = 450;
          MAXY = 260;

     var
          origo: point;


implementation

     procedure DrawXYaxes;
(* Draws XY-axes *)
     begin
          MoveTo(origo.h + MAXX, origo.v);
          LineTo(origo.h, origo.v);
          MoveTo(origo.h, origo.v - MAXY);
          LineTo(origo.h, origo.v);
     end; { DrawXYaxes }


     procedure LabelXYaxes;
     (* Labels XY-axes *)
          var
               i: integer;
     begin
          for i := 0 to maxTime do
               begin
                    MoveTo(trunc(origo.h + i * (MAXX /
                    maxTime)), origo.v);
                    LineTo(trunc(origo.h + i * (MAXX /
                    maxTime)), origo.v + 5);
               end;
          for i := 0 to urchin.maxDisp do
               begin
```

```
                    MoveTo(origo.h, trunc(origo.v - i * 10 *
                    (MAXY / urchin.maxDisp)));
                    LineTo(origo.h - 5, trunc(origo.v - i *
                    10 * (MAXY / urchin.maxDisp)));
               end;
     end; { LabelXYaxes }


     procedure Clear;
(* Activates and expands Drawing Window *)
(* Positions origo in lower left corner *)
(* Draws & Labels XY-axes *)
          var
               writeRect: rect;
               drawRect: rect;
     begin
          HideAll;
          SetRect(writeRect, 2, 385, 532, 475);
          SetTextRect(writeRect);
          ShowText;
          SetRect(drawRect, 2, 35, 532, 362);
          SetDrawingRect(drawRect);
          ShowDrawing;
          origo.v := MAXY + 20;{ Vertical displacement of
          origo from upper left corner }
          origo.h := 40;       { Horisontal displacement of
          origo from upper left corner }
          DrawXYaxes;
          LabelXYaxes;
     end; { Clear }


     procedure PlotDensity (oldDensity, newDensity: real);
     begin
```

```
            MoveTo(origo.h + trunc(time * MAXX / xMaxDisp),
            origo.v - trunc((oldDensity * MAXY) /
            urchin.maxDisp));
            LineTo(origo.h + trunc(time * MAXX / xMaxDisp),
            origo.v - trunc((newDensity * MAXY) /
            urchin.maxDisp));
      end; { PlotUrchin }


      procedure Plot;
(* Conditional plotting *)
      begin
            if urchin.adultPlot then
                  PlotDensity(urchin.oldAdultDensity,
                  urchin.adultDensity);
            if urchin.juvenilePlot then
                  PlotDensity(urchin.oldJuvenileDensity,
                  urchin.juvenileDensity);
            if kelp.plot then
                  PlotDensity(kelp.oldDensity * urchin.maxDisp,
                  kelp.density * urchin.maxDisp);
      end; { Plot }

end.        { Plotting unit }

unit Regression;

interface

      uses
            Globals, Plotting;

      procedure CrypticRegression;
      procedure AggregationRegression;

implementation

      var
```

```
        density: real;


    procedure CrypticRegression;
(* Estimates the proportion of cryptic urchins *)
        var
            %cryptic: real;
    begin                              { CrypticRegression }
        prefed := kelp.density;
        food := kelp.density;
        if crabLobster.density > EPSILON then
            decapods := 1;
        if wolffish.density > EPSILON then
            decapods := 0;
        if size = LARGE then
            density := urchin.adultDensity * (0.6 * 0.9)
    { Conversion from per-squaremeter-units to per-tank-
      units }
        else if size = SMALL then
    { (Regression is based on per-tank-units) }
            density := urchin.juvenileDensity * (0.6 *
            0.9);

        %cryptic := 0.501 + 0.047 * season + 0.377 * size -
        0.2 * refuges;
        %cryptic := %cryptic - 0.263 * decapods - 0.002 *
        density - 0.096 * prefed;
        %cryptic := %cryptic + 0.2 * food - 0.086 * season
        * size;
        %cryptic := %cryptic + 0.086 * season * decapods +
        0.175 * size * refuges;
        %cryptic := %cryptic - 0.003 * size * density + 0.2
        * size * prefed;
        %cryptic := %cryptic - 0.118 * size * food + 0.146
        * refuges * food;
```

```
            %cryptic := %cryptic + 0.045 * prefed * decapods +
            0.157 * season * size * decapods;
            %cryptic := %cryptic - 0.133 * size * refuges *
            food;
            if season = WINTER then
                 %cryptic := %cryptic - 0.003 * size *
                 decapods;

            if %cryptic < EPSILON then
                 %cryptic := 0;

            if (1 - %cryptic) < EPSILON then
                 %cryptic := 1;

            if size = LARGE then
                 urchin.%crypticAdults := %cryptic
            else if size = SMALL then
                 urchin.%crypticJuveniles := %cryptic;
       end;                          { CrypticRegression }


       procedure AggregationRegression;
  (* Estimates the index of mean crowding for adult urchins *)
            var
                 crowding: real;
       begin                               { AggregationRegression }
            density := urchin.adultDensity * (0.6 * 0.9);
  { Conversion from per-squaremeter-units to per-tank-units }
  { (Regression is based on per-tank-units) }
            if wolffish.density > EPSILON then
                 begin
                      noPredator := 0;
                      decapods := 0;
                 end
            else if crabLobster.density > EPSILON then
                 begin
```

```
                    noPredator := 0;
                    decapods := 1;
               end
          else
               begin
                    noPredator := 1;
                    decapods := 0;
               end;

          if density > EPSILON then
               begin
                    crowding := -1.911 + 0.746 * refuges +
                    0.312 * density;
                    crowding := crowding + 1.329 * noPredator
                    + 1.701 * decapods;
                    urchin.aggregation := crowding;
               end
          else
               urchin.aggregation := 0;

          if urchin.aggregation < EPSILON then
               urchin.aggregation := 0;
     end;                         { AggregationRegression }

end.                              { Regression unit }
```

```
unit Predation;

interface

     uses
          Globals, Plotting, Regression;

     procedure Predation;
     procedure SteadyOutbreakInitiation;
     procedure PulseOutbreakInitiation;
     procedure OutbreakTermination;

implementation

     var
          juvenileDensity: real;
          adultDensity: real;
          oldJuvenilesProportion: real;
          oldWolffish: real;
          oldMaxTime: integer;


     procedure KelpRecovery;
(* Logistic kelp recovery *)
     begin
          kelp.density := (1 + kelp.recoveryRate * (1 -
kelp.density)) * kelp.density;
     end;


     procedure KelpOvergrazing;
(* Exponential kelp destruction *)
     begin
          if kelp.density > kelp.minDensity then
               kelp.density := (1 + kelp.overgrazingRate) *
               kelp.density
          else
```

```
                kelp.density := kelp.minDensity;
     end;


     function PredationType2 (k, d, n: real): real;
(* Holling Type 2 functional predator response *)
     begin
          PredationType2 := 7 * (k * n) / (d + n);
     { #Eaten/Predator week }
     end;


     function PredationType3 (k, d, n: real): real;
(* Holling Type 3 functional predator response *)
     begin
          PredationType3 := 7 * (k * n * n) / (d * d + n *
          n);   { #Eaten/Predator week }
     end;


     procedure AdultCrabLobsterPredation;
(* CrabLobster predation on adult urchins *)
     begin
          if holling = 2 then
               urchin.adultDensity := urchin.adultDensity -
               PredationType2(crabLobster.k2adult,
               crabLobster.d2adult, adultDensity) *
               crabLobster.density
          else if holling = 3 then
               urchin.adultDensity := urchin.adultDensity -
               PredationType3(crabLobster.K3adult,
               crabLobster.D3adult, adultDensity) *
               crabLobster.density;

          if urchin.adultDensity < 0 then
               urchin.adultDensity := 0;
     end;       { AdultCrabLobsterPredation }
```

```
    procedure AdultWolffishPredation;
(* Wolffish predation on adult urchins *)
    begin
        if holling = 2 then
            urchin.adultDensity := urchin.adultDensity -
            PredationType2(wolffish.k2Adult,
            wolffish.d2Adult, adultDensity) *
            wolffish.density
        else if holling = 3 then
            urchin.adultDensity := urchin.adultDensity -
            PredationType3(wolffish.k3Adult,
            wolffish.d3Adult, adultDensity) *
            wolffish.density;

        if urchin.adultDensity < 0 then
            urchin.adultDensity := 0;
    end;        { AdultWolffishPredation }


    procedure JuvenileCrabLobsterPredation;
(* CrabLobster predation on juvenile urchins *)
    begin
        urchin.juvenileDensity := urchin.juvenileDensity -
        PredationType3(crabLobster.k3Juvenile,
        crabLobster.d3Juvenile, juvenileDensity) *
        crabLobster.density;

        if urchin.juvenileDensity < 0 then
            urchin.juvenileDensity := 0;
    end;        { JuvenileCrabLobsterPredation }


    procedure JuvenileWolffishPredation;
(* Wolffish predation on juvenile urchins *)
    begin
```

```
        urchin.juvenileDensity := urchin.juvenileDensity -
        PredationType3(wolffish.k3Juvenile,
        wolffish.d3Juvenile, juvenileDensity) *
        wolffish.density;

        if urchin.juvenileDensity < 0 then
            urchin.juvenileDensity := 0;
    end;        { JuvenileWolffishPredation }


    procedure CrypticTest;
    (* Checks if cryptic behaviour is being simulated *)
    begin
        if cryptic then             { Predators do not
                                    consume cryptic urchins }
            begin
                size := SMALL;
                CrypticRegression;
                juvenileDensity := urchin.juvenileDensity
                * (1 - urchin.%crypticJuveniles);
                size := LARGE;
                CrypticRegression;
                adultDensity := urchin.adultDensity * (1
                - urchin.%crypticAdults);
            end
        else                    { Cryptic behaviour is not
                                being simulated }
            begin
                juvenileDensity :=
                urchin.juvenileDensity;
                adultDensity := urchin.adultDensity
            end;
    end;        { CrypticTest }

    procedure CrabLobsterPredation;
(* CrabLobster predation on juvenile or adult urchins *)
```

```
(* according to experimentally determined numerical
preference quotient *)
     begin
          CrypticTest;
          if juvenileDensity / (adultDensity + EPSILON) > 253
               / 168 then
               JuvenileCrabLobsterPredation
          else
               AdultCrabLobsterPredation;
     end;       { CrabLobsterPredation }


     procedure WolffishPredation;
(* Wolffish predation on juvenile or adult urchins *)
(* according to experimentally determined numerical
preference quotient *)
     begin
          CrypticTest;
          if juvenileDensity / (adultDensity + EPSILON) > 301
               / 583 then
               JuvenileWolffishPredation
          else
               AdultWolffishPredation
     end;       { WolffishPredation }


     procedure NaturalMortality;
     begin
          urchin.adultDensity := urchin.adultDensity * (1 -
          naturalMortalityRate);
          urchin.juvenileDensity := urchin.juvenileDensity *
          (1 - naturalMortalityRate);
     end;       { NaturalMortality }


     procedure KelpDynamics;
     begin
```

```
      kelp.oldDensity := kelp.density;
      if urchin.aggregation > outbreakInitiationThreshold
      then
           KelpOvergrazing
      else if not pulse and (urchin.adultDensity <
           outbreakTerminationThreshold) then
           KelpRecovery;
end;       { KelpDynamics }


procedure WriteIt;
begin
     Writeln(time : 6 : 1, crabLobster.density : 8 : 3,
     wolffish.density : 8 : 3, urchin.recruitment : 6 :
     1, urchin.juvenileDensity : 8 : 2,
     urchin.adultDensity : 8 : 2, urchin.aggregation : 8
     : 2, kelp.density : 8 : 4);
     Writeln(crypticYes : 8, holling : 6,
     crabLobster.density : 8 : 3, wolffish.density : 8 :
     3, urchin.recruitment : 6 : 1, urchin.pulseDensity
     : 6 : 1);
end;

procedure TestWrite;
begin
     if testWriting then
          WriteIt;
end;


procedure ResultWriteSteady;
begin
     if not testWriting then
          begin
               WriteIt;
```

```
                    Writeln(steadyFile, crypticYes : 8,
                    holling : 6, crabLobster.density : 8 : 3,
                    wolffish.density : 8 : 3,
                    urchin.recruitment : 6 : 1);
               end;
     end;


     procedure ResultWritePulse;
     begin
          if not testWriting then
               begin
                    WriteIt;
                    Writeln(pulseFile, crypticYes : 8,
                    holling : 6, crabLobster.density : 8 : 3,
                    wolffish.density : 8 : 3,
                    urchin.pulseDensity : 6 : 1);
               end;
     end;


     procedure ResultWriteTermination;
     begin
          if not testWriting then
               begin
                    WriteIt;
                    Writeln(terminationFile, crypticYes : 8,
                    holling : 6, crabLobster.density : 8 : 3,
                    wolffish.density : 8 : 3,
                    urchin.recruitment : 6 : 1);
               end;
     end;


     procedure AnnualPredation;
(* Annual predation cycle and recruitment *)
(* Wolffishes are inshore only during the summer *)
```

```
    var
        i, j: integer;
begin
    urchin.oldAdultDensity := urchin.adultDensity;
    urchin.oldJuvenileDensity :=
    urchin.juvenileDensity;
    urchin.juvenileDensity := urchin.juvenileDensity +
    urchin.recruitment;
    Plot;
    urchin.oldJuvenileDensity :=
    urchin.juvenileDensity;
    season := SUMMER;
    for j := 1 to 20 do
        begin     { Summer loop }

            CrabLobsterPredation;
            WolffishPredation;
            NaturalMortality;
            AggregationRegression;
            KelpDynamics;
            time := time + 1.0;
            Plot;
            TestWrite;
            urchin.oldAdultDensity :=
            urchin.adultDensity;
            urchin.oldJuvenileDensity :=
            urchin.juvenileDensity;
        end; { Summer loop }
    urchin.adultDensity := urchin.adultDensity +
    urchin.juvenileDensity * oldJuvenilesProportion;
    urchin.juvenileDensity := urchin.juvenileDensity -
    urchin.juvenileDensity * oldJuvenilesProportion;

    AggregationRegression;

    oldWolffish := wolffish.density;
```

```
        wolffish.density := 0;
        season := WINTER;
        for i := 1 to 32 do
             begin      { Winter loop }
                  CrabLobsterPredation;
                  NaturalMortality;
                  AggregationRegression;
                  KelpDynamics;
                  time := time + 1.0;
                  Plot;
                  TestWrite;
                  urchin.oldAdultDensity :=
                  urchin.adultDensity;
                  urchin.oldJuvenileDensity :=
                  urchin.juvenileDensity;
             end; { Winter loop }

        if (time < 52) and pulse then
             oldJuvenilesProportion := 0
        else
             begin
                  if urchin.juvenileDensity > EPSILON then
                       oldJuvenilesProportion :=
                       urchin.juvenileDensity /
                       (urchin.juvenileDensity +
                       urchin.recruitment)
                  else
                       begin
                            oldJuvenilesProportion := 0;
                       end;
             end;

        wolffish.density := oldWolffish;
end;       { AnnualPredation }
```

```
    procedure Predation;
(* Simulates sea urchin population dynamics for maxTime years
*)
        var
            i: integer;
    begin           { Predation procedure }
        time := 0;
        oldJuvenilesProportion := 0;
        oldWolffish := 0;
        urchin.oldJuvenileDensity :=
        urchin.juvenileDensity;
        urchin.oldAdultDensity := urchin.adultDensity;
        MoveTo(origo.h, trunc(origo.v - urchin.adultDensity
        * MAXY / urchin.maxDisp));
        AggregationRegression;    { Checks the status of
                                  "noPredator"    }
        if noPredator = 1 then    { NB Cryptic behaviour is
                                    of no interest in the }
            cryptic := FALSE      { absence of predators  }
        else
            cryptic := crypticYes;

        for i := 1 to maxTime do
            begin
                AnnualPredation;
            end;        { Years loop }
    end;            { Predation procedure }


    procedure SteadyOutbreakInitiation;
        var
            i, j: integer;
    begin

        testWriting := testWritingYes;
        pulse := FALSE;
```

```
            i := 0;
            for j := 0 to 30 do
                 begin          { for loop }
                      kelp.density := kelp.maxDensity;
                      if wolffish.activePredator then
                           wolffish.density := j * 0.01;
                      if crablobster.activePredator then
                           crablobster.density := j * 0.01;
                      while kelp.density > 0.1 *
kelp.maxDensity do
                           begin     { while loop }
                                urchin.juvenileDensity := 0;
                                urchin.adultDensity := 0;
                                i := i + 1;
                                urchin.recruitment := i;
                                kelp.density :=
                                kelp.maxDensity;
                                Predation;
                           end;      { while loop }
                      ResultWriteSteady;
                      i := i - 4;
                 end;      { for loop }
            wolffish.density := 0.0;
            crabLobster.density := 0.0;
       end;           { SteadyCutbreakInitiation }


       procedure PulseOutbreakInitiation;
            var
                 i, j: integer;
       begin

            testWriting := testWritingYes;
            pulse := TRUE;
            oldMaxTime := maxTime;
```

```
        maxTime := 5;
        i := 40;
        for j := 0 to 30 do
            begin           { for loop }
                kelp.density := kelp.maxDensity;
                if wolffish.activePredator then
                    wolffish.density := j * 0.01;
                if crablobster.activePredator then
                    crablobster.density := j * 0.01;
                while kelp.density > 0.1 *
                kelp.maxDensity do
                    begin     { while loop }
                        urchin.pulseDensity := i;
                        urchin.juvenileDensity := i;
                        urchin.adultDensity := 0;
                        i := i + 1;
                        urchin.recruitment := 0;
                        kelp.density :=
                        kelp.maxDensity;
                        Predation;
                    end;      { while loop }
                ResultWritePulse;
                i := i - 4;
            end;      { for loop }
        wolffish.density := 0.0;
        crabLobster.density := 0.0;
        maxTime := oldMaxTime;
    end;            { PulseOutbreakInitiation }


    procedure OutbreakTermination;
        var
            i, j: integer;
    begin

        testWriting := testWritingYes;
```

```
          pulse := FALSE;
          i := 10;

          for j := 0 to 30 do
               begin          { for loop }
                    kelp.density := kelp.minDensity;
                    if wolffish.activePredator then
                         wolffish.density := j * 0.01;
                    if crablobster.activePredator then
                         crablobster.density := j * 0.01;
                    while kelp.density < 0.9 *
                    kelp.maxDensity do
                         begin     { while loop }
                              urchin.juvenileDensity := i;
                              urchin.adultDensity := 30;
                              i := i - 1;
                              urchin.recruitment := i;
{ Outbreaks are terminated at this level of recruitment }
                              kelp.density :=
                              kelp.minDensity;
                              redation;
                         end;       { while loop }
                    urchin.recruitment := urchin.recruitment
                    + 1;
{ Outbreaks are sustained at this level of recruitment }
                    ResultWriteTermination;
                    i := i + 10;
               end;       { for loop }
          wolffish.density := 0.0;
          crabLobster.density := 0.0;
     end;            { OutbreakTermination }

end.                 { Predation unit }
```

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