A study on the biology of Osangularia cf. venusta (Brady): an epiphytic foraminifera on the intertidal seagrass Halodule uninervis in Shelly Bay, Townsville, North Queensland.

Thesis submitted by

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ABSTRACT

A study on the biology of an epiphytic foraminifera (Osangularia cf. venusta) has been conducted in the intertidal zone at Shelly Bay near Townsville, Australia, during the period of 1988 to 1990.

The aims of the study were 1) to understand the general biology of O. cf. venusta, 2) to investigate the temporal patterns of O. cf. venusta distribution and its relationship with the substratum (seagrass blades), 3) to obtain information on the population dynamics of O. cf. venusta including growth rate, recolonization, and migration.

Sampling was carried out during low tide (< 0.5 metres), over three different time intervals : 1) monthly, 2) fortnightly, and 3) daily. Samples were fixed by using 70 % ethanol as soon as the field works were completed. O. cf. venusta specimens were collected by detaching them from the seagrass blades under a stereo microscope. Detailed observations of the specimen was made by means of a stereo microscope and a scanning electron microscope. Locomotion was observed by video recording the movements of O. cf. venusta individuals on the Halodule uninervis blades.

The study shows that individuals dislodging by physical and biological forces, may influence the population dynamics of O. cf.venusta especially the

"age" distribution. These factors were also suspected to affect the temporal abundance, density and the proportion of microspheric and megalospheric individuals in the population. Other factors such as the condition of the seagrass, its abundance and blade area are also strongly believed to affect the temporal abundance of Q. cf. venusta.

Generally, left coiled individuals dominated the population during the study period. This coiling direction preference, however, could not be correlated to the temperature variations of the surrounding environment.

"Twinned" specimens were observed in the Q. cf. venusta population during the study period. The study shows that the "twinned" phenomenon in Q. cf. venusta was probably initiated by the creation of a second aperture whilst the juvenile had only one chamber. The juvenile, then developed two rows of later chambers based on the two apertures.

The present study also reveals that Q.cf.venusta maintained its existence in the harsh intertidal environment by 1) reinforcing the test, 2) producing a large number of juveniles, 3) clinging on the blades of the intertidal seagrass Halodule uninervis, and 4) rapidly colonizing and recolonizing the "empty" seagrass blades.

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DECLARATION

I declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any university or other institution of tertiary education. Information derived from the published or unpublished work of others has been acknowledged in the text and a list of references is given.

B. Ludvianto

..27..August 1992.

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Chapter I

1.1. General Introduction

Foraminifera are single celled organisms that mostly secrete calcareous shells and live in the marine habitat and in the nineteenth century amazingly brought together a chemist, Brady; a grocer, Wright; a surgeon, Flint; and a post office official, Earland, into one "interest" of study. These pioneer workers in foraminifera, were fascinated by the beauty of foraminiferal tests and their usefulness in the geologic field (Haynes, 1981). The range of size of foraminifera (between 0.10 mm to more than 5 mm) allow them to be used as "index fossils" in oil exploration and other subsurface studies (Haynes, 1981). Of even greater value is their wide distribution in most sedimentary rock particularly in clay, silt , fine sand, coarse sand and limestone.

Besides their use in the geological studies, more recently, foraminifera have been used to investigate water mass movement (Boltovskoy and Wright, 1976), marine pollution (Bates and Spencer, 1979), marine environmental stress (Bock, 1976) and sediment production (Muller, 1976).

The studies of foraminiferal biology can be separated into two main topics i.e. 1) detailed investigations of the species and, 2) studies on the

relationship between species or group of species and the surrounding environment.

Detailed studies on the foraminiferal species have included investigations on

1) fine structure of foraminiferal protoplasm (Lee et al., 1965; Marzalek, 1969; Anderson and Bé, 1978; Alexander and Banner, 1984),

2) test morphology and test abnormality (Hottinger, Halicz and Reiss, 1991; Hansen and Reiss, 1972; Hottinger, Halicz and Reiss, 1991; Bolotovskoy, 1982; Boltovskoy, Scott and Medioli, 1991; Aktürk, 1976; Bé and Spero, 1981),

3) growth (Bradshaw, 1957; Murray, 1983; Hallock et al., 1986; Bijma et al., 1990),

4) life cycle, reproduction and alternation of generations (Lutze and Wefer, 1980; RÖttger, Krüger and de Rijk, 1990; Angell, 1990; RÖttger, Fladung, Schmaljohann, Splinder and Zacharias, 1986; Goldstein, 1988; Grell, 1988; Kloos, 1984) and,

5) behaviour (Kitazato, 1988 and Wienberg, 1991).

The studies on the relationship between foraminifera and their surrounding environments are

1) spatial and temporal distribution (Boltovskoy and Lena, 1969; Boltovskoy and Wright, 1976; Coleman, 1979; Michie, 1982 and 1987; Moodley, 1990; Jennings and Nelson, 1992; Sautter and Thunell, 1989 ,

2) migration (Walker, 1976; Bock, 1969),

3) population dynamics and sediments production (Murray, 1967 and 1983; Reynolds and Thunnell, 1986; Berger, 1971; Muller, 1974; Hallock et al., 1986; Erskian and Lipps, 1987),
4) association (Dobson and Haynes, 1973; Haward and Haynes, 1976; Zumwalt and Delaca, 1980; Bock, 1967 and 1969; Brasier, 1975; Severin, 1983 and 1987) and,
5) colonization and recolonization (Ellison and Peck, 1983; Buzas et al., 1989; Buzas, 1978; Finger and Lipps, 1981).

Living foraminifera can be observed in tide pools, estuaries and lagoons, intertidal zones, and inner shelf zones to the abyssal plains (Boersma, 1978; Brasier, 1980; Murray, 1973).

Foraminifera in the intertidal zone, have been extensively studied by many workers such as Reiter (1959), Cooper (1961), Boltovskoy (1963 and 1966) and Boltovskoy and Lena (1970). Because of the unique conditions of the intertidal zone (subject to twice-daily subaerial exposure, diurnal temperature changes, evaporation, rainfall and alteration of salinity), species of foraminifera that occupy this area are very well adapted to life in extreme conditions (Murray, 1973; Boltovskoy and Wright, 1976). Species may have flat tests, living attached to the substratum (Rotorbinella, Discorbis, Trochammina, Rotorbinella lomaensis (Bandy), R. turbinata (Cushman and Valentine), Discorbis monicana, Zalesny and Trochammina pacifica

(Cushman), or have thick and strong walls (Elphidium crispum, Quinqueloculina seminulum, Rotalia becarii) to survive living in the intertidal zone (Reiter, 1959; Boltovskoy and Wright, 1976).

According to Boltovskoy and Wright (1976) it is important to differentiate the living from the dead specimens when dealing with the foraminifera in the intertidal zone. This is because of the extensive sediment movement in this region that can cause faunal mixed up.

Many studies have shown that only a small percentage of the species found in the intertidal zones can be considered as living specimens. Reiter (1959) for instance reported only 17 were found living from 129 species observed in Santa Monica Bay, California. He also highlighted the seasonal variations in the number of individuals and species of foraminifera in Santa Monica Bay during his seven year study period. Cooper (1961) examined samples from San Diego, California northward to Colombia River, Oregon and stated that from the 120 species found only 64 species had live specimens. In Puerto Deseado, Argentina Boltovskoy (1963) and Boltovskoy and Lena (1966;1970) discovered that only 50 % of 130 species had live specimens.

Unfortunately, the method of differentiating the live and dead foraminifera found in the sediment is still the subject of debate. The most common method used to differentiate live foraminifera from dead is by the

use of the vital stain method that was introduced by Walton (1952) and the Sudan Black B fat staining method of Walker et all. (1974). These methods have proven unsatisfactory, because both the living and dead foraminifera are often stained together. This appears to be caused by the non-living protoplasm remaining inside the dead test for some period (Bernhard, 1988). Recently, De Laca (1986) introduced ATP analyses in order to differentiate the living foraminiferal from the dead population, however this method is both expensive and time consuming.

Boltovskoy and Wright (1976) stated that foraminiferal distribution is controlled by several ecological factors such as depth, temperature, salinity, nutrition, substratum, pH, light intensity, turbidity, organic content of substratum and the concentration of oxygen and calcium carbonate in the seawater.

Substratum, as one of the ecological factors, has been defined by foraminiferal investigators as the sediment and/or other organisms on the sediment (including weed and grass) where benthic foraminifera live. In the interest of ecology this definition should be refined so that foraminifera living on sediment are distinguished clearly from foraminifera living epiphytically or epizoically, thus the effect of substratum on the organisms would be more precise.

Seagrass such as : Posidonia, Cymodocea, Halophila, Halodule, Enhalus and, Thalassia have been reported to

be the substratum occupied by many species of foraminifera (Martin and Wright, 1988; Bock, 1969; Severin, 1987; Faber, 1991; Davies, 1970).

Epiphytic foraminifera usually attach themselves to the substratum by means of an organic matrix, as shown by Delaca and Lipps (1972) in Rosalina globularis. After death the attachment materials decompose and the test falls down to the sediments beneath the seagrass. Thus, only live specimens will be found attached to the seagrass blades.

Because, 1) the problem with differentiating between the live and dead foraminifera and 2) ease with which live foraminifera living epiphytically can be distinguished, it is concluded that biological and ecological studies of the intertidal foraminifera are more relevant to be undertaken on the epiphytic species.

Bock (1967) pioneered the study of epiphytic foraminifera living in seagrass beds. He concluded that seagrass (Thalassia testudinum) provides a habitat and means of dispersal for several foraminifera such as Archaias angulatus, Articulina mucronata, Fursenkoina complanata, Miliolina circularis, M. labiosa, Nubecularia cf N.lucifaga, Rosalina floridana, Sorites marginalis and Triloculina bermudezi in the Florida Keys. Davies (1970) in his study at Eastern Shark Bay, Western Australia found that Peneroplis planatus, Marginipora vertebralis, Vertebralina striata, Nuberculina sp, Spirilina sp, Patellina sp, Discorbis

dimidiatus all live on segrasses (including Posidonia and Cymodocea). He defined these organisms as epibiont foraminifera and suggested that these foraminifera contribute a significant amount of skeletal material to the carbonate sediment banks in this area.

In his research, Brasier (1975a) discovered that the diversity of foraminiferal tests is higher in the seagrass areas of Alligator Reef, South Jamaica. Murray (1970, in Brasier, 1975a) stated that in Abu Dhabi Lagoon, the diversity and standing crop of foraminifera was improved by the colonization of seagrass.

In a study of the importance of substratum in determining the character of foraminiferal biofacies in the lagoon of Barbuda, West Indies, Brasier (1975) concluded that the phytal substratum seems to control the distribution and standing crop of foraminifera. The word "phytal" was coined by Brasier to signify that the substrata where foraminifera lived consisted of weed and grass. However, he even included hard substrata derived from molluscs and corals into his "phytal" definition! He also found that the habitats with phytal substrata promoted an increase of foraminiferal standing crop. Although he listed foraminifera found on phytal surfaces, he did not, however, make a clear distinction between which "phytal" substrata supported which foraminifera, nor did he distinguished between weed and grass.

Blanc-Vernet (1969 in Brasier, 1975) and Davies (1970) stated that Peneroplis planatus has a parallel distribution and is associated with Cymodocea, and that other foraminifera such as Sorites marginalis and Amphisorus hemprichii seems to have a parallel distribution with Thallassia beds (which also included Halophila, Syringodium and Halodule).

Based on the above work and other research, Brasier (1975) used foraminifera to interpret the paleodistribution of a seagrass community. In this study he tried to match the appearance of certain foraminifera and seagrass species in time and space, and he concluded that "the distribution of recent and fossil seagrass are similar to the distribution of Recent and fossil seagrass-dwelling foraminifera".

Unfortunately, most of the studies on epiphytic foraminifera were either carried out in deeper water or undertaken only for the purpose of identifying the number of species. The study of the biology and ecology of a specific epiphytic foraminifera in the intertidal zone is still wanting.

Quantitative evidence on the biology and ecology of epiphytic foraminifera and their relationships with seagrass as a substratum thus needs to be gathered.

The pilot study that was conducted in early 1988 in the intertidal zone at Shelly Bay near Townsville, showed that the seagrass (Halodule uninervis) which occupied most of this area was inhabited by a species of

foraminifera called Osangularia cf.venusta (Brady). The published information on O.cf.venusta and its relationship with the substratum (H.uninervis) is very limited.

Coleman (1979) reported that specimens of Pararotalia venusta (which might be more correctly called Osangularia cf.venusta) were collected at depths ranging from 3 to 10 fathoms in Bowling Green Bay, North Queensland. Michie (1982 and 1987) collected Pararotalia venusta from Port Darwin, which was associated with calcareous sands and coral reef. He also stated that 10 % of his foraminiferal assemblages from the outer harbour region and off Lee Point, were comprised of P.venusta. These two reports, however, were based on sediment samples in which the method of differentiating the live and dead foraminifera still needs to be improved, and thus the place where P.venusta was found, is not neccessarily the actual habitat of this species.

There are at least three major advantages in using an epiphytic foraminifera in order to study the biology of intertidal foraminifera 1) the problems of reworked specimens is avoided, 2) there is no need for an extra step in the work to differentiate the living specimens from the their dead counterparts and 3) the specimens are always available in large numbers for the whole year, so statistically valid analyses can be performed.

During the study time, samples were taken over three different time intervals i.e : monthly,

fortnightly and daily. Seagrass blades were sampled during low tides that exposed the seagrass beds (<0.5m).

The present study was set up to investigate 1) the general biology of the intertidal epiphytic foraminifera 2) the patterns of the temporal distribution of O.cf.venusta and its relationship with the substratum (seagrass blades), 3) the population dynamics of O.cf.venusta including growth rate, recolonization and migration.

1.2. The history of the taxonomic position of Osangularia cf.venusta .

Specimens which are morphologically identical with the specimens collected by the author from Shelly Bay during the present study, were first recorded by Brady (1884) as Rotalia venusta, n. sp. from South Pacific Stations. Brady's specimens mostly came from the islands south of Papua from depth of 3 to 11 fathoms. He also obtained specimens from the west coast of Patagonia off Middle Island, at the depth of 345 fathoms. These specimens which were about 0.75 mm diameter, had sublenticular tests, in which the dorsal face was nearly flat and the ventral face was convex. The external surface of the test was granular or rugose. The sutures were limbate on the dorsal face and deeply excavated on the ventral. The last whorl consisted of eight chambers

and the aperture was an elongate fissure on the inner side of the final segment.

The most noticeble difference between the morphology of the specimens collected from Shelly Bay and Brady's (1884) descriptions, is on the characteristics of the aperture, especially the shape and the lack of apertural lip in Brady's specimens. The specimens collected from Shelly Bay have an aerial, arched, slit-like aperture that is characterised by the presence of a murus reflectus and an apertural lip.

Heron-Allen and Earland (1914 and 1915) discovered that Rotalia venusta was the most abundant and typical species in the Kerimba archipelago (Portuguese East Africa). This archipelago was characterised by extensive sandy beaches, stretches of rock-bound coast and mangrove swamps. The main islands are of coral formations and surounded by fringing and barrier reef. R.venusta was abundant in most of the sampling stations (depth 5 to 85 fathoms) and was reported to show variations in test morphology. According to Heron-Allen and Earland (1914) the test of R.venusta is normally inequilaterally biconvex with the dorsal face flatter than the ventral face. The specimens from the archipelago, however, had a highly convex dorsal face while the central portion of the the ventral face was excavate and was normally filled with secondary shell-matter. The peripheral edge which is normally lobulate, was found to be continuous or have marginal spines or

became denticulate, as in specimens from the station in Montepes Bay (a sample which also contained Zostera seagrass).

Finlay (1939) preferred to put Rotalia venusta under the genus Calcarina, because of the characteristics of the shape of the aperture of the R.venusta specimens. Hofker (1951) discovered specimens similar to Brady's (1884) specimens of Rotalia venusta from the Malay Archipelago. Based on the aperture appearance of his specimens, he considered these to be Parella venusta (Brady). He was convinced that the aperture of recent Parella venusta showed signs of unification of two parts that were found separate in the aperture of fossil counterparts. He also pointed out that the toothplate, apertural lip and keel were present. Barker (1960), however, preferred to follow Finlay (1939) and placed R. venusta back in the Calcarina.

After observing ten epiphytic specimens collected by the author from Shelly Bay, Yassini (1990, pers. comm.) suggested that Cribrorotalia venusta (Brady) is the proper species name for these specimens. Hottinger (1991, pers.comm), however, suggested the specimens collected from Shelly Bay be placed in Osangularia and he recommended Osangularia cf.venusta (Brady) as the best name for these specimens. His suggestion was mainly based on the overall morphological charcteristics of the specimens and especially on the shape and the position

of the aperture. In Osangularia, the aperture is characterised by having a murus reflectus or "a deeply sutural indentation of the apertural face of the test, longitudinally and obliquely folded below the aperture" (Loeblich and Tappan, 1988). This characteristic as well as other morphological features of Osangularia and also venusta are clearly present in the specimens collected from Shelly Bay and thus Hottinger's (1991) suggestion is followed for the species name in the present study.

Chapter II

Study site description and general materials and methods.

2.1. Site description

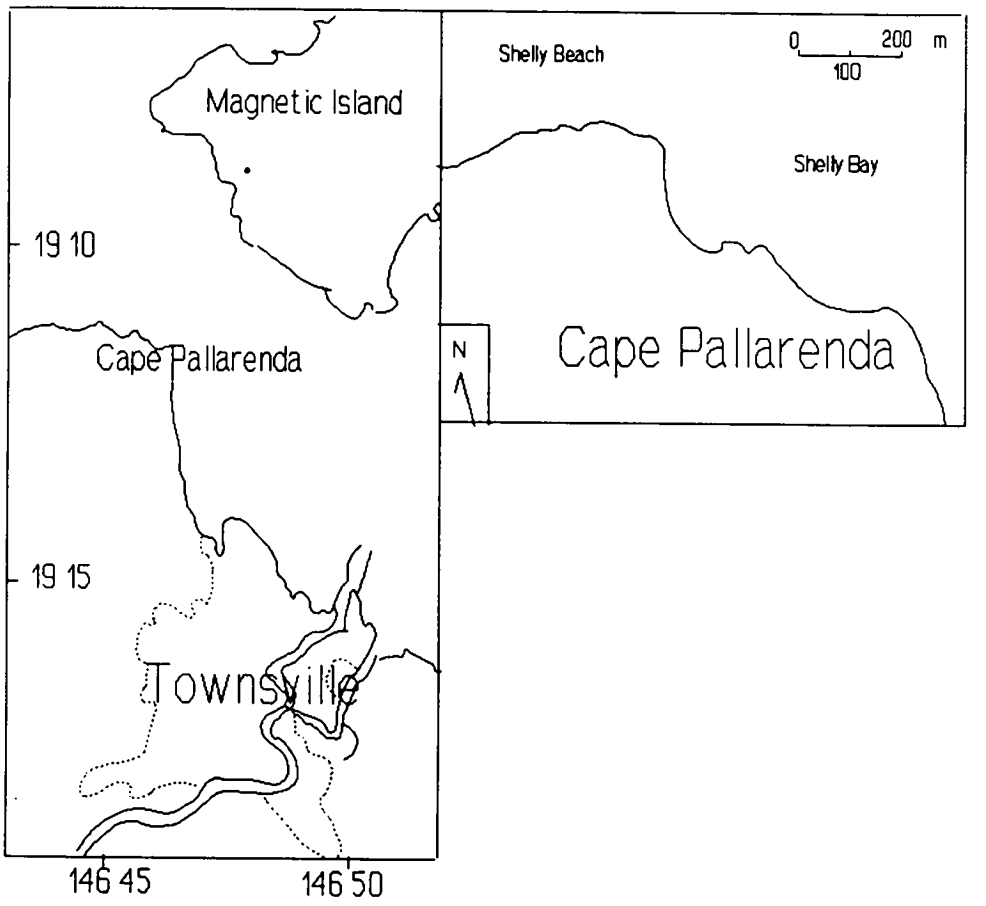
The study was carried out in Shelly Bay (19°11'S, 146°46'E, see fig 1) about 9.5 Kms northwest of Townsville Harbour, Queensland, Australia. The area was chosen specifically because of the abundance of the epiphytic foraminifera, seagrass and accessibility.

The study area was confined to a strip about 800 m long and 500 m wide that was exposed during low spring tides. The substratum was mostly well sorted sand with some pockets of clay sized materials in the area close to the north eastern shore.

The seagrass beds mostly consisted of Halodule uninervis and Halophila ovalis.

Halodule uninervis that was found in the area near to the north eastern shore of the Bay, has relatively longer blades, compared with other areas in the Bay. The blades of this seagrass, however, looked "clean" and

Figure 1: Study site at Shelly Bay, Townsville, North Queensland.


Magnetic Island
19 10
Cape Pallarenda
19 15
Townsville
146 45
146 50
Shelly Beach
0 200 m
100
Shelly Bay
N
Cape Pallarenda

when observed under the stereo microsocope, no foraminifera were detected. H.uninervis found in other areas of the Bay, has a relatively shorter blade and were always inhabited by foraminifera.

2.2. Materials and methods

2.2.1 General field methods

The sampling was carried out over three different time intervals:

a) monthly (October 1988 to September 1989)

b) fortnightly samples (January 1990 to March 1990)

c) daily (17th August to 21st August and 15th September to 18th September 1990).

Sampling was carried out during any low tide of less than 0.5 m. The seagrass blades were picked by means of forceps and scissors. Each leaf was placed in a separate plastic vial that was filled with sea water for transporting to the laboratory. In this way detached foraminifera could be related to a single leaf.

The sampling and experimental designs are presented in the Materials and methods section of each topic discussed in the following Chapters.

2.2.2 General laboratory methods

In the laboratory the H.uninervis blades with the epiphytic foraminifera on them were preserved in 70 % ethanol and stored in plastic vials.

Foraminifera specimens were obtained by detaching them from the seagrass blades by using an entomological needle, under a stereo microscope with 10 to 40 X magnification. The number of foraminifera were counted, as well as the number of chambers, coiling directions and the number of microspheric and megalospheric forms.

The differentiation of megalospheric and microspheric form and the determination of the number of chambers as well as the coiling direction of the test, required the immersion of the specimens in aniseed oil. A phase contrast microscope with 200 X magnification was used to observe the specimens.

The area of each seagrass blade was calculated, based on the length and width measured by callipers and an ocular micrometer respectively.

Video recording experiments were performed to study the growth rate of Osangularia.cf.venusta and its movements on a single H.uninervis leave.

Detailed observations of the external and internal features of the O.cf.venusta test were carried out by means of scanning electron microscopy (Phillips XL 20) in the SEM unit, James Cook University.

Chapter III

Temporal distribution of Osangularia cf.venusta and its relationship with the seagrass as a substratum.

3.1. Introduction.

Many workers have investigated the temporal distribution or periodicity phenomenon in foraminiferal populations (Boltovskoy and Lena, 1969; Buzas, 1969, 1978, 1982 and 1989; Ellison and Peck, 1983). Buzas (1969) stated that seasonal periodicity is common in the benthic foraminifera. Boltovskoy and Lena (1969) and Buzas (1969) reported that density periodicity was observed in foraminifera even in a short period of time.

Based on his caging experiments, Buzas (1978 and 1982) stated that predators play more important roles in regulating the temporal foraminiferal densities than the physio-chemical variables. In his investigation at Link Port, Buzas (1989) found that the maximum foraminiferal densities were observed in the warmer months. He also found that time was the most significant variable in his investigation, and he concluded that the foraminiferal density demonstrated periodicity.

Lee (1974) stated that patchy spatial distribution was very common in benthic foraminifera. He also

contended that even in small sediment samples ($\pm$ 1 cm^3) patchy distribution in benthic foraminifera could be observed.

In order to recognise the temporal and spatial distribution of the epiphytic foraminifera and their relationship with seagrass as the substratum, the following investigations were conducted on the seagrass-foraminifera association found at the study site. A pilot study showed that Halodule uninervis is spread broadly along the beach of Pallarenda (9.5 Km northwest of Townsville harbour) and has a patchy association with Halophila ovalis. Osangularia.cf.venusta is the most abundant foraminifera species that can be found on the seagrass blades at Pallarenda.

Based on the above findings the aim of this research was to study the monthly abundance and density variation of O.cf.venusta, and its relationship with the seagrasses of Pallarenda.

3.2. Materials and methods

3.2.1. Field work:

3.2.1.1. Seagrass preference.

To find out which kinds of seagrasses O.cf. venusta prefers, two sites at Pallarenda (Shelly Bay, AB; and Shelly beach, OB, see figure 2) were chosen

depending on the co-occurence of Halodule uninervis and Halophila ovalis .

At each site within the seagrass beds, a set of 4 random locations were selected. At each location 8 seagrass blades were picked at random from a 78.5 cm^2 quadrat by using forceps and scissors. Each leaf was placed in a separate plastic vial for transporting to the laboratory. In this way detached foraminifera could be related to a single leaf.

3.2.1.2. Temporal distribution of O.cf.venusta and its relation to the area of seagrass blades (experiment 1)

Temporal distribution variations were investigated for two periods of sampling with a slightly different sampling design between them. The first design (see figure 3) was developed to gain general information on the temporal distribution of O.cf.venusta , for a six month period. This first sampling period was carried out during October 1988 to March 1989. The sampling was conducted by placing a transect with six fixed locations (location 1 to 6) within the seagrass beds. Each location was 100 metres apart and used as regular sampling plot (see figure 2).

The second design (see figure 4) was employed

Figure 2: Study area and sampling site in Shelly Bay.

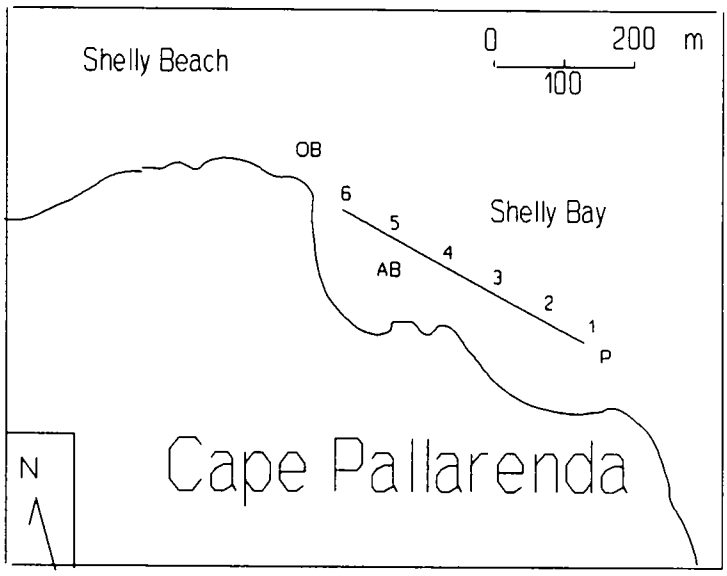

Shelly Beach
0
200 m
100
OB
6
5
4
AB
3
2
1
P
Shelly Bay
N
Cape Pallarenda

Figure 3: Sampling design used for studying the temporal mean abundance of O.cf.venusta during October 1988 to March 1989.

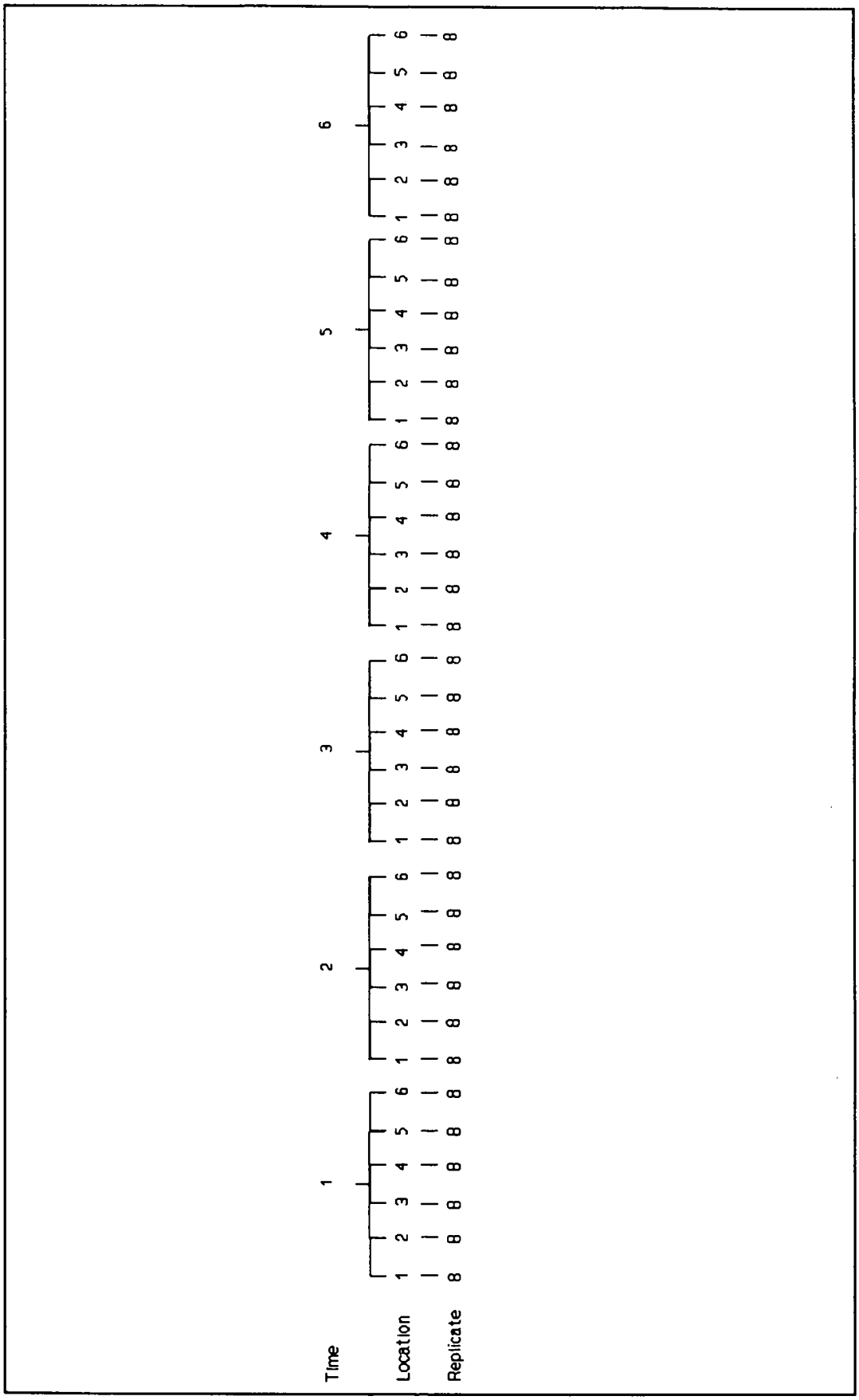

Time
Location
Replicate
1
2
3
4
5
6

Figure 4: Sampling design for studying the temporal abundance of O.cf,venusta during April 1989 to September 1989.

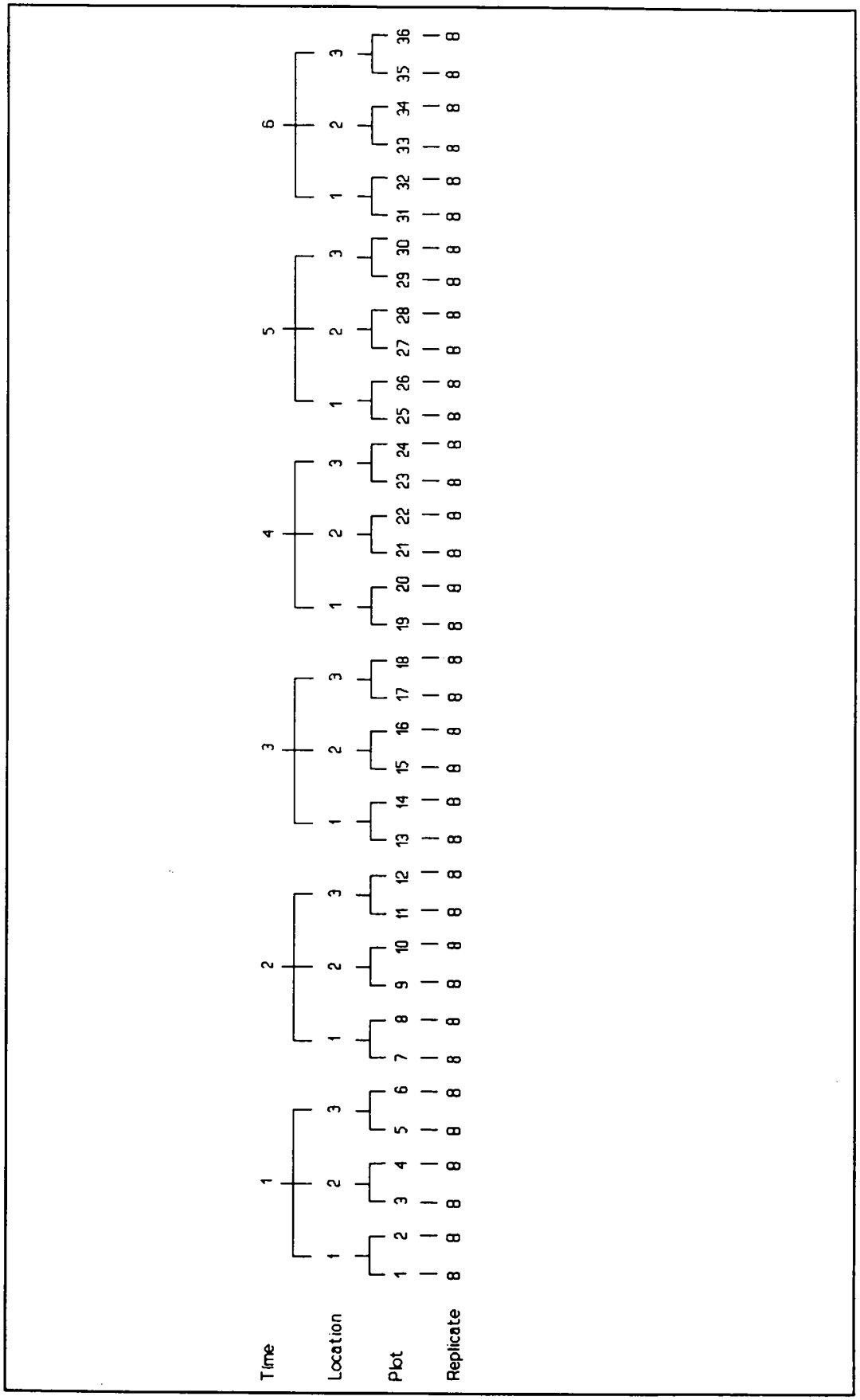
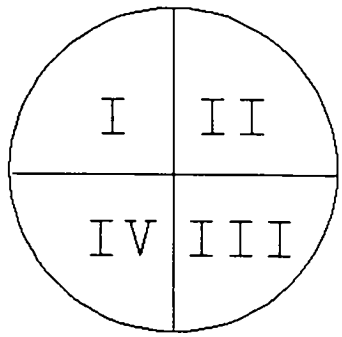

Time
Location
Plot
Replicate

Figure 5: Quadrants at each location of Experiment 1, period 2 (April 1989 to September 1989).



I,II,III,IV= Quadrants

during April 1989 to September 1989. This design was introduced to obtain more detailed information, especially the effects of space and time on the O.cf.venusta population.

The sampling was conducted monthly during low tide (less than 0.5 m) periods. The three locations in this second design were actually in the locations 1, 3 and 5 of sampling design 1. At each location (which was a circle of 5 metres diameter and divided into four equal quadrants, see figure 5), two randomly selected plots were set up on every sampling date. These two plots were selected randomly from the four quadrants by using a random number generated by a calculator.

3.2.1.3. Temporal distribution of O.cf.venusta and its relation to the abundance of the seagrass blades (experiment 2).

In order to investigate the relationship between the temporal distribution of O.cf.venusta and the abundance of seagrass blades, two field studies were undertaken. The first study was carried out for the period between October 1988 to March 1989, on the same dates as experiment 1 (see section 3.2.1.2). During this sampling period, an area of 5 x 5 metres was selected near location 1 (P) in fig.2 as a study site to determine the abundance of relevant organisms. Three quadrats (78.5 cm^2 each) were placed haphazardly at this

site. At each quadrat all of the seagrass blades were picked at the base end of the leaves and placed into plastic bags filled with seawater.

A second study was carried out for the period of sampling April to September 1989, at the same dates as experiment 1 (see section 3.2.1.2). A second 5 x 5 metre study site was selected 5 metres away from the first study site. The two sites were set up to investigate the patterns of the temporal distribution of O.cf.venusta , the seagrass (H.uninervis) and their temporal and spatial interaction. The same seagrass sampling method as employed in the first study, was used in both study sites.

3.2.2. Laboratory work:

All samples were fixed in 70% ethanol. Five samples (from 8) from each species of seagrass within each location were selected at random. The number of O. cf. venusta on each leaf were recorded.

3.2.2.1. Experiment 1.

The total number of O.cf.venusta on each blade were counted. The area of each leaf was measured (to the nearest 0.01 mm^2) by using a microscope micrometer to measure the width and callipers to measure length. By dividing the number of O.cf.venusta on each leaf by the

area of each leaf, the density of O.cf.venusta was obtained.

3.2.2.2. Experiment 2.

The total number of O.cf.venusta and the seagrass blades of each quadrat, at each site were recorded.

3.3. Analysis of data.

The data were analysed by employing several statistic methods :

Data	Method
Seagrass preference	Two way analysis of variance.
O.cf.venusta abundance	Two way analysis of variance, October 1988 to March 1989, (month fixed, location random). Three way analysis of variance, April to September 1989, (month fixed, location and plot random).
Relationship between O.cf.venusta abundance and area of blades	Simple correlation
Relationship between O.cf.venusta abundance and number of blades.	Simple regression and correlation
Seagrass blades abundance	Two way analysis of variance.

The data were transformed to Log (x) or Log (x+1), if necessary to satisfy the data normality requirement for the analysis of variance (Zar, 1984, Winer, 1972).

In order to obtain data on the seasonal variation of the abundance, density and blade area data from experiment 1 at locations that were monitored for a one year period (locations 1, 3, and 5) were plotted against dates of sampling.

3.4. Results

3.4.1. Seagrass preference of O.cf. venusta at Shelly Bay, Pallarenda.

Halodule uninervis and Halophila ovalis are common species of seagrass found in the area of Shelly Bay, Pallarenda. These two species of seagrass are used by O.cf.venusta as its substratum. Based on the statistical analysis (two way analysis of variance) that is presented in table : 1 , it was concluded that in Shelly Bay, there is a significant difference between the number of O.cf.venusta on Halophila ovalis and Halodule uninervis with a greater mean number of O.cf.venusta on Halodule uninervis than on Halophila

Source	DF	MS	F	P
Species (S)	1	5.93083	61.74	< 0.05 *
Location (L)	3	8.822E-01	0.92	> 0.05
S x L	3	9.607E-02	0.81	> 0.05
Replication (R) S x L x R	32	1.1962E-01		

Table 1: Result of the ANOVA on the O.cf.venusta mean abundance between the two species of seagrass (Halophila ovalis and Halodule uninervis) found in Shelly Bay, testing the Null hypothesis :

Ho_1 : There is no significant difference between the two seagrass species.

Ho_2 : There is no significant difference among locations

Ho_3 : There is no interaction effect between species and location on the O.cf.venusta mean abundance

Data were transformed to Log (x + 1)

* : significant .

Source	DF	MS	F	P
Species (S)	1	7.7520E-04	0.04	> 0.05
Location (L)	3	4.8878E-02	2.12	> 0.05
S x L	3	2.2433E-02	1.25	> 0.05
Replication (R) S x L x R	32	1.7959E-02		

Table 2: Result of the ANOVA on the O.cf.venusta mean abundance between the two species of seagrass (Halophila ovalis and Halodule uninervis) found in Shelly Beach, testing the Null hypothesis :

Ho_1 : There is no significant difference between the two seagrass species.

Ho_2 : There is no significant difference among locations

Ho_3 : There is no interaction effect between species and location on the O.cf.venusta mean abundance

Data were transformed to Log (x + 1)

ovalis. Therefore, this study was based mainly on the relationship of O.cf.venusta on Halodule uninervis .

3.4.2. Monthly temporal density and abundance and its relationship with the area of the blades.

The investigation on the temporal abundance of O.cf.venusta that were carried out over two separate sampling periods and using two designs, provided almost the same results.

The first period of investigation (October 1988 to March 1989) revealed that the temporal abundance of O.cf.venusta was significantly affected by the interaction between the times (dates of sampling) and the locations in the seagrass bed (see table 3). The average abundance ranged from 3 individuals/blade to 101 individuals/blade.

The second investigation that was undertaken during the period of April 1989 until September 1989, also demonstrated a significant importance for time and space factors in determining the abundance of O.cf.venusta (see table 4). The average number of individuals in this period ranged from 0.75 individuals/blade to 48 individuals/blade.

The second period of investigation also suggested more about the importance of the interaction of time and space factors at a smaller spatial scale (the plots) in

determining the average number of individuals per blade. The plots were only 2.5 metres apart and there was a significant difference in the average number of O.cf.venusta living on the blades.

Figures 6a, b, c show the average abundance of O.cf.venusta per blade at three locations that were monitored over a one year period. Generally, it can be seen that at location 1 the number of individuals per blade was relatively higher compared with the other two locations. It ranged from 2.18 to 62.75 individuals, and the average was 28.95 individuals per blade. At location 3 and 5, the average numbers of individuals per blade were 13.83 and 15.09 respectively.

On April 1989 the number of individuals per blade was noticeably smaller at all three locations. This small number was initiated in February 1989 and continued until April before it increased again on May 1989.

The monthly density patterns of the three locations are presented in figures 7a, b, c. The average density of O.cf.venusta at location 1 was 0.976 individuals/mm^2/month, while locations 2 and 3 had 0.5288 and 0.5833 individuals/mm^2/month respectively.

A relatively higher density (number of individuals/mm^2) was detected at all locations in

Source	DF	MS	F	P
Month (M)	5	2.8806	5.84	< 0.05 *
Location (L)	5	7.3716E-01	13.61	< 0.05 *
M x L	25	4.9358E-01	9.12	< 0.05 *
Replication (Rep) M x L x Rep	252	5.4144E-02		

Table 3: Result of the ANOVA on the monthly (October 1988 to March 1989) mean abundance of O.cf.venusta, testing the Null Hypothesis :

Ho_1 : There is no mean abundence difference among Months

Ho_2 : There is no mean abundance difference among Locations

Ho_3 : There is no interaction effect between Months and Locations

Data were transformed to Log (X + 1)

* : significant .

Source	DF	MS	F	P
Month (M)	5	4.9671	5.92	< 0.05 *
Location (L)	2	3.4320	10.16	< 0.05 *
M x L	10	0.83945	2.48	< 0.05 *
Plot (P) M x L x P	18	0.33763	5.35	< 0.05 *
Replication (R) M x L x P x R	252	6.3163E-02		

Table 4: Result of the ANOVA on the monthly O.cf.venusta mean abundance during the period of April 1989 to September 1989, testing the Null Hypothesis :

Ho_1 : There is no significant difference among Months

Ho_2 : There is no significant difference among Locations

Ho_3 : There is no interaction effect between Month and Location

Ho_4 : There is no significant difference between Plots

Data were transformed to Log (x + 1)

* : significant .

Figure 6 a, b, c: Monthly O.cf.venusta mean abundance at location 1, 3, and 5.

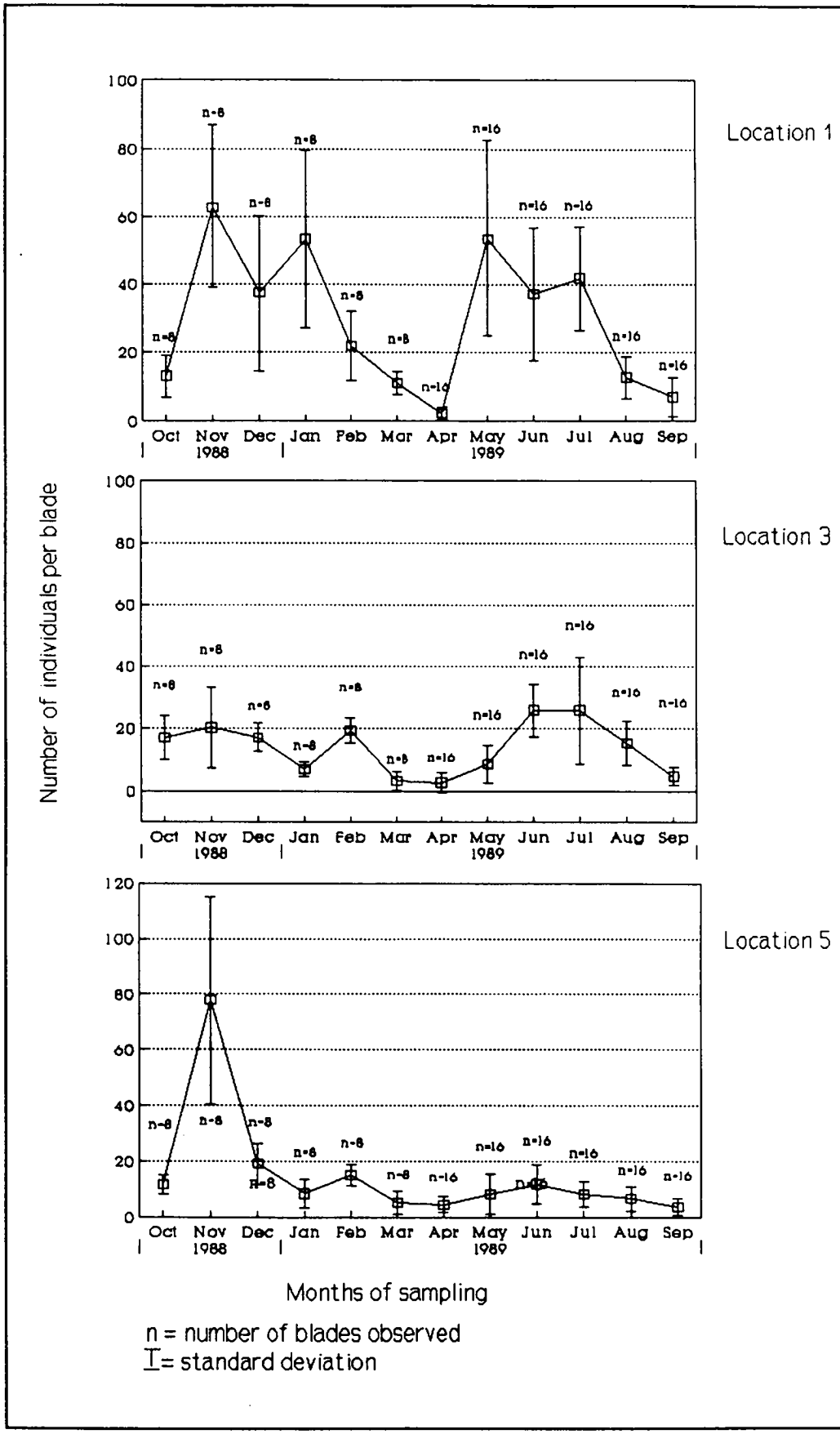

Location 1
Location 3
Location 5
Number of individuals per blade
Months of sampling
Oct
Nov
1988
Dec
Jan
Feb
Mar
Apr
May
1989
Jun
Jul
Aug
Sep
n = number of blades observed
I= standard deviation

Figure 7 a, b, and c: Monthly O.cf.venusta density at location 1, 3, and 5.

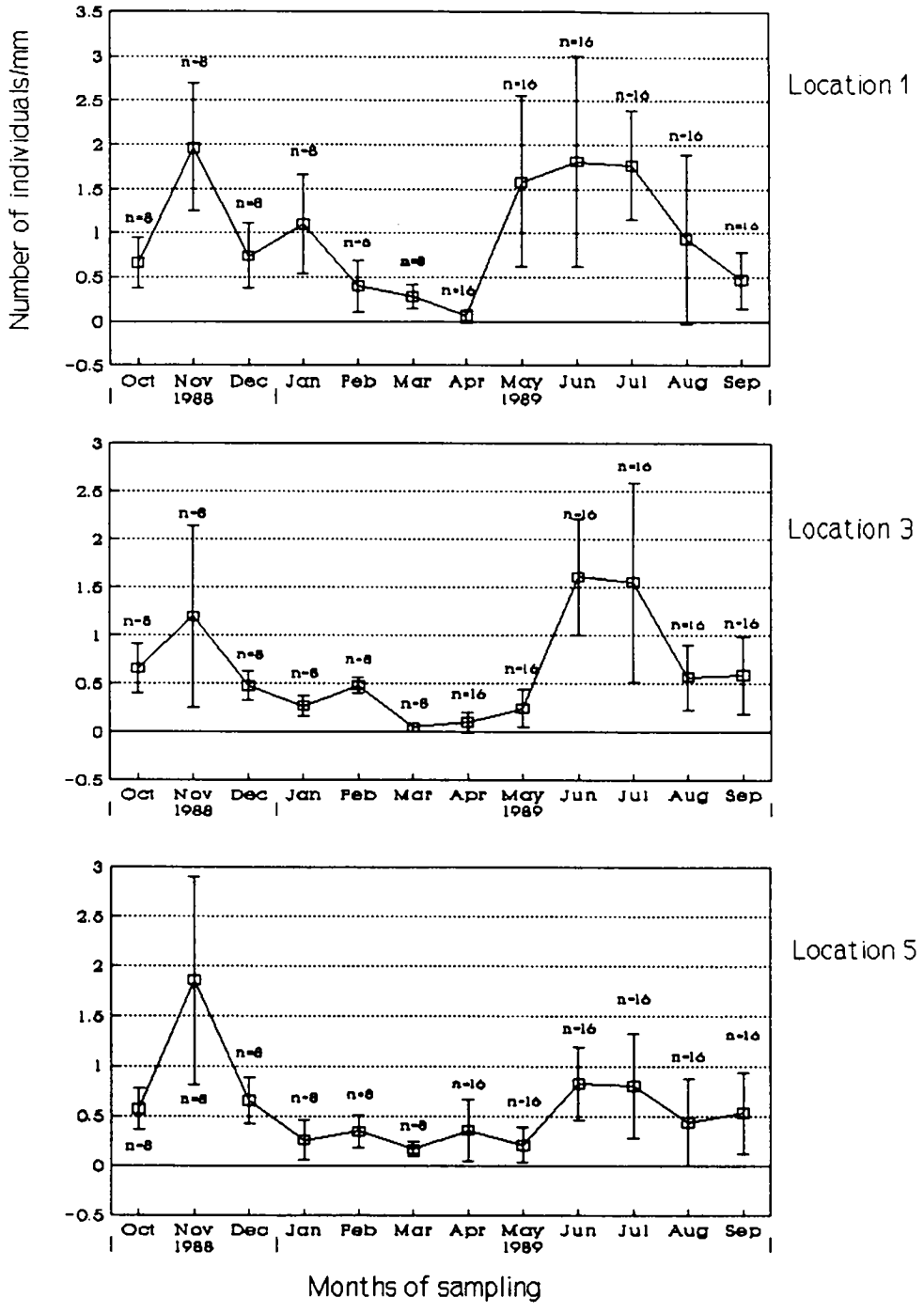
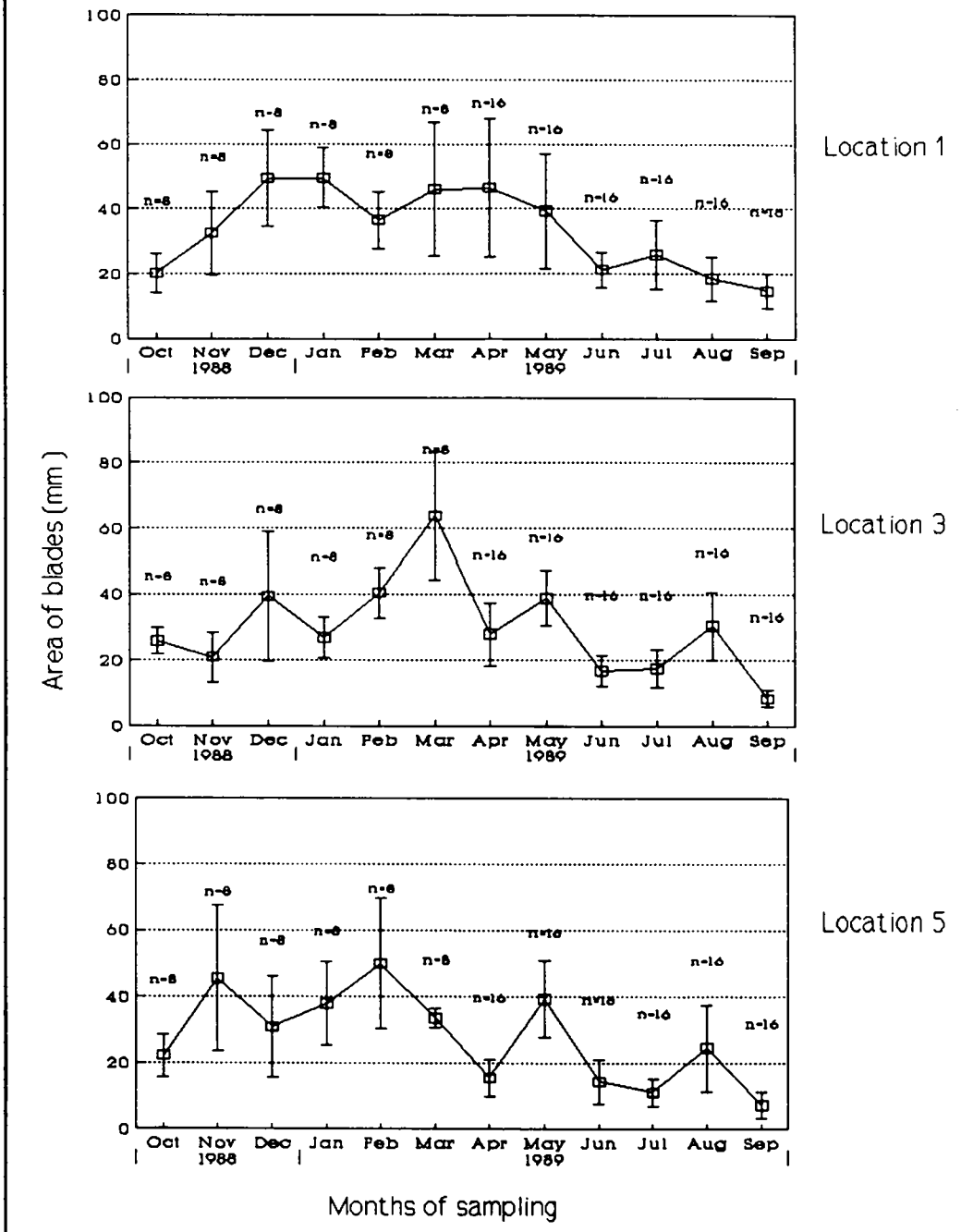

Number of individuals/mm
Location 1
Location 3
Location 5
Oct
Nov
1988
Dec
Jan
Feb
Mar
Apr
May
1989
Jun
Jul
Aug
Sep
Months of sampling
n = number of blades observed
I = Standard deviation

Figure 8 a, b, and c: Monthly mean area of seagrass blade at location 1, 3, and 5.


Location 1
Location 3
Location 5
Area of blades (mm)
Months of sampling
Oct
Nov
1988
Dec
Jan
Feb
Mar
Apr
May
1989
Jun
Jul
Aug
Sep
n = number of blades observed
I = Standard deviation

November 1988, June and July 1989.

The area of the individual seagrass blades was higher at location 1 (33.34 mm^2) compared with the blades at locations 2 and 3 where their average areas were 29.76 and 27.67 mm^2 respectively (see figure 8a. b, c).

Table 5 shows the correlation coefficient for the relationship between the average abundance of O.cf.venusta and the average area of the seagrass blades. The correlation between these two variables are mostly significant ($p<0.05$). In March 1989, April 1989, May 1989 and August 1989, however, no significant correlation could be detected ($p>0.05$).

3.4.3. Monthly temporal O.cf.venusta abundance in relation to the temporal abundance of the blades.

Experiment 2 which was designed to recognise the relationship between the abundance of O.cf.venusta and the abundance of the seagrass blades, revealed significant relationship between these two factors ($p<0.05$, see tables 6 and 7). The relationship could also be clearly observed in figures 9 and 10.

The analysis of variance of the temporal abundance of seagrass blades is shown in table 8. The later table also suggests that the seagrass blades were significantly different between times or dates of sampling ($p<0.05$). There was, however, no significant

difference detected between plots in terms of the abundance of the seagrass blades ($p>0.05$).

3.5. Discussion

Q.cf.venusta lives on the blades of both seagrass Halophila ovalis and Halodule uninervis. The statistical analysis, however, shows that Q.cf.venusta preferred to live on the blades of H.uninervis.

Faber (1991) suspected the existence of substances that were exuded by the rhizomes of seagrass plants in explaining the foraminifera substrate preference in the Halophila meadows. He found that the epiphytic foraminifera Peneroplis planatus preferred to live on the horizontal rhizome and stems rather than the erect blades or sediments. This phenomenon was not investigated in this work, and it is not known if a particular seagrass species produces special substances to attract Q.cf.venusta. However, this study suggests that the seagrass preference may be governed by the living nature and shape of blades of the two seagrass species.

Month of sampling	r
October 1988	0.4580
November 1988	0.5148
December 1988	0.4520
January 1989	0.4731
February 1989	0.3280
March 1989	-0.0281 ns
April 1989	-0.2225 ns
May 1989	0.0460 ns
June 1989	0.5592
July 1989	0.6529
August 1989	-0.2817 ns
September 1989	0.5173

Table 5: Summary of the simple correlation coefficients between the O.cf.venusta abundance and the area of blades (n=48), testing Ho :ρ = 0 against Ha :$\rho \neq 0$

ρ = correlation coeficient in the population
r = correlation coefficient in the sample
r (0.05)2.46 = 0.285
ns= non significant

Source	DF	MS	F	P	R^2
Regression	1	9.4538E+05	4.74	<0.05*	0.2284
Residual	16	3.1929E+05			
Total	17				

Table 6: Result of the ANOVA on regression between the number of O.cf.venusta and the number of blades per 18 plots (1 plot = 78.53 cm^2) during the period of October 1988 to March 1989, testing the Null hypothesis :

Ho : there is no significant simple regression between the number of O.cf.venusta and the number of blades

* : significant .

Source	DF	MS	F	P	R^2
Regression	1	3.4920	11.36**	<0.01	0.2504
Residual	34	3.0751E-01			
Total	35				

Table 7: Result of the ANOVA on regression between the number of O.cf.venusta and the number of blades per 36 plots (1 plot = 78.53 cm^2) during the period of April to September 1989, testing the Null hypothesis :

Ho : there is no significant simple regression between the number of O.cf.venusta and the number of blades

** : highly significant .

Source	DF	MS	F	P
Month (M)	5	410.51	3.78	< 0.05 *
Plot (P)	1	25.00	0.23	> 0.05
M x P	5	174.60	1.61	> 0.05
Replication (R) M x L x R	24	108.56		

Table 8: Result of the ANOVA on the monthly blades abundance during the period of April 1989 to September 1989, testing the Null Hypothesis :

Ho_1 : There is no significant difference among Months

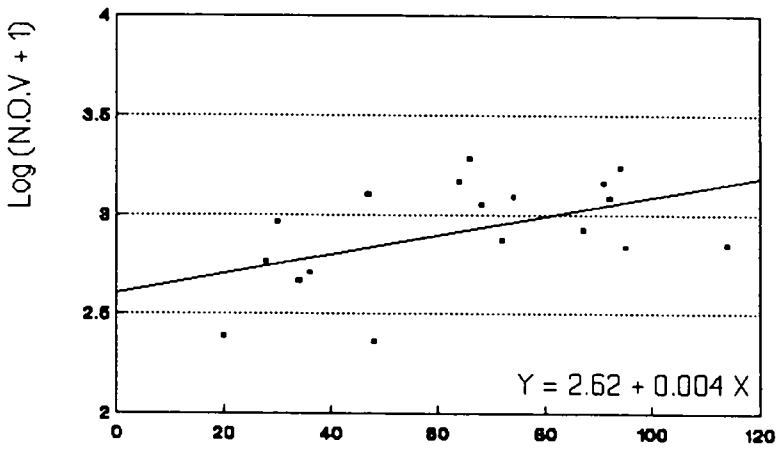
Ho_2 : There is no significant difference between Plots

Ho_3 : There is no interaction effect between Month and Plots

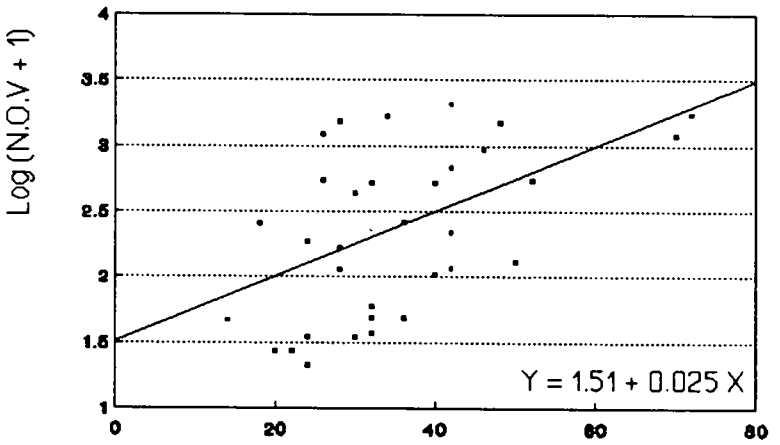
* : significant .

Figure 9: Number of O.cf.venusta vs number of seagrass blades per plot in experiment 2 during October 1988 to March 1989.

Figure 10: Number of O.cf.venusta vs number of seagrass blades per plot in experiment 2 during April 1989 to September 1989.



Number of seagrass blades per plot



Number of seagrass blades per plot

N.O.V. = Number of Q.cf.venusta

H.uninervis has relatively long, ligulate blades whereas H.ovalis has short rounded blades. The blades of H.uninervis were also noted to be mostly in the erect position in the water column, whilst the blades of H. ovalis tend to lie close to the sediment surface. In addition, it was also observed that most of the time H.uninervis blades were found free from sediment particles, whilst the opposite condition occurred on the blades of H.ovalis. Clinging on the erect blade in the water column and free from sediment particles is possibly the ideal living condition for O.cf.venusta.

The abundance and density data, which were gathered for a one year period, during October 1988 to September 1989 suggest that O.cf.venusta exhibited different periodicity in different locations. Thus, the abundance of O.cf.venusta was seemingly not solely ruled by time, but also by a space factor. The space factor could be on a big scale, such as the location of sampling, or on a small scale, such as seagrass blades.

The results from the close observation of three locations (1, 3 and 5) highlighted the importance of space on the bigger scale (macrospace) in regulating the O.cf.venusta population. Location 1, in which the average area of seagrass blades was relatively higher, exhibited greater abundance and density of O.cf.venusta compared with the other two locations. In addition, the significant relationship between the number of O.cf.venusta and the area of seagrass blades) and also

the results from experiment 2, that emphasized the the relationship between the number of blades and the number of Q.cf.venusta) indicates, even more, the importance of microspace (the blades) in governing the epiphytic foraminiferal population.

Severin (1983 and 1987) reported that, in Papua New Guinea, there was no correlation between seagrass area and Marginopora vertebralis density. The present study, therefore highlights that there are specific behavioural differences between two tropical epiphytic foraminiferal species in terms of their relationship with the seagrass as their substratum.

During the course of investigation, it was noted that during the low tides, location 1 was always inundated longer compared with the other two locations. In addition, the seagrasses in location 1 appeared to remain covered by seawater during the low tide, whilst location 3 and 5 were exposed. It was also noticed that the seagrasses in location 1 were more dense compared with locations 3 and 5. Thus, it is reasonable to assume that the local conditions of depth, the density, and area of seagrass blades, singlely or together, play an important role in regulating the Q.cf.venusta population.

There are at least three strong possibilities which must be taken into account in explaining the patchyness of the spatial distribution of Q.cf.venusta and their temporal fluctuations. These possibilities are : 1) the

effect of the environmental factors (e.g. waves and currents) in detaching the foraminifera from the seagrass blades, 2) the migration of foraminifera between blades and 3) the natural development and reproduction of the epiphytic foraminiferal population.

The effect of waves and currents can be inferred from the data gathered during the tropical cyclone season (February 1989 to April 1989). The population of foraminifera decreased dramatically, especially in April 1989, when specimens were collected just one day after the tropical cyclone Aivu passed close to the study site.

The possibility of foraminiferal migration is investigated in Chapter V section 3, and the reproduction and population development is discussed in chapter V section 1.

Chapter IV

Morphology of Osangularia cf.venusta :its abnormality and uses in the temporal study

4.1. General morphology of O.cf.venusta.

4.1.1. Introduction

Foraminiferal classification, according to Loeblich and Tappan (1964, 1988) is based mainly on the characteristics of the test . These characteristics include chamber form, chamber arrangement, ornamentation, apertural structure, chamber wall composition, crystal form, lamellar character, perforation , canal system and internal modifications such as endoskeletal pillars and toothplates.

There are many variations of foraminiferal chamber form such as globular, ovate, pyriform, tubular, cyclical, hemispherical, radial, elongate, angular, tubuluspinate and fistulose. The arrangement of the chambers may be rectilinear, arcuate, zigzag, planispiral, peneropline, trochospiral, plano-convex, streptospiral, milioline, uniserial, biserial, triserial and quadriserial (Loeblich and Tappan, 1964). Brasier (1980) and Haynes (1981) mentioned that in some cases

one species of foraminifera can have more than one chamber arrangement , for instance planispiral in the early juvenile chambers and biserial in the later chambers, as is found in Spiroplectamina. In Eggerella, the juvenile has trochospiral chambers and the adult has a triserial chamber arrangement.

The test of foraminifera may develop some variations of external surface ornamentation such as spines, keels, rugae, striae, costae, granules or reticulate and pustules (Brasier, 1980). Other ornamentation described as punctate, limbate sutures, ribbed , fissures and pitted can also be found in foraminiferal tests (Loeblich and Tappan, 1964).

Foraminifera have two main openings on their tests. The main aperture and the supplementary aperture, or its modification such as canal opening and pores. The aperture is highly variable but often species specific (Loeblich and Tappan, 1964). Some additional modification such as lip, tooth, plates, rims, tegilla, bullae , phialine, umbilical teeth and umbilical bos may also be found (Loeblich and Tappan, 1964; Boltovskoy and Wright, 1976; Brasier, 1980).

Boltovskoy and Wright (1976) stated that the chamber wall may be constructed in 4 ways: 1) chitinious, 2) agglutinated, 3) calcareous and 4) silicious. The calcareous foraminifera have six wall structures : 1) microgranular walls, 2) procellaneous walls, 3) radial hyaline walls, 4) finely granular

hyaline walls, 5) monocrystalline walls and 6) spicular walls. The finely granular hyaline walls have a lamellar structure when a thin section of the test is studied with light or electron microscope. These lamellar structures are monolamellar, rotaliid, bilamellar, and multilamellar (Loeblich and Tappan, 1964; Boltovskoy and Wright, 1976 and Haynes, 1981). The "rotaliid" wall is unique because when new chambers form, a layer of the ultimate chamber also covers the apertural face of the penultimate chamber and forms a septal flap . This structure is slightly different to the bilamellar chamber structure in which the apertural face of the penultimate chambers is not covered by the new layer of shell material of the ultimate chamber (Loeblich and Tappan, 1964; Boltovskoy and Wright, 1976; Brasier, 1980; Haynes, 1981).

Haynes (1981) stated that the inner layer of the ultimate chamber in the "rotaliid" wall structure can modify the intercameral foramen and create a toothplate in the penultimate chamber. In asterigerinids, Hansen and Reiss (1972) found that the toothplate was formed by a doubled inner lining of the chamber wall. This toothplate separated the chamber lumen from the stellar-chamberlet. Hottinger et.al (1991), however, emphasized that there is no association between toothplate and stellar-chamberlet, instead, they introduced the term umbilical plate for a structure that separates the chamber lumen from the foliar or stellar-chamberlet.

They also highlighted that the toothplate always protrudes distally and adaxially with a free edge through the main aperture. Billman, Hottinger and Osterle (1980) in their work on rotaliid foraminifera emphasized other internal chamber structures such as the foraminal plate and umbilical cover plate. They defined the foraminal plate as an inward oblique extension of chamber wall, running through the intercameral foramen and thus forming the umbilical cover plate. Hottinger et.al. (1991) separated the umbilical plate and cover plate from the umbilical cover plate, defined by Billman et.al.(1980). According to Hottinger et.al. (1991) the umbilical plate is only found in the ultimate chambers because it extends from the distal to proximal chamber wall and is attached to the intercameral foramen and to the main aperture without protruding into it. A cover plate is never found in the ultimate chamber. It completely separates the main chamber lumen from the foliar chamberlet and no perforations exist in this plate.

The perforations or pores in the chamber walls have been noted for a long time in the calcareous foraminifera. Based on the diameter of the pores, Boltovskoy and Wright (1976) stated that, there are at least two groups of calcareous foraminifera. The first group are Nodosariidae, Buliminidae, Polymorphinidae, and Heterohelicidae that have pores with diameter ranges from 1-6 μ. The second group are Rotaliidae,

Acervulinidae, and Nonoionidae with pores ranging from 6-15 μ. Haynes (1981) stated that externally the pores could have an oval, round or slit-like shape. He also mentioned that the internal openings of pores in the chamber lumen are usualy larger in diameter than the external openings.

The real function of the pores, according Boltovskoy and Wright (1976) still needs to be clarified. Berthold (1976, in Haynes, 1981) and Boltovskoy and Wright (1976), however, stated that some functions of the pores were to allow : a) the process of osmoregulation, b) gas exchange, c) excretion of dissolved organic substances, d) gamete release and d) especially in planktonic foraminifera, to increase buoyancy.

The present study attempts to describe the general morphology including both the external and internal appearence of the calcareous foraminifera Osangularia.cf.venusta (Brady). This description is very important as it ensures that the biology of only one species is described and the correct taxonomic position of O.cf.venusta is determined.

4.1.2. Material and methods

Live specimens were used for observing the morphology of the forams. To do this, live specimens of

the seagrass Halodule uninervis, upon which the foraminifera is epiphytic, were collected from Shelly Bay. The blades were immersed in filtered seawater and the live forams photographed.

The morphology of Q.cf.venusta was also studied by using dry specimens immersed in aniseed oil. Pictures were taken by using a camera connected to a light microscope, using both transmitted and reflected light.

Detailed observations of the external and internal features of Q.cf.venusta test were carried out by means of scanning electron microscopy (Phillips XL 20) in the SEM unit, James Cook University.

4.1.3. Results

4.1.3.1. Megalospheric and microspheric morphology.

Q.cf.venusta has a low trochospiral chamber arrangement with no carina or keel, and may be coiled either sinistrally or dextrally. All chambers are visible from the dorsal side, whilst only the chambers from the last whorl are visible from the ventral side. The megalospheric and microspheric specimens were differentiated by measuring the diameter of the first chamber (proloculus). The proloculus diameter of the megalospheric specimens ranged from 40 to 80 μ, whereas the diameter of the proloculus of the microspheric forms ranged from 5 to 10 μ. The microspheric forms have more

whorls than the megalospheric ones (see figures 11 and 12).

From the dorsal side the sutures were oblique, and only slightly depressed while from the ventral side they were deeply incised. The dorsal side of the chambers were slightly inflated and pustulate near the periphery. The ventral side of the chambers were more inflated and the chamber wall more heavily pustulate . The pustules on the ventral side near the umbilicus, at the umbilical plug and adjacent to the chamber of the previous whorl, in front of the aperture, were long and spike-like (see figures 13, 14, 15, 18, and 19). The "spike-like" pustules can have one or more pointed tips. The area near the periphery of the ventral side and on the dorsal side the pustules were rounded and short (see figures 16 and 17).

The apertural face was covered by short, conical pustules, which became infrequent in the area surrounding the apertural lip. The same kinds of pustules were also found covering the apertural lip.

Externally, the pores were round in shape and distributed among the pustules. The average diameter of the pores of the dorsal side was about 1.7 u whereas the average diameter of the ventral pores was 1.8 u.

Figure 11: Osangularia cf.venusta, megalospheric specimen, dorsal view (⟵ 0.12 mm).

Figure 12: Osangularia cf.venusta, microspheric specimen, ventral view (⟵ 0.12 mm).

Figure 13: Apertural view. Note the shape of the pustules in front of the aperture.

Figure 14: Two different types of pustules. Note the pores with "lip" distributes among pustules.

Figure 15: Long, sharp pointed pustules near the umbilical plug.

Figure 16: Short, rounded pustules near periphery at the ventral side.

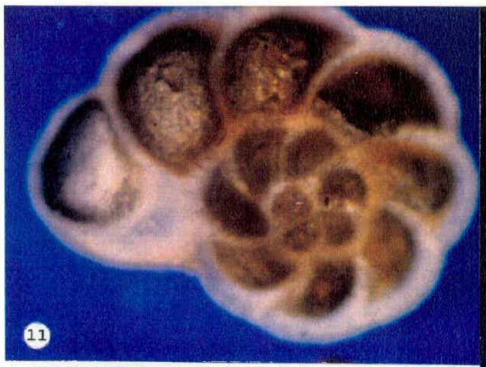
Figure 17: Short, rounded pustules at the dorsal side.

Figure 18: Umbilical side. Note the umbilical plug.

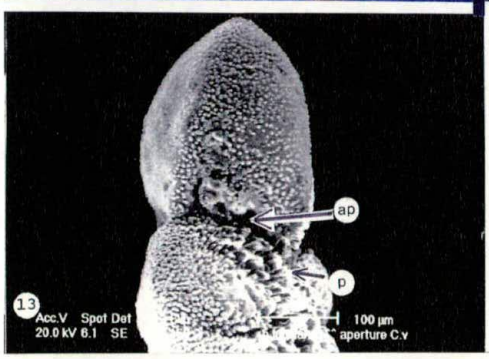
Figure 19: Detail of the umbilical plug. Note the multiple tips of the pustules.

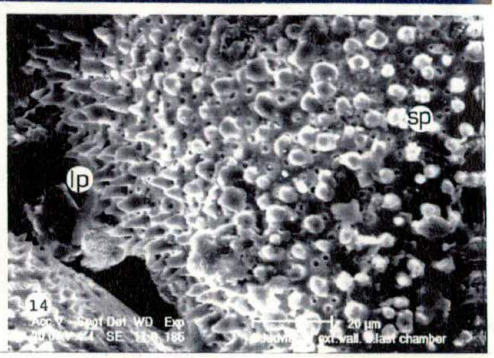
Figure 20: Pores viewed from the internal chamber wall. Note the pores "lip-like" structure.

ap = aperture
lp = long pustules
p = pustules
sp = short pustules
up = umbilical plug


11


12


ap
p
13
Acc.V Spot Det
20.0 kV 6.1 SE
100 µm
aperture C.v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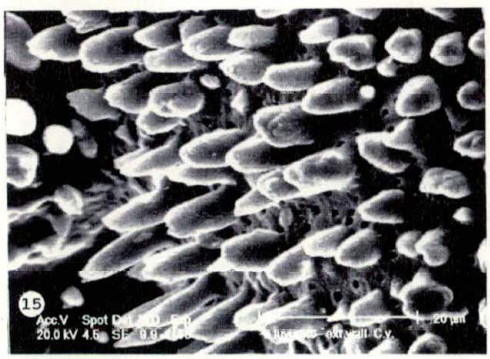
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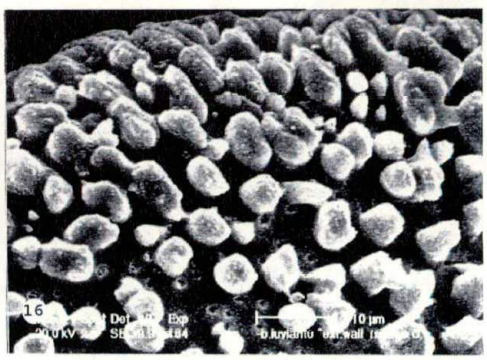
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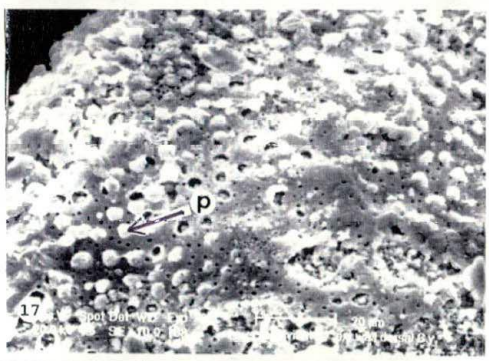
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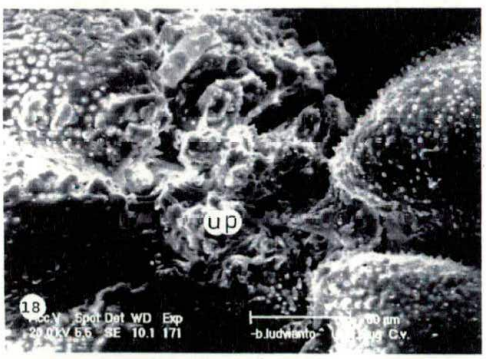

up
18
Acc.V Spot Det WD Exp
20.0 kV 5.5 SE 10.1 171


20 µm

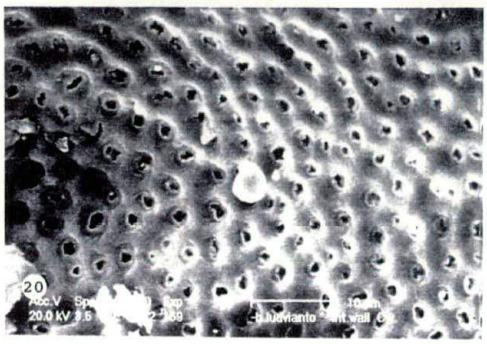

20
Acc.V Spot Det WD Exp
20.0 kV 5.5 SE 12.2 189

Figure 21: Pores viewed from the internal chamber wall. Note the anastomose inner lamellae.

Figure 22: Cross section of the ultimate chamber wall. Note the position of pores and the shape of pustules.

Figure 23: Cross section of the ultimate chamber wall. Note the pustules and the pores that have a narrower internal opening.

Figure 24: Cross section of the penultimate chamber wall.

Figure 25: Apertural view of Q.cf.venusta showing the shape and position of the main aperture. Note the **thick lip** (——— = 0.10 mm).

Figure 26: Brood chamber aperture. Note the heavily pustulate, thick aperture lip and shape of pustules infront of the aperture.

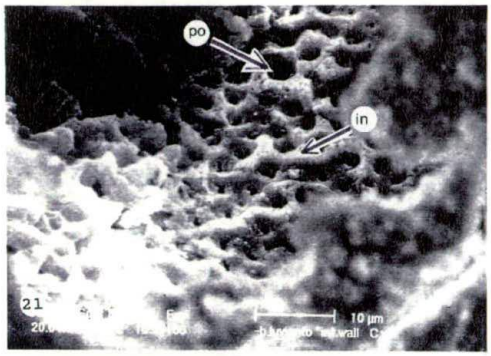
Figure 27: Brood chamber aperture. Note the pore at the "china wall-like" plate.

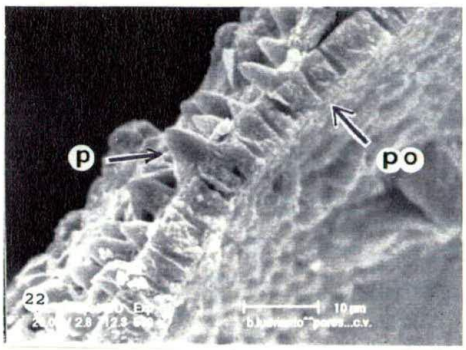
Figure 28: Brood chamber aperture. Note the " bending" that creates a second arhed opening.

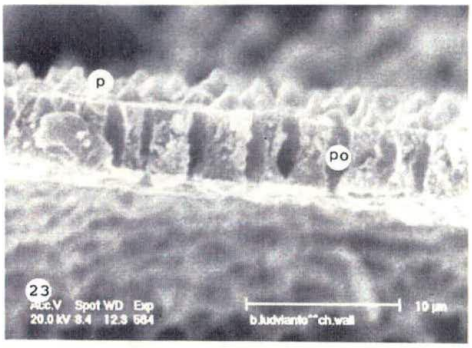
Figure 29: Broken ultimate chamber, showing the " china wall-like" plate.

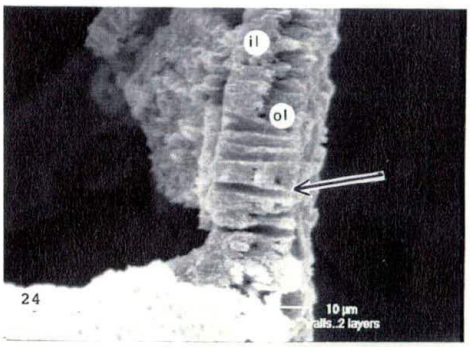
Figure 30: Detail of the " china wall-like " plate. Note the " U shape opening ".

ap = aperture
b = bending
cw = "china wall-like" plate
icf= intercameral foramen
il = inner lamina
in = inner lamellae
ol = outer lamina
op = "U shape axial opening"
p = pustule
po = pore
sf = septal flap


po
in
21
10 µm

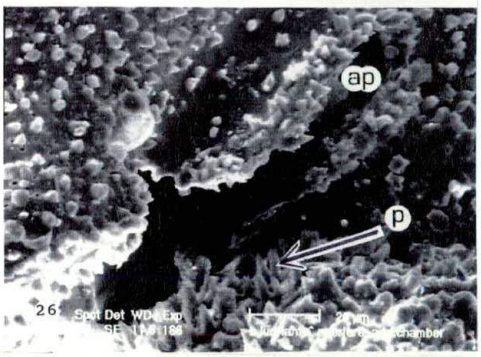

p
po
22
10 µm

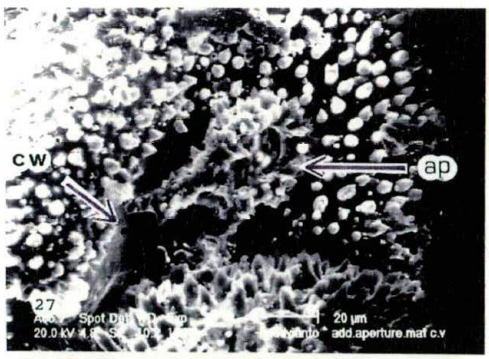

p
po
23
Acc.V Spot WD Exp
20.0 kV 3.4 12.3 584
10 µm

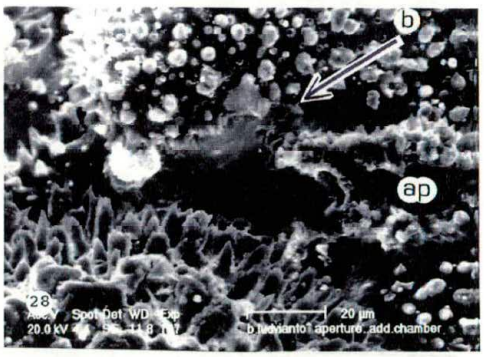

il
ol
24
10 µm


ap

25


ap
p
26
20 µm


cw
ap
27
20 µm


b
ap
28
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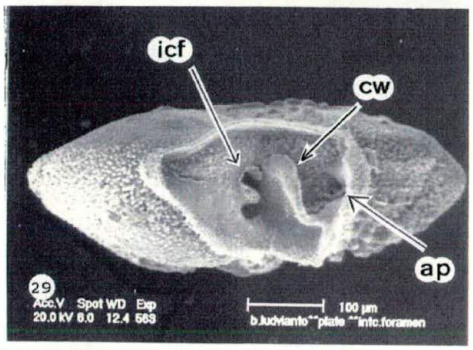
icf
cw
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29
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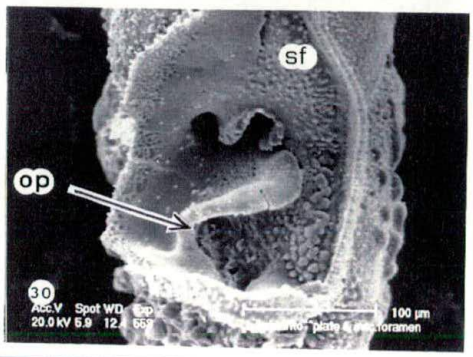
20.0 kV 8.0 12.4 563
100 µm


sf
op
30
Acc.V Spot WD Exp
20.0 kV 5.9
100 µm

Internally, the pore openings were bordered by a "lip like" structure that can be fully opened (round shape) or slightly closed (slit shape). The pores were separated from each other by an anastomosed thickening of the inner chamber walls to form a honeycomb-like feature (see figures 20 and 21). A cross section of the chamber wall showed that the pores have some variation in shape (see figures 22 and 23). Figure 24 shows that the pores at the two layers of the penultimate chamber wall were perfectly aligned the pores of the inner layer or lamina continued smoothly into the pores of the outer lamina.

Figure 25 shows the arched aereal aperture bordered by a thick lip (see also figures 26 to 28). A small posterio-equatorial bend on the ventral end of the aperture lip creates a smaller arched continuation of the aperture.

Figures 29 and 30 show that the main aperture was partly separated from the chamber lumen by a "china wall-like" plate which runs from the basal border of the intercameral foramen of the penultimate chamber to the distal chamber wall. This is attached to both the ventral side of the apertural lip and the chamber wall on the axial-umbillical side. This plate was about 9 μ thick and gradually thickened toward the distal chamber wall ($\pm$ 12 μ thick). Figure 32 shows that the plate was a distal extension of the inner lamella of the distal

chamber wall surrouding the intercameral foramen of the previous chamber.

The chamber wall of O.cf.venusta seemed to be constructed in the rotaliid pattern as described byBrasier (1980) and Haynes (1981). In O.cf.venusta, however, the inner lamellae of the newly constructed chamber that covered the apertural face of the old chamber (and called the septal flap) left a small portion of the pustules as " pustule remains". The area between the pustule remains was smooth and no pores were observed (see figure 35).

The inner lamellae of the chamber wall consist of two surfaces : the smooth surface and the anastomose "honeycomb-like" surface. The smooth surface was observed in : 1) the ventral part of the wall that adheres to the previous chamber (and forms the septum), 2) the axial-umbilical side of the chamber wall in conjuction with the plate, 3) the internal area of the aperture or intercameral foramen, and 4) on the apertural face of the previous chamber (see figures 29 to 33). The structure of the inner lamella was similar to the structure of the plate. It is mostly imperforate, but in the septum area and the part of the plate which separates the chamber lumen from the umbillical area, simple pores (without lip and anastomose thickened

Figure 31: Internal structure of the aperture, in relation to the "china wall-like" plate.

Figure 32: The "china wall-like" plate at the third chamber before the ultimate chamber.

Figure 33: Broken ultimate chamber showing the inner lamellae and the outer lamella in relation to the whole chamber structure.

Figure 34: The inner lamellae. Note the gradually changing of the surface appearence from smooth to thickened anastomose structure bordering the pores.

Figure 35: Apertural face of the penultimate chamber. Note the pustules remains.

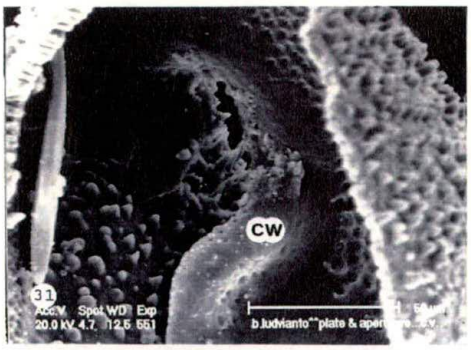
Figure 36: Mature microspheric with brood chambers (—— = 0.66 mm)

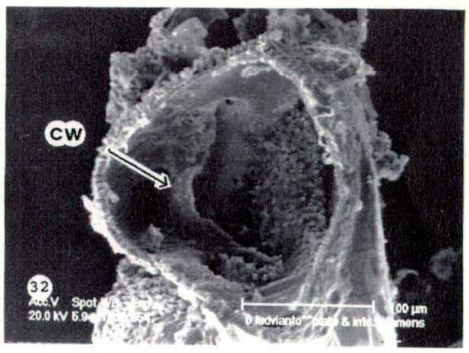
Figure 37 and 38: Mature microspherics. Note the shapes and positions of the brood chambers in relation to the chambers at the last whorl (Fig. 37. —— = 0.15 mm; Fig. 38.—— = 0.18 mm).

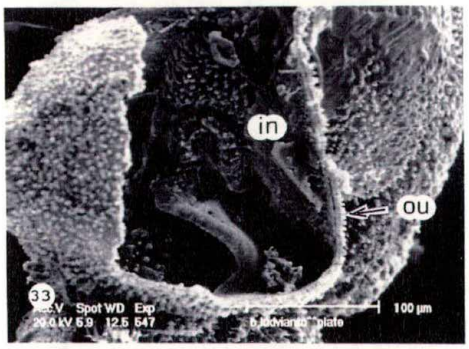
Figure 39: Mature microspheric with one brood chamber. Note the postion of the second aperture of the brood chamber (—— = 0.15 mm).

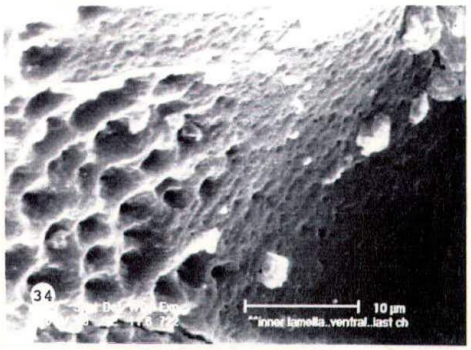
Figure 40: Mature microspheric specimen with two brood chambers. Note the second aperture at the ultimate chamber, and the position of the apertures at the brood chambers.

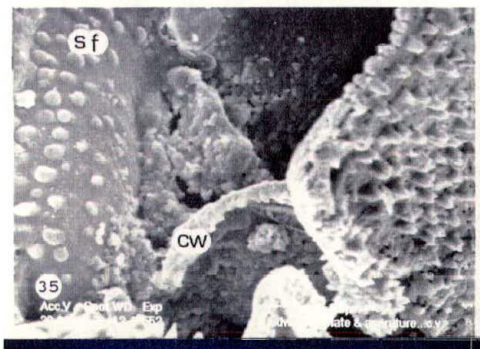
ap = aperture
bc = brood chamber(s)
cw = "china wall-like" plate
il = inner lamellae
in = inner lamellae
sf = septal flap
u = ultimate chamber

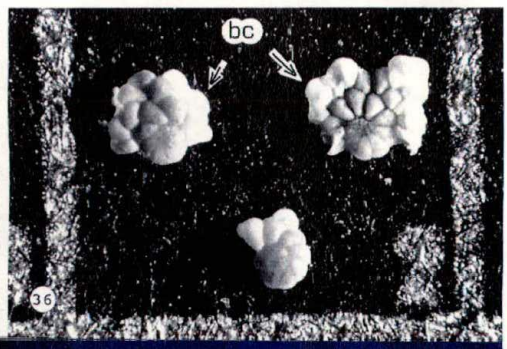

cw
31
Acc.V Spot WD Exp
20.0 kV 4.7 12.5 551
b.ludvianto^^plate & aper

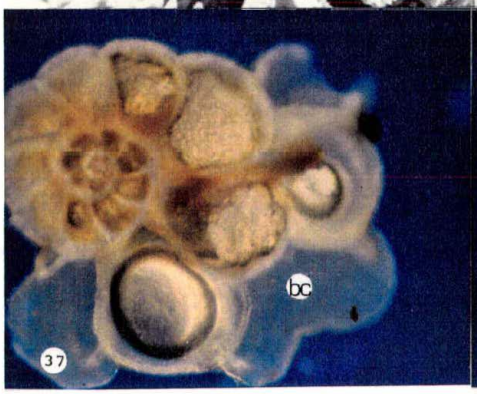

cw
32
Acc.V Spot
20.0 kV 5.9
b.ludvianto^^


in
ou
33
Acc.V Spot WD Exp
20.0 kV 5.9 12.5 647
b.ludvianto^^plate
100 µm

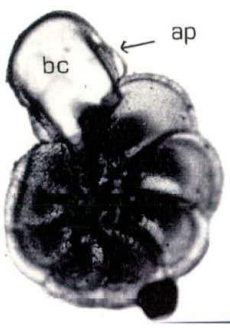

34
10 µm
^^inner lamella..ventral..last ch

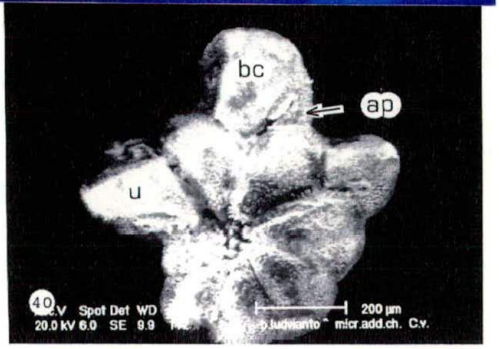

sf
cw
35
Acc.V


bc
36


bc
37


bc
38


ap
bc


bc
ap
u
40
Acc.V Spot Det WD
20.0 kV 6.0 SE 9.9
200 µm
micr.add.ch. C.v.

39

structures) were observed. The "honeycomb-like" surface was observed in other parts of the chamber wall especially in the dorsal and ventral parts near the periphery. This structure is the continuition of the smooth inner lamella that thickened and bordered the internal pores (see figure 34).

4.1.3.2. Mature microspheric morphology

In general, there were no major morphological differences between immature microspheric and mature microspheric forms, other than the existence of brood chambers. These chambers develop in a very irregular pattern. They can be initiated from the last chamber or from any other chamber in the last whorl (see figures 36 to 40). Once an initial brood chamber has formed subsequent brood chambers may use this as a base (see figures 36 and 38).

The existence and position of the second aperture seems to guide the direction and development of the brood chamber. There was no clear pattern in the number of the brood chambers that can be developed from the last whorl of the microspheric form. Figure 39 shows an initial brood chamber that was formed on the last chamber of the microspheric individual. Two apertures opposite one another were developed in the initial brood chamber and thus the next two brood chambers could either be formed on the distal and proximal side of the

brood chamber or one brood chamber could be developed in one of the apertures of the initial brood chamber.

Brood chambers can be formed in two ways. They may be based on the last chamber, and grow in the direction of the original coiling direction of the individual, so that second aperture is formed. Alternatively a second aperture can be formed in the septum area near the periphery and the intercameral foramen of the previous chamber. Here the brood chamber grows in the opposite direction to the original coiling direction of the individual.

It was also noted that there was no clear pattern to the direction of the development in brood chambers. However, the new brood chambers were always in the equatorial plane direction with no dorsal or ventral development.

The shape of the aperture of the brood chambers is exactly the same as the shape of the aperture of the microspheric individual. The brood chambers may have two apertures positioned opposite one another. The pustules of the periphery in front of the brood chamber aperture are long and pointed (see figures 26 to 28). Figure 41 shows the second aperture and the intercameral foramen that were formed near the periphery of the chamber of the last whorl of a microspheric individual. Judging from the position of the intercameral foramen and the arrangement of the chambers, the intercameral foramen

shown is most likely the second foramen of that particular chamber.

The "china wall-like" plate in the brood chamber is presented clearly at figures 41 and 42. This plate is positioned identically in both megalospheric and microspheric individuals.

Figure 43 shows that two plates are found in the chamber that has two apertures. Unlike the ordinary "china wall" plate, the second plate emerges from the equatorial-ventral side of the intercameral foramen and is attached to the internal structure of the second aperture lip. The second brood chamber will probably be formed in the posterio-equatorial side of this ultimate chamber.

The structure of the brood chamber wall is identical in both the microspheric and megalospheric individuals. It consists of an inner and outer lamella. The inner lamella adheres to the previous chamber and continues to the axial-umbillical wall in conjuction with the "china wall" plate and ends at the internal part of the aperture. It was observed to have a smooth surface. The inner lamella continues, to become the thickened border of the pores elsewhere in the internal chamber wall, and creates an anastomose surface (see figure 44).

Figure 41: Broken brood chamber showing the position of the intercameral foramen of the base chamber and the "china wall-like" plate.

Figure 42: Detail position of the "china wall-like" plate in relation to the intercameral foramen of the base chamber.

Figure 43: Broken brood chamber showing the relationship between the "china wall-like" plate with the internal intercameral foramen.

Figure 44: Detail of the internal chamber wall of the brood chamber. Note the pores with "lip structure".

Figure 45: Mature microspheric with juveniles (——— = 0.15 mm).

Figure 46: Two live mature microspheric individuals with the juveniles that had just been released and spread along the blade. Note the cracked brood chamber with some juveniles still in it (——— = 0.43 mm).

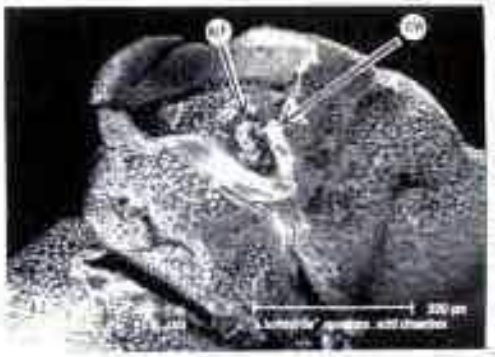
Figure 47: Remains of the brood chambers (——— = 0.17 mm).

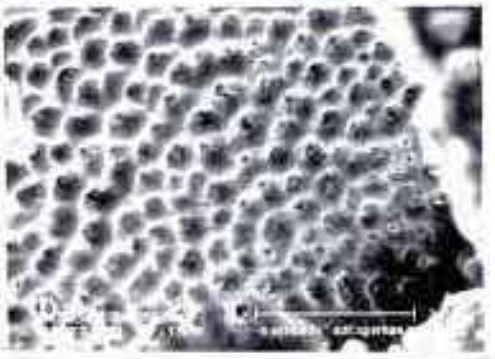
Figure 48: Broken ultimate chamber showing the origin of the aperture lip.

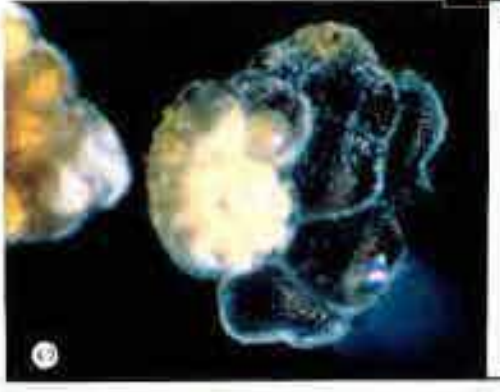
Figure 49: Cross section of the base chamber of the mature microspheric specimen. Note the inner and outer lamina (bc: brood chamber, bsc: base chamber, il: inner lamina, ol: outer lamina).

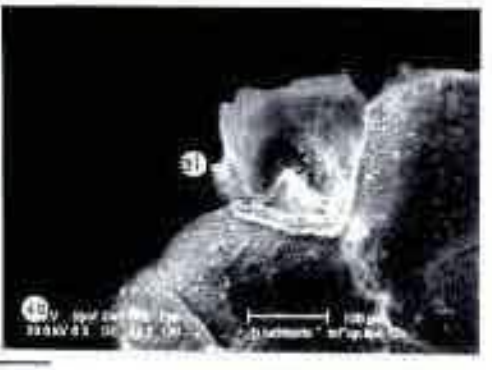
Figure 50: Enlargement of Figure 48, showing the detailed of the connection between the two lamina. Note the "tube" like structure of the pores (il: inner lamina, ol: outer lamina, po:pore).

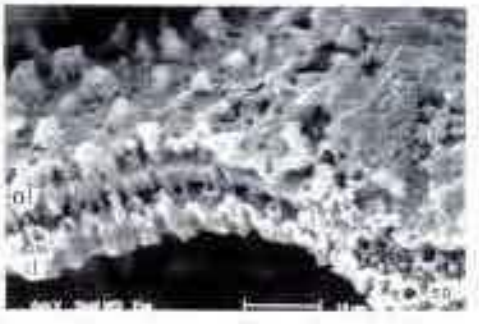
al = aperture lip
bc = brood chamber(s)
cw = "china wall-like" plate
icf= intercameral foramen
j = juvenile(s)











In cross section, the chamber wall of the base chamber (the chamber in the last whorl on which the brood chamber is formed) was found to have a bilaminar structure (see figures 49 and 50). The figures also show that the wall of the brood chamber only consists of one lamina, which contains two lamellae (an inner and outer lamella).

Figures 49 and 50 also show the tube-like structure that was found at each pore of the base chamber walls. This structure seems to be derived from the inner part of the pore that grows externally into the pore of the outer layer of the chamber wall .

It was difficult to determine how many brood chambers one microspheric foraminifera could make during its life. Figure 45 shows a mature microspheric individual with only two brood chambers built on the last chamber, that had already released juvenile megalospheric individuals. Figure 46 shows an adult that had four brood chambers from which the juveniles had already been released. The breaking of the ventral part of the brood chambers seems to be initiated before releasing their juveniles.

4.1.4. Discussion

The test of foraminifera has attracted many workers, especially geologists and paleontologists, who study them in relation to paleoenvironment interpretation (Boersma, 1978 and Murray, 1991). The test, according to Marszalek et.al (1969 in Murray, 1991) acts as a protective device against predation and unfavourable environmental conditions, a space for deposition unwanted material, a structure that is needed in the reproduction process and a device that helps to control the buoyancy of the individual. Murray (1991), however, questioned the function of the test as a protective device against predation, he argued some foraminifera were actually attacked by predators because of their test colour. He also did not like the suggestion that the test can assist in the reproduction process.

In Q.cf.venusta one function of the test is to form a case in which the juveniles are retained as they grow. Based on the variations in the appearences of pustules it can be speculated that they become eroded with time. The way Q.cf.venusta lives, by clinging on the blade of the intertidal seagrass H.uninervis, exposes it to water movements and abrasion by entrained sand particles. This suggests a protective function of the test.

Loose (1970, in Boltovskoy and Wright, 1976) suggested that species living in turbulent water tend to develop a thick test wall as a survival adaptation. In

this study, it seems that with an average thickness of 5 μ of the ultimate chamber wall, that Q.cf.venusta use their pustules to protect the test from the direct effect of water and sand abrasion.

Besides characteristics of life habits and habitats, protoplasmic characteristics, ontogenic changes, reproductive processes and geologic ranges, test morphology is still the major part of foraminifera that is studied and used in taxonomy (Boersma, 1978, Boltovskoy and Wright, 1976).

The most noticeably characteristic of the test of Q.cf.venusta was the shape and structure of the main aperture and the additional apertures. The aperture that is basically an aerial, arched, slit-like opening has a bend at the ventral end of the heavily pustulose aperture lip. This bend creates an image of a second smaller arched structure viewed from the apertural side. Figure 30 shows that the intercameral foramen has a similar structure to the main aperture. In the intercameral foramen, however, the bend was covered by the smooth surface of the inner lamella of the ultimate chamber.

Studying figures 16, 17, 20, and 38, it appears that the bend structure is the point where the "china wall" plate was more or less split in two directions. The first half of the plate continuing to become the aperture, and the second half attached to the inner lamella of the axial-umbillical chamber wall. It also

can be recognised that the lip of the aperture was derived purely from the outer lamella and not from the inner lamella (see figure 48).

The shape of the aperture in O.cf.venusta was quite comparable with the species described by Hofker (1951) as Parella venusta. The difference is that in Hofker's specimens the apertural lip bordered the whole aperture whilst in O.cf.venusta the lip was only confined to the first arch.

Hofker (1951) suggested that the two apertures were separated by the reduced toothplate that runs from the lip of the intercameral foramen through the basal chamber wall and ending at the ventral side of the aperture. He, furthermore, stated that the part of the apertural face between the two foramina was formed by the toothplate. In O.cf.venusta, however, the nearest plate structure that can be observed is the "china wall" plate and this plate does not separate the two openings of the aperture. It appears that this plate was initially to become the basal chamber wall which separates the chamber lumen from the chamber of the previous whorl. It does, however, twist ventrally and creates a "U-shape" ventral opening near the aperture. Consequently,the chamber is connected to the ambient environment not only by the aperture but also by the " U shape" opening.

The general structure of the plate, which is poorly perforated, smooth and rounded at its edges confirms

that this plate is an extension of the inner lamella of the previous chamber wall (see figure 30 and 32). Billman et.al. (1980) and Hottinger et.al (1991) described four different kinds of plates found in the rotalliid chamber lumen. These plates are tooth plate, cover plate, foraminal plate and umbilical plate. In terms of the attachment structure and its function which separates the chamber lumen from the axial space, the "china wall-like" plate can be compared with the toothplate. The "china wall-like" plate, however, does not have a free, serrated distal end protruding adaxially to the aperture, which is found in the tooth plate. Consequently, the "china wall" plate could not simply be defined as a toothplate.

4.2. Test abnormality in O.cf.venusta

4.2.1. Introduction.

In the history of microfossil observation, Bogdanovicz and Dmitrieva (1950 and 1952 in Boltovskoy and Wright, 1976) found a high proportion of "pathological" specimens in the Tertiary sediment . They suggested that this kind of morphological abnormality is caused by sudden hydrological changes in the past environment.

According to Boltovskoy and Wright (1976) there are at least two different types of test abnormality. One that is caused by mechanical factors that usually affect the newly constructed portion of the wall (commonly in the last few chambers), and another that is caused by ecological factors, that can usually be seen on the whole of the specimen.

There are several abnormal specimens that have been reported to be caused by ecological factors. However, according to Boltovskoy and Wright (1976) they can be condensed into three phenomenon : a) kummerform, b) twinned specimens and c) odd wall structure that appear as strong and sometimes shapeless calcareous spines.

The term kummerform refers to foraminifera in which the last chamber in the test is equal to or smaller than the previous one. This phenomenon is reported for Globigerinoides ruber, Globoquadrina dutertrei and Globigerina pachyderma. (Hecht & Savin, 1971, 1972; Olsson, 1973 in Boltovskoy and Wright, 1976). The odd wall structure phenomenon has been reported by Boltovskoy and Boltovskoy (1970, in Boltovskoy and Wright, 1976) in Globigerina quenqueloba, G.bulloides, G.pachyderma, Globigerinita glutinata and G.uvula from Subantartic and Antartic waters.

The twinned shape phenomenon has been reported by Earland (1933, 1934 and 1936 in Boltovskoy and Wright, 1976), Boltovskoy and Boltovskoy (1970, in Boltovskoy and Wright, 1976) and Boltovskoy (1982). Boltovskoy and

Wright (1976) concluded that in twinned foraminifera both specimens are from the same species, and that the size of one test is always smaller than the other. Boltovskoy (1982) found twinned planktonic specimens Globorotalia opima nana from a site located at 35 ° S, 18° E, depth 2,949 m. He also stated that most twinned specimens usualy have different test sizes, but that in some very rare cases both tests can be the same size.

4.2.2. Results

The "twinned" specimens that were found in this study had the same morphological characteristics as their "single" O.cf.venusta counterparts. The two tests were attached to one another via their dorsal regions (see figures 51 to 54).

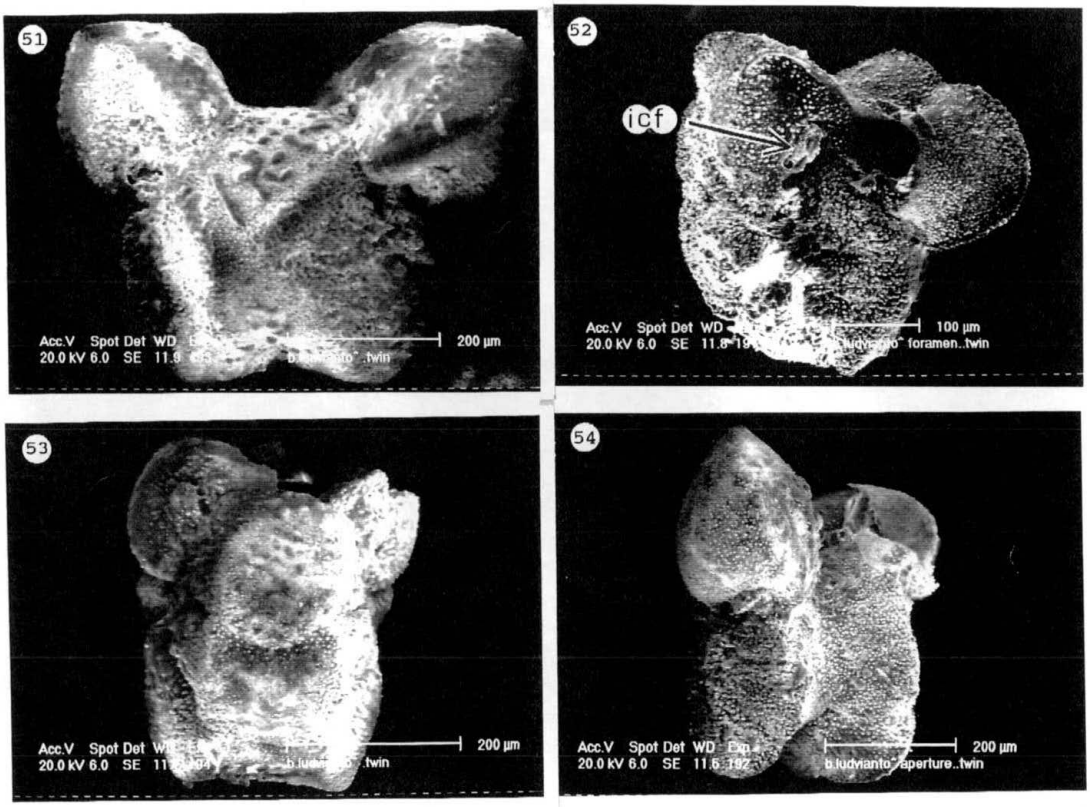
The two tests may be found fused perfectly in the early chamber, so that it looks like one individual with two umbilical plugs. In such specimens the last two or three chambers seem to split equatorially and create two rows of chambers with one main aperture in each last chamber (see figure 52). Other specimens were found having a "test connection" structure as the extension of the dorsal chamber wall of each test (see figure 51). The "test connection" structure may join the chambers at their periphery (figure 53) or it may only join the early chambers as seen in figure 54

Figure 51: Twinned specimen. Note the position of the two apertures.

Figure 52: The intercameral foramen of the penultimate chamber of the twinned specimen.

Figure 53: Equatorial view of "twinned" specimen, showing the complete joining of the early chamber.

Figure 54: Apertural view, showing partial joining of the early chambers.


51
Acc.V Spot Det WD
20.0 kV 6.0 SE 11.9
200 µm
52
icf
Acc.V Spot Det WD
20.0 kV 6.0 SE 11.8
100 µm
foramen..twin
53
Acc.V Spot Det WD
20.0 kV 6.0 SE
200 µm
54
Acc.V Spot Det WD
20.0 kV 6.0 SE 11.5
200 µm
b.ludvianto_aperture..twin

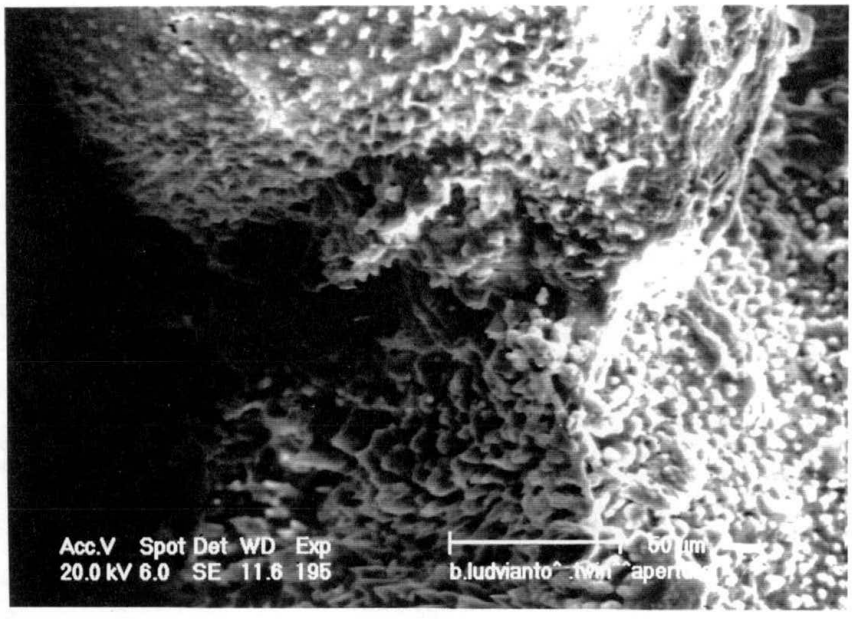
The tests have the same chamber shape and arrangement, suture structure, and pustule ornamentation as their "single" O.cf.venusta specimen counterparts. The aperture(s) and the intercameral foramen were exactly the same as the "ordinary" O.cf.venusta (see figures 51 and 55).

Most of the twinned specimens were of equal test size.

4.2.3. Discussion

Boltovskoy (1982) was not convinced by the suggestion that the twinned specimens were actually undergoing a process of plastogamy as stated by Erland (1934, in Boltovskoy, 1982). Plastogamy is a mode of sexual reproduction in which two or more mature foraminiferal individuals join their tests by the apertures in order to exchange their gametes (Erskian and Lipps, 1969 and Boltovskoy and Wright, 1976). Boltovskoy's (1982) objection was especially grounded on the fact that most twinned specimens consist of two different sized individuals. The position of the apertures, that were far apart, was also another reason for rejecting plastogamy. Boltovskoy (1982) speculated that in planktonic specimens where the size of the

Figure 55: Detail structure of the external chamber wall and aperture.


Acc.V Spot Det WD Exp
20.0 kV 6.0 SE 11.6 195
60 µm

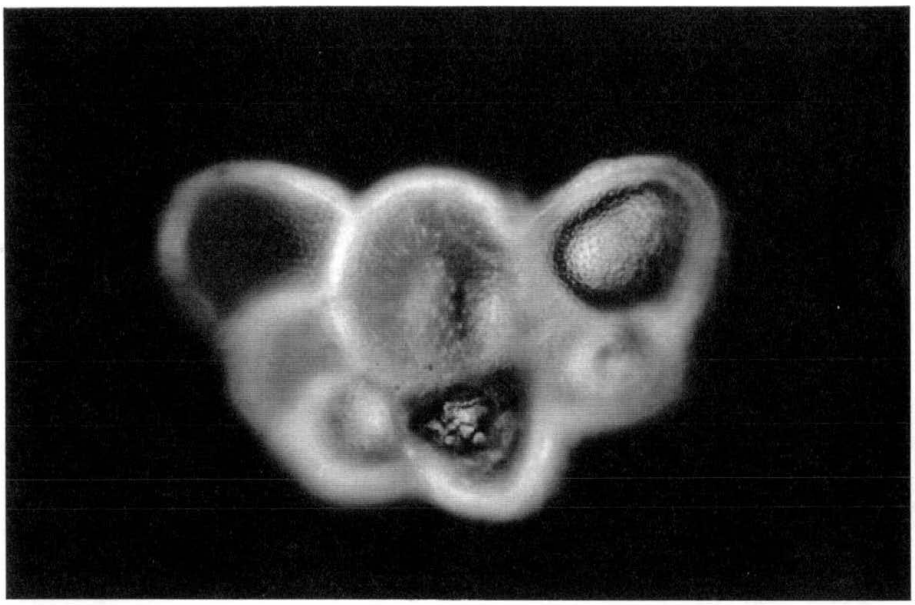
individuals was not the same, the smaller individuals could be the zygote, that in some way was prevented from abandoning its parent. This zygote still had a pseudopodial contact with its parent and grew attached to the parent. He, however, could not find an explanation for twinned specimens with two individuals of the same size.

In O.cf.venusta most of the individuals were the same size, they have widely separated apertures and are connected at their dorsal side. It is thus difficult to suggest that the twinned specimens were actually plastogamic specimens of two individuals.

Figure 56 shows a juvenile O.cf.venusta that is believed to be the young specimen of a twinned individual. The twinned phenomenon in O.cf.venusta is believed to have been initiated in the early stages of the individual development. It can be seen from the figure, that the young twinned specimen, with one proloculus, has already had three later chambers arranged in two directions or rows. It was most probable that the proloculus had two intercameral foramens. Each intercameral foramen then guided the development of the next chamber, and thus two rows of chambers developed.

The capability of O.cf.venusta to form more than one intercameral foramen has already been demonstrated

Figure 56: Early development of "twinned" individual of O.cf.venusta (⊢——⊣ 0.024 mm).



clearly in mature microspheric individuals (see 4.1.3.2). It is, therefore, reasonable to assume that this capability could also be established in the juvenile twinned individuals. Accordingly, I believe that the twinned specimens were not comprised of two different individuals, but rather of only one individual, that has two rows of chambers.

4.3. Coiling direction as one of the morphological characteristics in O.cf.venusta

4.3.1.Introduction

Trochospiral foraminifera grow by the addition of new chambers either in a clockwise (right) or counter-clockwise (left) direction. Coiling direction has been commonly used in many stratigraphic and phylogenetic studies of foraminifera (Bolli 1950; 1951; Ericson, Wollin and Wollin, 1954; Nagappa, 1957; and Bandy, 1960). The interpretation of regional and inter-regional correlation (Ericson, Wollin and Wollin, 1954; Nagappa, 1957; and Saito, 1976) with the shifts of coiling preference serves as a valuable tool for stratigraphers working on sediment sequences

An evolutionary study by Nagappa (1957) on a species of Globorotalia in West Pakistan supported Bolli's (1950) suggestion that random coiling direction

occurred in the early stages of its stratigraphic range, with a preferred coiling direction being observed in the later stages of its evolutionary life-span. The value of coiling ratios of left to right direction have been well established by Bolli (1950, 1951) on the various species of Globorotalia and Globotruncana. Stratigraphic correlation studies using coiling ratios were first applied on 2 deep sea cores in the North Atlantic (25 kms. apart) by Ericson, Wollin and Wollin (1954) who noted that sequences of the proportion of left and right coiling tests in these two cores were perfectly matched. They subsequently subdivided the surface sediment of the North Atlantic region into three provinces based on the coiling dominance of Globorotalia truncatulinoides , namely a left coiling province that was established for at least two thousand years and two right coiling provinces that were established for at least 10,000 years.

Studies on coiling direction of planktonic specimens have shown patterns of coiling to be correlated with environmental conditions. Specimens of Globigerina pachyderma , Globorotalia pachyderma, G.truncatulinoides and Neogloboquadrina pachyderma found in the higher latitudes were dominated by sinistral coiling, while those in the lower latitudes showed mainly dextral coiling (Bandy, 1960; Bé, 1960; Jenkin, 1967 and 1971; Vella, 1974).

Longinelli and Tongiorgi (1964) showed that the deposition of calcium carbonate in foraminiferal shells occurred at different times of the year for the different coiling types found in the same geographic location.

Although temperature has been considered as the main factor affecting coiling preference, several studies have shown inconclusive results. Cifelli (1971) has reported that no fixed correlation between coiling preference and seawater temperature was found for Globorotalia truncatulinoides. Olsson (1974) has cautioned against using coiling ratios of the different forms of Globigerina pachyderma to interpret the cold cycles of the Pliocene to lower Pleistocene period, as he believes the two different types of coiling directions in G.pachyderma actually represented two different species (G.pachyderma and Globorotalia pseudopachyderma).

Thiede (1971) discovered that the coiling ratio of G.truncatulinoides from the continental slope off Southern Portugal and Marocco varied with the shell size. He reported a greater ratio of sinistral coiling occurred in larger size specimens.

The different causes of coiling direction have largely concentrated on planktonic foraminifera. Little work has been undertaken on benthic foraminifera (Scott ,1976). Hallock and Larsen (1979) working on the benthic foraminifera Amphistegina detected an increase of

dextral A.lesonii and sinistral A.lobifera in water heated by thermal effluent.

As more studies on coiling preference have emerged it has become increasingly clear that further information is required to fully understand shell development in relation to climatic conditions.

Studies of coiling direction on in situ living foraminifera are still limited. For this reason a study of the living epiphytic foraminifera Q.cf.venusta has been conducted to determine the pattern of coiling direction in a tropical area.

4.3.2. Materials and methods

The data for coiling directions were obtained from observing the specimens collected from the temporal distribution study and the recolonization study (see Chapter III and Chapter V, section 2). All specimens from the recolonization study were observed, but only specimens from location 1, experiment 1 from the temporal distribution study were used in the present study. The number of left or right coiled individuals was determined by immersing the specimens in aniseed oil and observing under a phase contrast microscope. In this way coiling direction of the individuals was easily noted and the megalospheric and the microspheric individuals differentiated.

Detailed investigation of the seasonal pattern of the coiling direction was carried out by analysing the proportion of left coiled specimens for two different periods of sampling (monthly sampling for the six month periods, and fortnightly sampling for 60 days period). The left coiling specimens were chosen because on average it seemed that more of these were encountered during the study time (see figs.59 to 61).

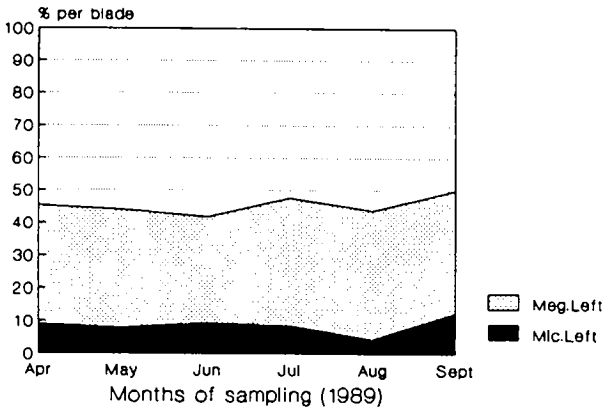
A two way nested analysis of variance (Zar, 1984) was employed to determine the monthly pattern of the proportion of the left coiled specimens. Both variables, Months and Plots, were considered as fixed factors.

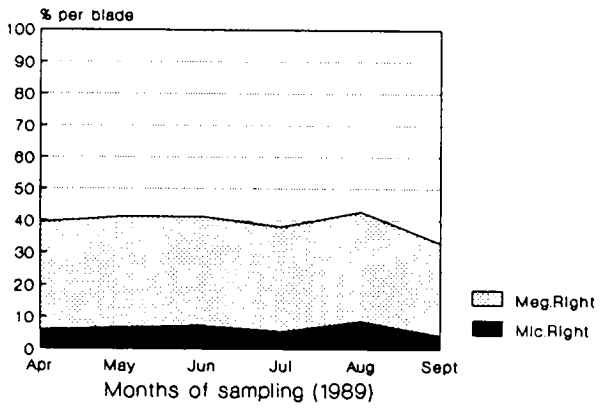
A three way repeated measurements analysis of variance (Winer, 1971; Rowell and Walters, 1976) was used to recognise the fortnightly pattern of the proportion of left coiled specimens. The Site variable was considered random, the Starting date and Period variables were considered as fixed factors. The data were transformed into Arcsine to meet the normality assumption before an analysis of variance could be used. A Wilk-Shapiro test of data normality was employed to test the result of the transformation. A sphericity test was employed to recognise the equality of variances,

Figure 57: Monthly percentage of left coiled megalospheric and microspheric individuals per blade.

Figure 58: Monthly percentage of right coiled megalospheric and microspheric individual per blade.

Figure 59: Monthly percentage of left and right coiled Q.cf.venusta per blade.


% per blade
100
90
80
70
60
50
40
30
20
10
0
Apr
May
Jun
Jul
Aug
Sept
Months of sampling (1989)
Meg.Left
Mic.Left


% per blade
100
90
80
70
60
50
40
30
20
10
0
Apr
May
Jun
Jul
Aug
Sept
Months of sampling (1989)
Meg.Right
Mic.Right

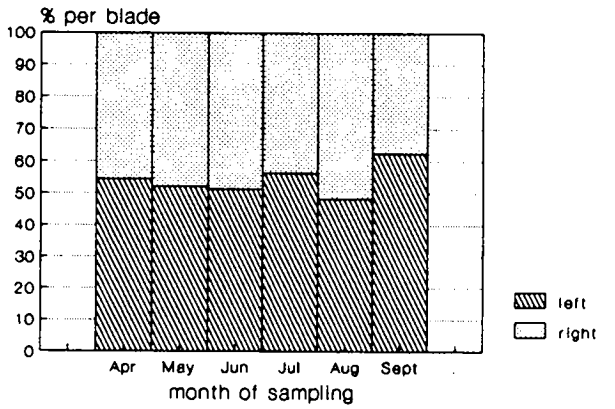
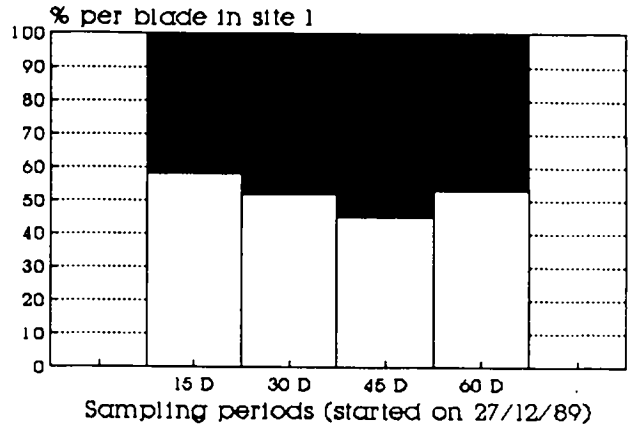
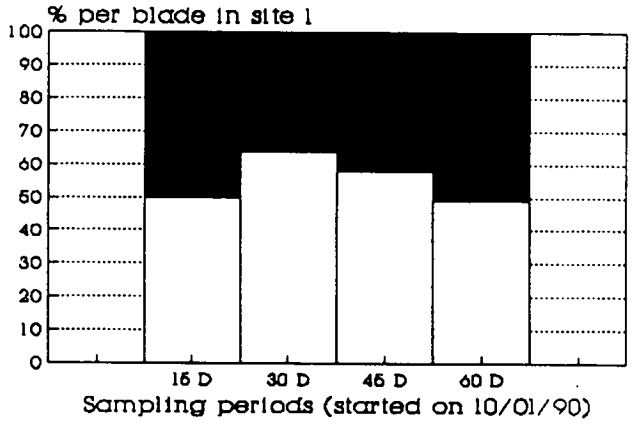
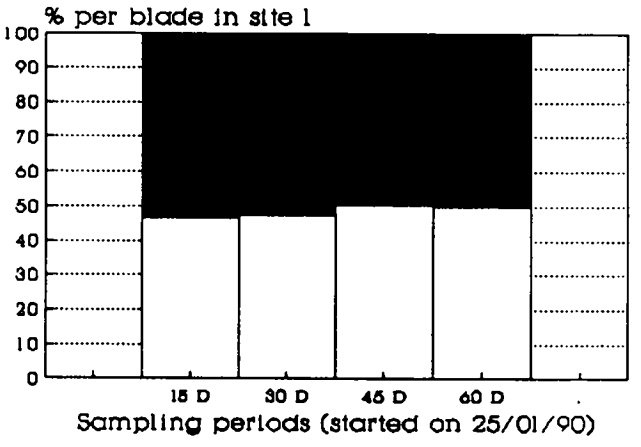

% per blade
100
90
80
70
60
50
40
30
20
10
0
Apr
May
Jun
Jul
Aug
Sept
month of sampling
left
right

Figure 60: Fortnightly percentage of left and right coiled Q.cf.venusta per blade at site 1.


% per blade in site 1
100
90
80
70
60
50
40
30
20
10
0
15 D
30 D
45 D
60 D
Sampling periods (started on 27/12/89)

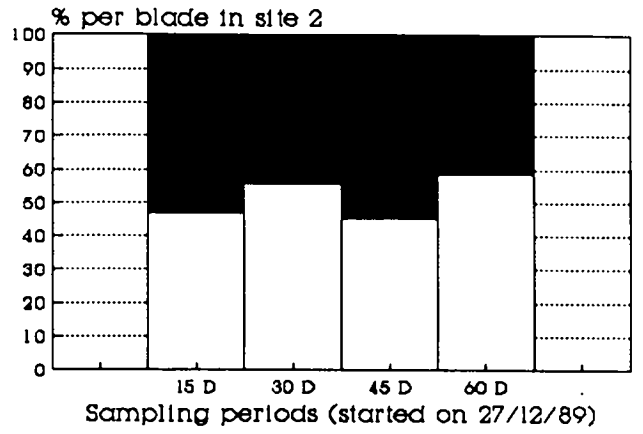

% per blade in site 1
100
90
80
70
60
50
40
30
20
10
0
15 D
30 D
45 D
60 D
Sampling periods (started on 10/01/90)

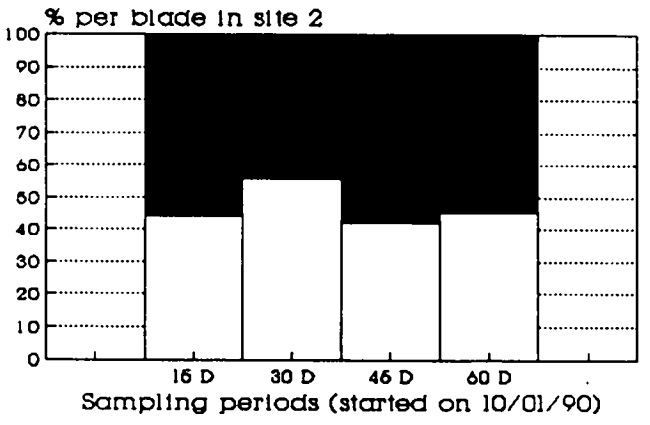

% per blade in site 1
100
90
80
70
60
50
40
30
20
10
0
15 D
30 D
45 D
60 D
Sampling periods (started on 25/01/90)

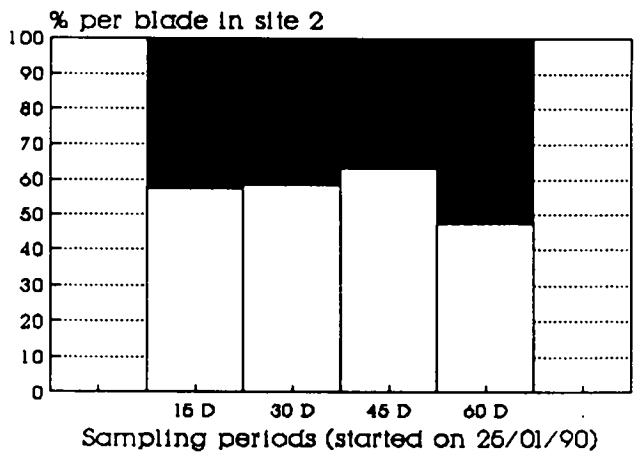
Right

Left

Figure 61: Fortnightly percentage of left and right coiled Q.cf.venusta per blade at site 2.


% per blade in site 2
100
90
80
70
60
50
40
30
20
10
0
15 D
30 D
45 D
60 D
Sampling periods (started on 27/12/89)


% per blade in site 2
100
90
80
70
60
50
40
30
20
10
0
15 D
30 D
45 D
60 D
Sampling periods (started on 10/01/90)


% per blade in site 2
100
90
80
70
60
50
40
30
20
10
0
15 D
30 D
45 D
60 D
Sampling periods (started on 26/01/90)

Right

Left

before a univariate analysis of variance can be utilised and exact F ratio can be obtained (Death, pers.comm; SAS manual, 1987 and Hyunh and Feldt, 1970).

There were two methods of measuring the field temperature. The first method involved placing the thermometers in three places i.e. 1) surface coastal seawater, 2) immersed sediment (sediment at the sampling plot that was still covered with ± 10 cm of seawater), and 3) exposed sediment adjacent to the sampling plots during the low tide. These measurements were made on a monthly basis at the same time as the sampling dates.

In order to determine the relationship between proportion of left or right coiled specimens in the monthly samples and the temperatures (surface seawater, immersed sediment and exposed sediment), a simple regression analysis of variance was employed.

The second method of measuring the field temperatures was employed fortnightly by placing the thermometer in the immersed sediment at the sampling plots when the seagrass blades were removed.

A simple regression analysis was utilised to recognise the relationship between the proportion of left coiled specimens in the fortnightly samples and the immersed sediment temperatures.

4.3.3. Results

Two generations of O.cf.venusta were found in the seagrass beds of Shelly Bay, the microspheric and the megalospheric. These two generations were differentiated mainly on the size of the first chamber. Both generations consist of sinistrally and dextrally coiled specimens (figs 57 and 58).

4.3.3.1. Monthly study

Plots of left and right dextral coiling show a slight decrease of the sinistral specimens during the months of May and June and increasing again during July and September . The coiling direction plots also showed that the sinistral coiling specimens were generally in greater proportions than the dextral ones (see figure 59)

A two way nested analysis of variance revealed that the monthly proportion of the sinistrally coiled individuals were not significantly different ($p>0.05$, see table 9) .

4.3.3.2. Fortnightly study.

A study of the fortnightly pattern of the coiling direction was carried out in conjunction with the recolonization study. The study was based on the seagrass blades recolonized by O.cf.venusta after certain period of time (15, 30, 45 and 60 days).

The Anova showed that the interaction between experiment starting date and period of recolonization factors played a significant role ($p<0.05$) in determining the proportion of left coiling direction individuals on the blades (see table 10). The sites factor and the interaction between sites and starting date factors were also found to significantly contribute to the proportion of left coiled individuals ($p<0.05$, see table 10). The comparisons of the "among periods factor" (especially period 1 or 15 days, which were considered to be the initial time for O.cf.venusta to recolonize the clean blades) showed that there was no significant difference ($p>0.05$) among period 1 (15 days) in term of the proportion of left coiled individuals in the population (see table 12).

A Polynomial contrasts test (Rowell and Walters, 1976 and Statistix ver.3.5, 1991) was carried out, and showed strong support for a linear trend of the proportion of left coiled individuals with the period of recolonization factor (see table 11).

Source	DF	MS	F	P
Month (M)	5	7.0435E-02	3.37	> 0.05 ns
Plot (PL) M x PL	6	2.0905E-02		
Replication(Rep) M x PL x Rep	84	5.0242E-02		

Table 9: Result of the ANOVA on the temporal proportion of left coiled individuals of O.cf.venusta (April to September 1990).

The Null Hypothesis was:

Ho: There is no difference in the proportion of left coiled individuals in the population during the six month study period

ns : non significant; $\alpha = 0.05$.

Source	df	MS	F	P
Between group				
Sites (SI)	1	4.3022E-01	10.64	0.0172 *
St.Date(SD)	2	2.4275E-02	0.60	0.5785
SIxSD	2	2.6441E-01	6.54	0.0311 *
Subject (sub) subxSIxSD	6	4.0435E-02		
Within group				
Period (P)	3	1.7753E-01	3.13	0.0514
SDxP	6	1.7950E-01	3.16	0.0268 *
SIxP	3	8.0979E-02	1.43	0.2675
SIxSDxP	6	2.9044E-02	0.51	0.7915
SIxSDxPxsub	18	5.6726E-02		
SIxSDxPxsubxrep	96	1.1074E-01		

Table 10: Result of the ANOVA testing the effect of Sites, Starting dates of experiments and Periods of sampling on the proportion of left coiling direction individuals.

* significant; α = 0.05 level of significance

Degree	SS	F	P
1	4.4826E-01	7.90	0.0116 *
2	1.0772E-03	0.02	0.8919
3	8.3264E-02	1.47	0.2414

Table 11: Polynomial Contrast for testing the trends of the proportion of left coiled direction during the Periods of sampling.

Degree 1 = linear trend (* significant)
2 = quadratic trend (non significant)
3 = cubic trend (non significant)

$\alpha = 0.05$

Source	df	MS	F ratio		F (2,6;0.05)
among P1's (Site 1)	2	2.0981E-02	0.518	ns	5.1433
among P 1's (Site 2)	2	6.7591E-02	1.671	ns	5.1433
among P 2's (Site 1)	2	7.8253E-02	1.935	ns	5.1433
among P 2's (Site 2)	2	1.2810E-02	0.310	ns	5.1433
among P 3's (Site 1)	2	1.0481E-01	2.59	ns	5.1433
among P 3's (Site 2)	2	1.6534E-01	4.089	ns	5.1433
among P 4's (Site 1)	2	4.4529E-01	11.012	*	5.1433
among P 4's (Site 2)	2	1.9252E-01	4.761	ns	5.1433
error term	6	4.0435E-02			

Table 12: Summary of the Anova testing the different of the left coiled proportion among Periods at different Starting dates of the experiments.

Note.

The MS values were originally calculated at each Period for each Sites by using an ANOVA model of

Y = u + SD + Sub(SD) + Residuals.

with Y = number of individuals per blade
SD = Starting Dates of the experiments
Sub = The subject (containers) that were sampled repeatedly The ANOVA table is :

Source of variance	df	MS
SD	2	
Sub (SD)	2	
SD * Sub * Rep	4	

The MS value of the SD factor drawn from this calculation was then treated as source of variance among Periods and was devided by the MS value of the error term of the "Between group" at table 10 that is 4.0435E-02 to create the F ratio value (De'ath, pers.comm). This F ratio were then compared with the F distribution table at the df of 2 and 6 with 0.05 level of significance.

4.3.3.3. Relationship between the proportion of sinistrally coiled individuals with temperatures

Figure 62 shows the monthly temperature measurements on the exposed sediment, immersed sediment and surface seawater. Table 13 shows that, there was no significant correlation between the proportion of left and right coiled specimens and temperature, during the 6 month study period.

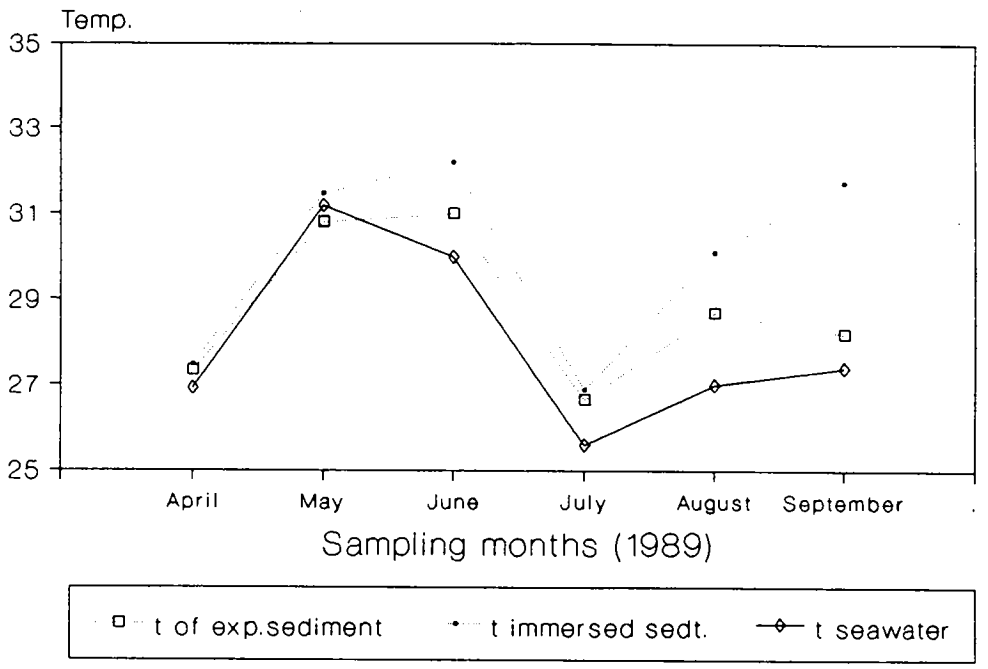
Figures 63 and 64 show the fortnightly immersed sediment temperature measurements, in Site 1 and Site 2 in relation to the percentage of left coiled individuals per blade. Table 14 shows that no significant correlation was detected between the proportion of sinistrally coiled individuals and the immersed sediment temperature during the 60 day study period.

4.3.4. Discussion

A monthly sample of the population of O.cf.venusta from the intertidal seagrass beds in Shelly bay showed that sinistral coiling forms predominated (see fig.2). Bandy (1960) stated that 98% of temperate and tropical Globigerina pachyderma are dextrally coiled. The results

Figure 62: Monthly temperature in Shelly Bay, during April 1989 to September 1989.

t.of exposed sedt: temperatures of exposed sediment,
t.immersed sedt : temperatures of immersed sediment,
t.surface swtr : temperatures of surface coastal seawater.


Temp.
35
33
31
29
27
25
April
May
June
July
August
September
Sampling months (1989)
t of exp.sediment
t immersed sedt.
t seawater

Regression	Coef.of determination	P
% left x T.exsd	0.2060	p > 0.05
% right x T.exsd	0.5980	p > 0.05
% left x T.imsd	0.0002	p > 0.05
% right x T.imsd	0.1665	p > 0.05
% left x T.swtr	0.1956	p > 0.05
% right x T.swtr	0.4232	p > 0.05

Table 13: Summary of the simple regression between the percentage of left (% left) or right (% right) and the monthly temperatures.

T.exsd = temperature of exposed sediment,
T.imsd = temperature of immersed sediment,
T.swtr = temperature of surface sewater.

Regression	Coef.of determination	P
left x T (SD 1 S1)	0.0012	p > 0.05
left x T (SD 1 S2)	0.0112	p > 0.05
left x T (SD 2 S1)	0.1082	p > 0.05
left x T (SD 2 S2)	0.8516	p > 0.05
left x T (SD 3 S1)	0.4226	p > 0.05
left x T (SD 3 S2)	0.6821	p > 0.05

Table 14: Summary of the regression analysis on the relationship between the proportion of left coiled direction (% left) and immersed sediment temperature (T).

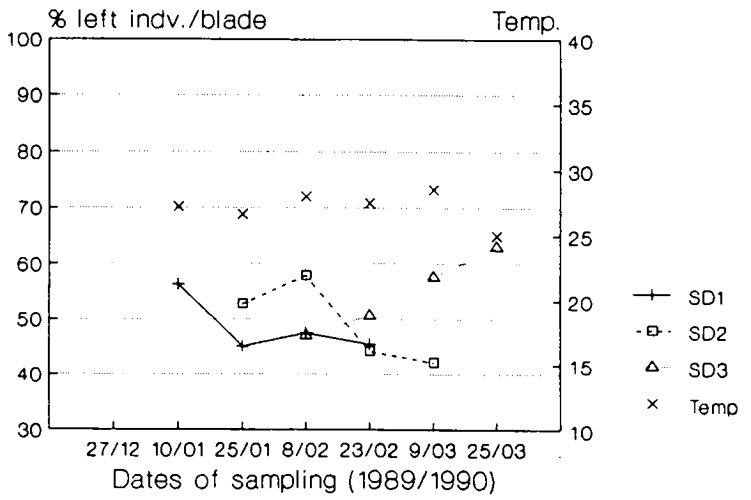
SD 1 = starting date of experiment 1
SD 2 = starting date of experiment 2
SD 3 = starting date of experiment 3
S1 = Site 1
S2 = Site 2

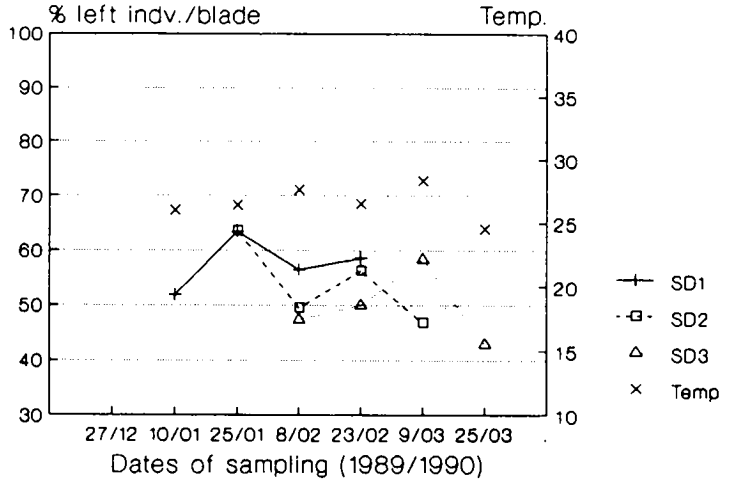
Figure 63: Fortnightly immersed sediment temperature in relation to the percentage of left coiled individual per blade at site 1.

SD1: Experiment 1 started on the 27th of December 1989,
SD2: Experiment 2, started on the 10th of January 1990,
SD3: Experiment 3, started on the 25th of January 1990.
Temp: Immersed sediment temperatures (°C).

Figure 64: Fortnightly immersed sediment temperature in relation to the percentage of left coiled individuals per blade at site 2.

SD2: Experiment 1, started on the 27th of December 1989,
SD2: Experiment 2, started on the 10th of January 1990,
SD3: Experiment 3, started on the 25th of January 1990.
Temp: Immersed sediment temperatures (°C).


% left indv./blade
Temp.
100
90
80
70
60
50
40
30
40
35
30
25
20
15
10
27/12 10/01 25/01 8/02 23/02 9/03 25/03
Dates of sampling (1989/1990)
SD1
SD2
SD3
Temp


% left indv./blade
Temp.
100
90
80
70
60
50
40
30
40
35
30
25
20
15
10
27/12 10/01 25/01 8/02 23/02 9/03 25/03
Dates of sampling (1989/1990)
SD1
SD2
SD3
Temp

of this study, however, showed that only 35.20 - 53.17 % of Q.cf.venusta were dextrally coiled. Thus there is a specific difference in coiling preference between at least two tropical species. Sinistral coiling was the favoured coiling direction for Q.cf.venusta in Shelly bay over the six month period of study.

Most workers agree that sea water temperatures seems to play an important role in governing the coiling preference of foraminifera (especially the planktonic ones). The current study investigates the possibility of the effect of surrounding temperature on the Q.cf.venusta coiling preference in Shelly Bay.

The monthly surface sea temperatures during the study period (April 1989 to September 1989) show a slightly different pattern when compared with those of Kenny (1974) and Walker (1981) which were taken in Townsville harbour and site P34 in Cleveland Bay off Townsville respectively. Generally, the surface sea temperature reading in the present study is higher for the same seasonal period then that of Kenny (1974) and Walker (1981). In addition, it is also obvious that in their data the surface sea temperature in the Townsville region decreased during May and June and reached its minimum on July. This study shows that, instead of decreasing slowly and reaching its minimum in July, the surface sea temperature in May 1989 rose to about 31° C, before dropping to its minimum of less than 26 ° C in July 1989. This kind of pattern, is comparable to the

surface sea temperature reading carried out by Clayton (1987) in Shelly Bay. Thus, it is assumed that the difference in the patterns of the surface sea temperatures reading between the present study and those of Kenny (1974) and Walker(1981) is attributed to the position where the study were undertaken. The temperature difference might also be caused by the different method in placing thermometer in the surface seawater. Kenny (1974) positioned his thermometer in the top 25 cm of seawater with minimum water depth of 1 metre. Walker (1981) read his temperature data in station P34 in Cleveland Bay, which has a 10 metre depth. The surface sea temperature readings in the present study, however, were carried out in the top 25 cm of surface seawater with the maximum depth of 0.5 metres. This was done in order to gain data on the surface sea temperature in a position as close as possible to the sampling plot.

The present study shows that there were no significant relationships between the proportion of left coiled individuals and the surface sea temperature, as well as the immersed and exposed sediments temperatures. It is therefore suspected that the changing of the surrounding temperature of the O.cf.venusta population from seawater (at the high tide) to the exposed sediment (at the low tide), on a monthly basis appears to have little effect on the number of left coiled individuals in the population.

Other results that can be gathered from the monthly study is that the immersed sediment temperatures were always warmer than the other two temperature measurements. Probably this is because the coastal seawater had not yet absorbed the maximum heat radiation from the sun, and at the same time the exposed sediments had been cooled down by the wind. On the other hand, the seawater that covers the immersed sediments, seems to be able to retain the heat radiation from the sun and, therefore, the temperatures of the immersed sediment was always higher than the surface seawater and the exposed sediments.

The shorter interval of the fortnightly sampling shows that the immersed sediment temperatures fluctuated between 25 to 30°C and, it was not correlated significantly with the proportion of left coiled individuals during the study period.

Cifelli (1971) reported that a slight change of the surface temperatures (from 22.7 to 23.9 ° C) in a North-South transverse along longitude 65°W in the Sargasso Sea was associated with the shifting of coiling direction preference from left dominated (69 % left) to the right dominated (67 % right) in the Globorotalia truncatulinoides specimens. Hallock (1979) reported an increase of the proportion of dextral Amphistegina lesonii and sinistral A.lobifera coincided with an increase of 4 ° C of the seawater temperature.

In the present study on O.cf.venusta it is indisputable that, even though the surface seawater temperature range and variations (from 26.65 to 31.00 ° C) was much higher than the temperature range that G.truncatulinoides experienced in the Sargasso Sea, and also A.lobifera and A.lesonii in Hallock's (1979) work, such variations did not have a great effect on shifting the coiling direction preference of O.cf.venusta from left to right. Unfortunately, there was no information on the effect of exposed sediment and immersed sediment temperature on the biology of other epiphytic foraminifera, therefore no comparison can be made at this stage.

It is probable that the temperature measurements taken at the time of sampling had not yet had any effect on the O.cf.venusta population. If there was any influence of the temperature on the coiling direction pattern as suggested by other workers, the effect of it might only be detected by doing a continuous temperature reading before and during the sampling periods, to accommodate any temperature lagging effects.

In order to understand the temporal and spatial patterns of the left coiled individuals in the population a monthly and fortnightly study on the patterns of the left coiled individuals was undertaken.

The monthly sampling study showed that there were no significant differences among the sampling times at that study site. Thus the proportion of the left coiled

O.cf.venusta did not significantly change from April 1989 to September 1989 and that the left coiled individuals seemed to maintain their numbers in the population on a monthly basis.

The fortnightly study showed the proportion of sinistrally coiled individuals was significantly influenced by the association of time and space factors. There were two time factors involve in this study 1) the length of the recolonization period and 2) the starting dates of the experiments.

The length of the recolonization period variable did not show a significant effect on the proportion of left coiled individuals in the population. This suggests that O.cf.venusta population seems to maintain its coiling direction preference in the short term (fortnightly).

The importance of the association between the starting dates of the experiments and the period and also its association with the site variable in determining the proportion of left coiled individuals in the population is highlighted clearly in this study.

The effect of the association between the starting date and period variable was probably through the differences in the environmental conditions of each experiment. These differences, such as variations of length of exposure to air and other as yet unidentified factors might vary at the beginning and for the duration of the investigation.

The significantly different proportions between the two study sites and the significant effect of the association between the starting date and site variable, suggest that the space factor also plays a greater role in stimulating the difference in the proportion of left coiled individuals in the population than the time factor.

The natural conditions at each study site during the study period, e.g. depth and length of subaerial exposure, were possibly some of the environmental factors that may govern the number of foraminifera on seagrass blades. In turn, these factors could also control the proportion of left coiled individuals in the population. It was noticed that, gradually, site 1 was subaerially exposed longer compared to site 2 during the course of the investigation. This was quite extraordinary since it was noted that, during the previous one year temporal distribution study (October 1988 to September 1989), site 1 was always covered with seawater longer than the other sites. Even though no qualitative data were obtained, it was noticeable that site 1 had become shallower during the study period (January to March 1990). This was caused by slow lateral movements of sediments from the southeastern part of the bay towards site 1. This slow depth change in site 1 is perhaps one among many other environment factors that might play a role in determining the number

of left coiled individuals in the Q.cf.venusta population.

Severin (1987), in his study on the temporal distribution of Marginopora, suspected that the frequency of subaerial exposure that occurred in his study site was the factor responsible for preventing the seagrass being occupied by foraminifera. This kind of situation probably also occurred in the Q.cf.venusta population during the present study. Presumably the length and frequency of subaerially exposure affects the number of left coiled individuals that live on seagrass blades indirectly by disrupting the settlement of new Q.cf.venusta .

4.4. Microspheric and megalospheric generations: their occurrence and temporal patterns in the population

4.4.1.Introduction.

According to Boltovskoy and Wright (1976) and several other workers (Boersma, 1978; Haynes,1981 and Brasier, 1980; Goldstein, 1988; Röttger, Krüger and de Rijk, 1990) the life history of foraminifera is characterised as having two generations : the megalospheric generation, that contain one nucleus and have a relatively large initial chamber; and the microspheric generation, containing several nuclei and

having a relatively small initial chamber or proloculus. The megalospheric generations or gamont is the sexual form and it is commonly called form (A). The microspheric generation is the asexual form (form B) or agamont or schizont. The megalospheric forms are usually produced by the microspheric forms through protoplasm division in the last chamber. The microspheric generations are formed through gametogenesis when two gametes produced by the megalospheric form join to make a zygote (Boltovskoy and Right, 1976).

In addition, there are variations in the reproduction cycle by some foraminifera. A third generation called the megalospheric schizont occurs in foraminifera that have a trimorphic life cycle. This has been reported in the small foraminifera Elphidium crispum, Quinqueloculina circularis, Planorbulina mediterranensis and Nubecularia lucifaga and the larger foraminifera Heterostegina depressa (Röttger, et all , 1986). This form according to Rhumbler (1909, in Röttger, Krüger and de Rijk, 1990) is found when the microspheric generation (agamont) produce a megalospheric schizont instead of gamont by protoplasmic multiple fission. Mature megalospheric schizonts then produce megalospheric (gamont) offspring by following the same multiple fission process as their microspheric counterparts.

Kloos (1984) in his foraminiferal collection from a bay on Curaçao, Netherlands Antilles, found that there

were two generations of the megalospheric form (A 1 and A 2) and no microspheric forms in the adult specimens of Sorites orbiculus during the period of July 1979 to September 1979. He concluded that Sorites orbiculus reproduced only by means of apogamic schizogony and no meiosis occurred. Walker (1976) in his investigation on the life cycle of six species of tide pool benthic foraminifera, Cibicides lobatulus, Rosalina floridana, Quinqueloculina seminulum, Pateoris haurinoides, Spirilina vivipara and Eggerella advena observed no gamontic generation during a 14 month biweekly sampling study. He assumed that the gametogenesis of these six species of foraminifera occurred only in the deeper water, and the juvenile schizont forms were then transported to the intertidal zone where they attached to algae.

Boltovskoy and Wright (1976) stated that the microspheric form is, in most cases, significantly less in number than the megalospheric forms. They also noted that the ratio of the micro- to megalospheric forms and the number of megalospheric forms produced by microspheric forms in a particular time could reflect the reproductive rate of the species.

Q.cf.venusta is an epiphytic foraminifera found on the blades of the intertidal seagrass Halodule uninervis in Shelly Bay. The life cycle of this species has not been discussed so far. Its domination and abundance on the seagrass blades throughout the year are assumed to

be caused by the ability of this species to survive and reproduce in the harsh environment of the intertidal area. The aims of this study were : to observe the life cycle of O.cf.venusta, to determine the percentage of each generation (microspheric and megalospheric) in the population, and to observe their temporal percentage patterns throughout the study periods.

4.4.2. Materials and methods.

Specimens of O.cf.venusta were immersed in aniseed oil so that the microspheric and megalospheric forms could be distinguished. This cleared the specimens and allowed the structure of the chambers to be seen with a phase contrast microscope. The determination of microspheric and megalospheric forms were based on the measurements of the proloculus. The proloculus of the microspheric form ranged from 5 u to 10 u whilst in the megalospheric form it ranged from 40 u up to 90 u.

The study of the percentage of each generation and the temporal pattern of the proportion of the microspheric and megalospheric individuals in the population was conducted in two different sampling periods i.e. fortnightly and monthly, in conjunction with the recolonization and temporal distribution study. The specimens used in this study came from the recolonization and the temporal distribution study (see

Chapter 5, section 2, and Chapter III). All specimens of the recolonization study and specimens from location 1, experiment 1 from the temporal distribution study were used for determining the proportion of the microspheric and megalospheric in the population.

The presence of juvenile megalospheric O.cf.venusta in or around their microspheric parent could be seen when mature microspheric individuals with brood chambers were immersed in aniseed oil.

4.4.3. Results.

Based on the specimens observed, the life cycle of O.cf.venusta was characterised by an alternation of two generations, the microspheric and the megalospheric.

Data on the number of individuals of each generation are presented in tables 15 and 16.

The megalospheric generation always outnumbered the microspheric ones. The percentage of the microspheric generation ranged from 0 to 18.34 % /blade/month, and the percentage of the megalospheric generation ranged from 81.66 to 100 % /blade/month.

Figures 66 and 67 show the temporal trend of the fortnightly percentage of microspheric specimens/blade at two study sites. The percentage of microspherics from the three experiments (see section 5.2.2. for experimental set up and sampling methods) at site 1

seems to follow similar seasonal variation. At site 2, however, no clear seasonal trends could be traced.

The highest percentage of the microspheric generation recorded in the fortnightly study was 12.83 %, and it was observed in the foraminiferal population whose population development has been followed for a 6 weeks period. The lowest percentage was registered in two occasions : 1) on the 23rd of February, and 2) on the 25th of March, from site 1 experiment 3. On these occasions no microspheric specimens can be found.

Figure 45 (see page 63) shows megalospheric juveniles that are just about to be released by a mature microspheric parent.

4.4.4. Discussion.

The monthly sampling shows that, generally, the microspheric generation is present throughout the whole one year study period. Its percentage in the population, however, seems to fluctuate from one month to the other. This is not surprising, since Myers (1943, in Boltovskoy and Wright, 1976) also reported some seasonal fluctuations in the proportion of microspheric

Months	Micro	Mega	Total individuals / 8 blades	Total individuals / 16 blades
Oct.1988	0	104	104	
Nov.1988	33	486	519	
Dec.1988	13	284	297	
Jan.1989	16	401	417	
Feb.1989	16	93	109	
Mar.1989	5	77	82	
Apr.1989	5	29		34
May 1989	115	696		811
Jun.1989	88	454		542
Jul.1989	91	577		668
Aug.1989	25	177		202
Sept.1989	16	99		115

Table 15: Number of individuals of each generation per eight and sixteen blades of Halodule uninervis (Micro.= Microspheric; Mega.=Megalospheric).

Exp.	Dates	Sites	Micro	Mega	Total individuals / 6 blades
I	27/12/1989 (*)				
	10/01/1990	1	9	174	183
		2	5	134	139
	25/01/1990	1	4	161	165
		2	7	169	176
	08/02/1990	1	3	75	78
		2	6	229	235
	23/02/1990	1	4	98	102
		2	2	66	68
II	10/01/1990 (*)				
	25/01/1990	1	22	210	232
		2	10	327	337
	08/02/1990	1	2	61	63
		2	11	189	200
	23/02/1990	1	1	37	38
		2	1	68	69
	09/03/1990	1	10	100	110
		2	4	71	75
III	25/01/1990 (*)				
	08/02/1990	1	16	134	150
		2	3	231	234
	23/03/1990	1	0	38	38
		2	1	59	60
	09/03/1990	1	7	156	163
		2	2	63	65
	25/03/1990	1	0	6	6
		2	1	17	18

Table 16: Number of individuals of each generation in six blades of Halodule uninervis. (Exp. = Experiments ; Micr. = Microspheric; Mega.= Megalospheric; (*) = Starting dates of the experiments).

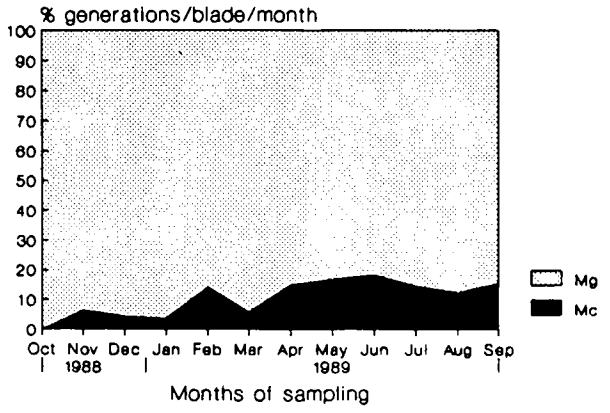
Figure 65: Monthly percentage of megalospheric and microspheric individuals per blade during October 1988 to September 1989.

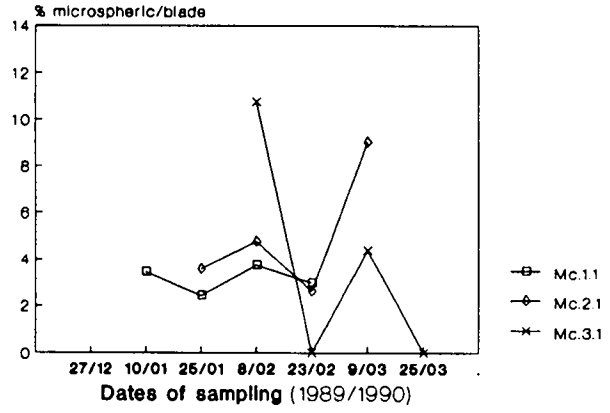
Figure 66: Fortnightly percentage of microspheric individuals per blade at Site 1.

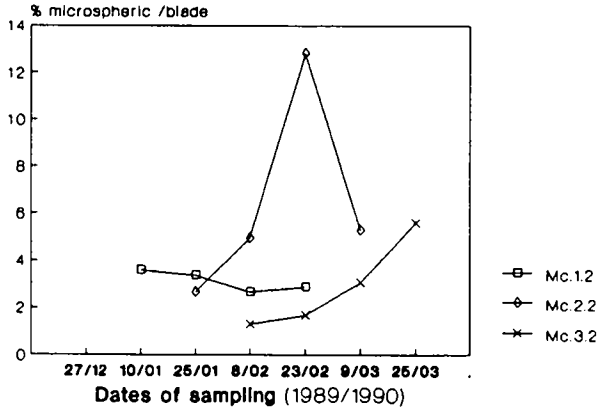
Mc.1.1: Experiment 1, started on 27/12/1989
Mc.2.1: Experiment 2, started on 10/01/1990,
Mc.3.1: Experiment 3, started on 25/01/1990.

Figure 67: Fortnightly percentage of microspheric individuals per blade at Site 2.

Mc.1.2: Experiment 1, started on 27/12/1989
Mc.2.2: Experiment 2, started on 10/01/1990,
Mc.3.2: Experiment 3, started on 25/01/1990.


% generations/blade/month
100
90
80
70
60
50
40
30
20
10
0
Oct Nov Dec Jan Feb Mar Apr May Jun Jul Aug Sep
1988
1989
Months of sampling
Mg
Mc


% microspheric/blade
14
12
10
8
6
4
2
0
27/12 10/01 25/01 8/02 23/02 9/03 25/03
Dates of sampling (1989/1990)
Mc.1.1
Mc.2.1
Mc.3.1


% microspheric /blade
14
12
10
8
6
4
2
0
27/12 10/01 25/01 8/02 23/02 9/03 25/03
Dates of sampling (1989/1990)
Mc.1.2
Mc.2.2
Mc.3.2

individuals in Tretomphalus.

In the shorter term study (fortnightly sampling), the percentages of microspheric individuals from the two study sites, show no similarity in their temporal patterns. Such observation highlights the role of time and space in governing the trends of the microspheric and megalospheric individuals in the Q.cf.venusta population.

According to Boltovskoy and Wright (1976), in foraminifera the microspheric form is often less abundant than the megalospheric form. In some cases they observed the opposite situation to occur. If conditions were not favourable, the number of megalospheric were reduced, and were sometimes absent. They postulated that unfavourable condition will occur during winter in the littoral zone of high latitudes, or in the sublittoral zone of mid-latitude.

In this study, the megalospheric form contributed at least 81.66 % of the monthly population and 87.17 % of the fortnightly population. It is obvious that the megalospheric generation dominated all samples. It is therefore, reasonable to believe that the patterns of the percentage of microspheric and megalospheric generations in the population of Q.cf.venusta seemed quite comparable with Boltovskoy and Wright's (1976) finding, and that stressing conditions did not occur.

Recently, there have been a few studies to investigate the seasonal pattern of the microspheric and

megalospheric generation in foraminiferal populations. Most of them were only carried out in the field for a very limited sampling time or in the laboratory. Boltovskoy and Wright (1976) reported that in Patellina and Calcarina, the microspheric form contributed 20 % of the population. In Elphidium , they found that 30 % of the population were microspheric individuals. Goldstein (1988) stated that only 223 microspheric specimens were found from thousands of Saccammina alba specimens she examined. She also mentioned that the microspheric specimens were only observed during a single season (March and April 1982). Seasonal study on Tretomphalus (Myers, 1943 in Boltovskoy and Wright, 1976) showed that ratio microspheric to megalospheric in autumn was 1 : 140, in winter was 1 : 24 and in spring was 1 : 340.

It is thus clear, from these few studies, that the foraminiferal population normally consists of a small percentage of microspheric specimens, and the variations in their percentages are seasonal.

This present study of O.cf.venusta shows both the long period variations for each generation (microspheric or megalospheric), and also the shorter period variation. Considering that the microspheric specimens were always outnumbered by their megalospheric counterparts, it is believed that there are at least three possibilities concerning the survival and adaptation of O.cf.venusta that lives epiphytically on the seagrass blades. These possibilities are 1) the

juveniles and immature microspheric form of this species have a low survival capability and adapt poorly as an epiphytic foraminifera , 2) when this form survives and reaches maturity, it has the capability of producing a large number of megalospheric juveniles and, 3) the megalospheric form of this species has a high survival capability and adaptability living in the harsh intertidal environment.

Chapter V

Population study

5.1. Population dynamics

5.1.1. Introduction

Studies on foraminiferal population dynamics have been made by several workers in many different places. The aims of their studies involved gathering information on foraminiferal sediment production, reproduction phase, growth rate, mortality and survivorship (Hallock et.al., 1986; Muller, 1974; Murray ,1967; Murray, 1973; Murray, 1983; Wefer, 1976).

Hallock et.all. (1986) stated that a study of the sediment production of foraminifera is fundamentally supported by population biology data. In his population dynamic study of the benthic foraminifera Nonion depressulus Murray (1983) mentioned that in foraminiferal production is important to distinguish between the living and dead foraminiferal assemblages. He also suggested that the study of this relationship is needed for the paleoecological interpretation of fossil assemblages. Murray (1967) stated that the annual production of foraminifera is the number of tests as well as their size and volume contributing to the sea floor during a one year period. He suggested that the annual production of foraminifera could be detected by employing regular sampling over a period of time. He

also recognised four main factors that influence the production of benthic foraminifera i.e. initial size of standing crop, the proportion of individuals which reproduce, frequency of reproduction and the number of juveniles from each reproduction.

Muller (1974) discovered that the sediment production of Amphistegina madagascariensis from Makapau Point, Oahu, Hawaii was 500 gram $CaCO_3/m^2$/year. Murray (1983) observed the production of Nonion depressulus was 144 tests per 10 cm^2 per year and the annual biomass production was 0.1267 mm^3 per 10 cm^2 or about 3.7 gram $CaCo_3/m^2$ in the Exe estuary, England. In Largo Sound, Florida Hallock et.al. (1986) calculated that the annual sediment production by Archaias angulatus was 60 gram $CaCO_3/m^2$/year.

Besides gaining information on the sediment production some workers successfully determined the reproduction phase of the foraminifera based on the size distribution of the specimens. Murray (1983) found eight or nine reproductive phases per year by observing the size distribution patterns of Nonion depressulus from the Exe estuary, England. He detected these phases by observing the existence of small specimens on the size distribution plots (the size of Nonion depressulus ranging from 120 to 300 um). Wefer (1976) in his study of benthic foraminifera in Baltic Sea, examined the size distribution of seven common species and found that the reproduction cycles (represented by the existence of

small sized individuals between 50 um to 150 um) were coincident with the changing of abietic and biotic environmental factors such as oxygen content, salinity, temperature, symbiotic algae and food availability. He also observed that the reproduction of the 7 species occurred 2 to 4 times in a year. Bradshaw (1957) stated that reproduction occurred at temperature between 20° C and 30° C in laboratory cultured Streblus becarii var. tepida. Zohary et.all (1980, cited in Reiss and Hottinger 1984) detected the existence of small individuals of Amphisorus hemprichii (less than 1.0 mm diameter) in April and May samples and interpreted this as the time of reproduction of A.hemprichii in the Gulf of Elat. They believed that this reproduction phase was activated by the increasing surface water temperature. In a life history study of Baculogypsina sphaerulata on an Okinawan reef flat, Sakai and Nishihara (1981) reported that asexual reproduction took place in June and July. They also found, at the same time, that specimens with brood chambers reached their highest numbers.

Several workers have managed to determine the growth rate of foraminifera from size distribution data. Murray (1983) interpreted the size distribution and plotted the peaks against month, and found that N.depressulus grew at the rate of 30 to 40 μm per month in the Exe Estuary, England. Hallock et.all (1986) observed a growth rate of 200 - 250 μm per month and

mortality rate of 24 % by examining the size frequency distribution of a live population of Archaias angulatus in shallow-shelf communities of the Florida-Bahamas carbonate province. Bradshaw (1957) showed that between 10 ° C and 30 ° C the growth rate of Streblus becarii var. tepida increased with rising temperature. Bijma et.all.(1990) in a study of seven planktonic species concluded that the increase in test size was larger at the optimum temperature and salinity, rather than at extremes.

Murray (1973) stated that observing the size of individuals is a reliable approach of recognising the age of foraminifera. Boltovskoy and Wright (1976) recommended the used of "number of chambers added" for determining the growth rate of foraminifera. There are some variations in the number of chambers added depending on the species, age and environmental conditions. The growth rates that have been reported ranging from 2 chambers a day in Elphidium to 1 chamber per two or three days in Heterostegina depressa (Jepps. 1956 and Rottger, 1972 as cited in Boltovskoy and Wright 1976). The rate of growth was not constant, with some species decreasing growth rate to one chamber every several days in the latter stages of growth (Myers, 1943 in Boltovskoy and Wright, 1976).

The present investigation attempted to study the population dynamics of Osangularia.cf.venusta, especially to identify and obtain information on

reproduction and growth rate (number of chambers added) using monthly and biweekly sampling periods .

5.1.2. Materials and methods

An attempt to use time lapse video recording of live foraminifera in the laboratory to measure the rate of chamber addition proved unsuccessfully. After a period of two days with no addition of chambers, individuals O.cf.venusta detached from the H.uninervis blade for no clear reason. No growth rate data, could be deduced from this method, although it provided interesting behavioural information described in section 5.3.3.2.

A second attempt was made to follow the growth of several individuals O.cf.venusta that were kept in the laboratory while they were still attached to H.uninervis blades . Living seagrass, with the sediment in which they lived was taken from their natural habitat and transplant into plastic containers (11 x 16 x 5 cm), and kept in tank supplied with flowing seawater. This approach failed, as by day two or three, individuals O.cf.venusta detached from the seagrass blades and could no longer be observed.

As the observations of live individuals did not successfully provide growth rate information, a detailed observation based on specimens gathered from the monthly

temporal distribution study (see section 3.2.1.2 for method of sampling), and from the recolonization study (see section 5.2.2 for method of sampling) was undertaken.

All megalospheric specimens from the recolonization study and megalopsheric specimens from location 1 experiment 1 of the temporal study (sampled monthly during April to September 1989) were used in this growth rate investigation. Megalospheric specimens were chosen because of their abundance in the Q.cf.venusta population, as described in section 4.4. In addition, mature microspheric specimens from experiment 2 of the temporal study (sampled during April 1989 to September 1989) were observed to detect the reproduction phase on a monthly basis. Only the microspheric specimens were observed for their maturity, because no significant morphological maturity could be determined in the megalospheric specimens. A mature microspheric form was distinguished by its additional brood chambers (see figures 37 and 38, Chapter IV). In addition, the existence of small megalospheric specimens having less than five chambers in their tests during the study period was also used to determine the reproduction phase of the population.

The laboratory methods are described in section 4.4.2. The only difference was the necessity to count the number of chambers in each specimen.

In the tests of Q.cf.venusta all chambers can be seen clearly from the dorsal side once the specimens were submerged in aniseed oil. The used of high magnification was necessary to clearly see the number of chambers to be counted.

In order to see whether or not there is an obvious size difference between the microspheric and the megalospheric forms, 150 specimens of each form were picked at random from all of the specimens available and their number of chambers and mean sizes were plotted.

5.1.3. Results

The present study reveals that, even though, the microspheric forms have the same number of chambers as their megalospheric counterparts, their overall size was noticeably smaller. Microspheric forms with 24 chambers for instance, were found to be the same size as a megalospheric form with 17 chambers (see figure 68). Thus, in order to avoid confusion in obtaining information of the "age" structure of Q.cf.venusta population, the number of chambers of each generation was the preferred unit of growth in this study.

During the one year study, the megalospheric form was found to have chambers ranging in number from 3 to 19 (see fig.69). Megalospheric juveniles (specimens with

Figure 68: Relationship between the number of chambers and size in microspheric and megalospheric specimens.

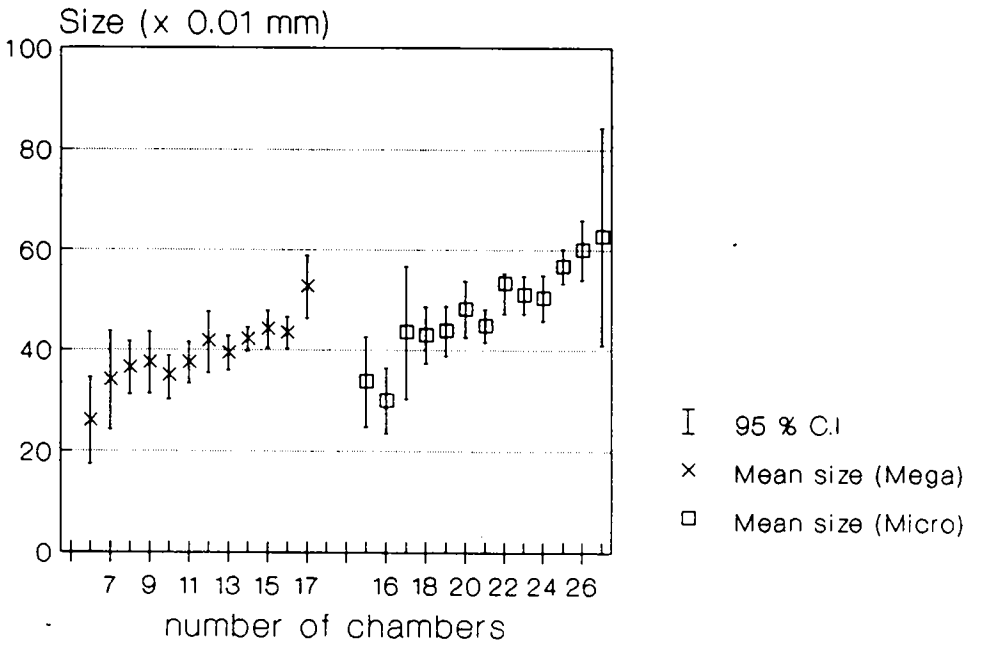
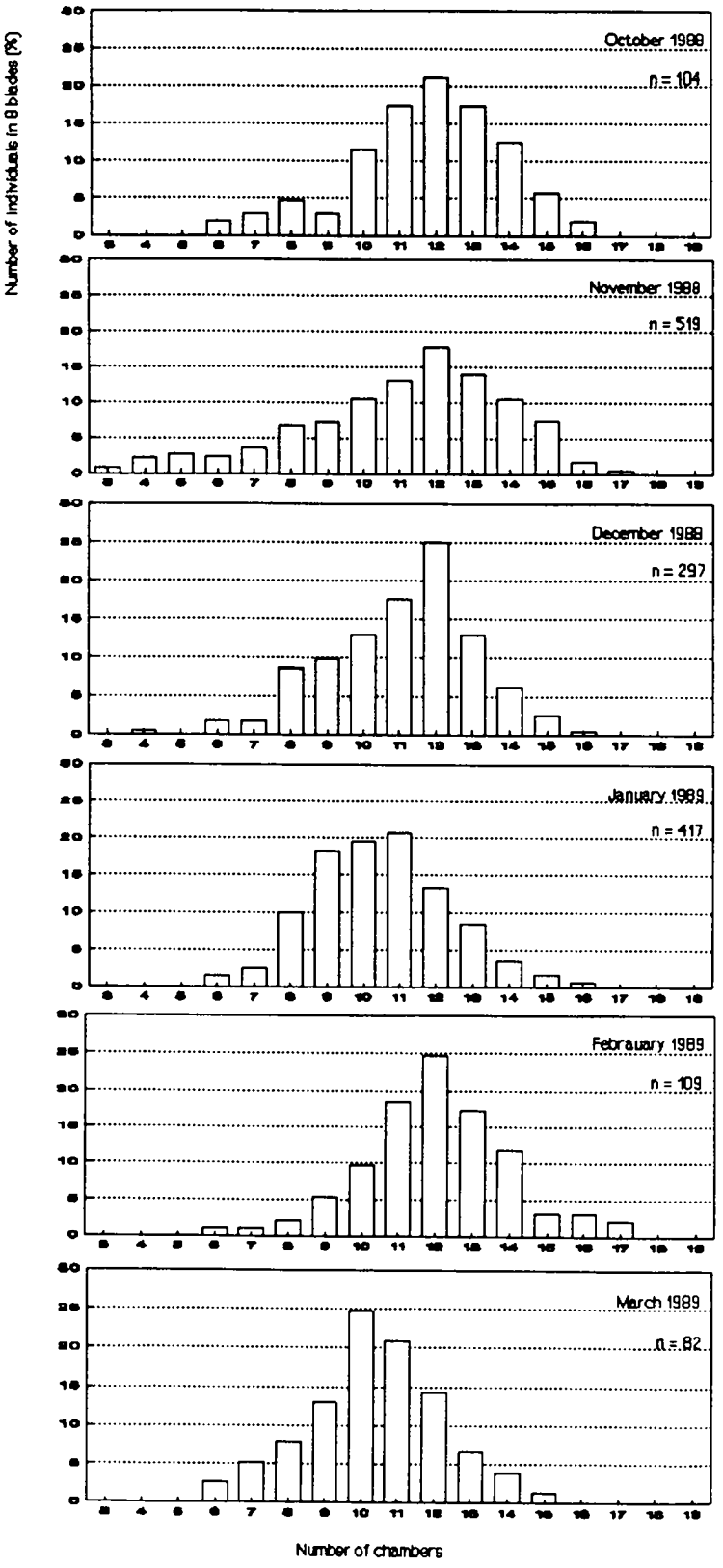
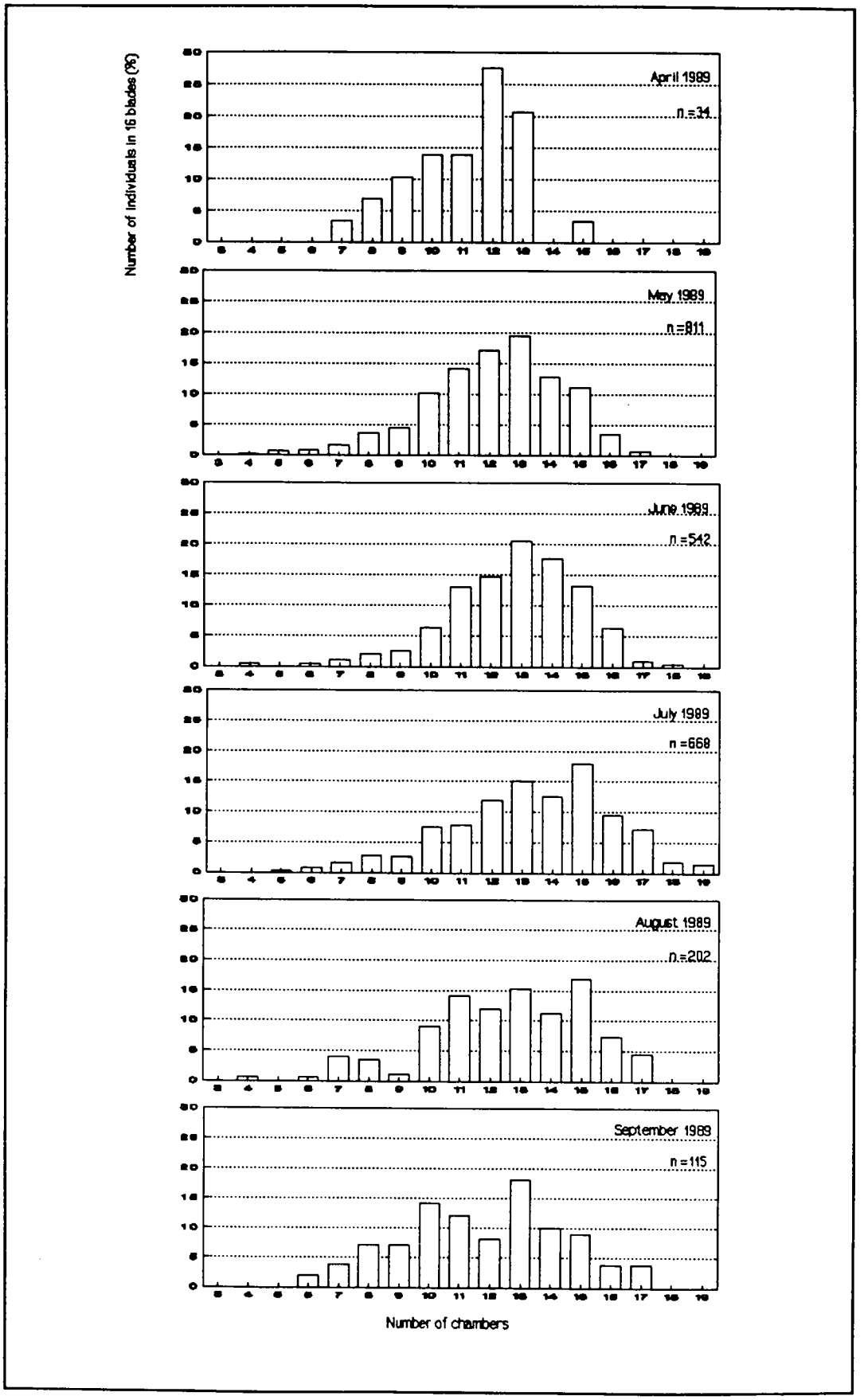

Size (x 0.01 mm)
100
80
60
40
20
0
7 9 11 13 15 17 16 18 20 22 24 26
number of chambers
I 95 % C.I
× Mean size (Mega)
□ Mean size (Micro)

Figure 69: Monthly number of chambers of megalospheric individuals (n: number of specimens observed).



Continue overleaf


Number of individuals in 16 blades (%)
April 1989
n = 34
May 1989
n = 811
June 1989
n = 542
July 1989
n = 668
August 1989
n = 202
September 1989
n = 115
Number of chambers

less than 5 chambers) were found in November and December 1988 and in May, June and August 1989. This figure also shows the monthly frequency distribution of the number of chambers in the population. In general, this figure shows that, the modes of the monthly number of chambers of megalospheric forms gave no clear pattern of progression as a reflection of the population growth rate.

A close inspection of the mean number of chambers (see figure 70), shows a strong suggestion of seasonal patterns in the population. This figure also demonstrates a gradual increase of the mean number of chambers (at the rate of 0.58 to 0.99 number of chambers/month) in the population during the winter period (March to July 1989). It also can be seen that, in summer (October to February) and late winter (August and September), the mean number of chambers in the population tends to decrease gradually.

The megalospheric specimens in the fortnightly study had 4 to 18 chambers. Juveniles were detected on three separate occasions i.e. January 25th (see fig.75), February 8Th (see fig.73), and March 9th (see fig.72).

Based on the observation of the modes of the number of chambers, no clear indication of the biweekly foraminiferal growth rate (see figures 71 to 76) could

Figure 70: Monthly mean number of chambers of specimens collected from Experiment 1 of the temporal distribution study.

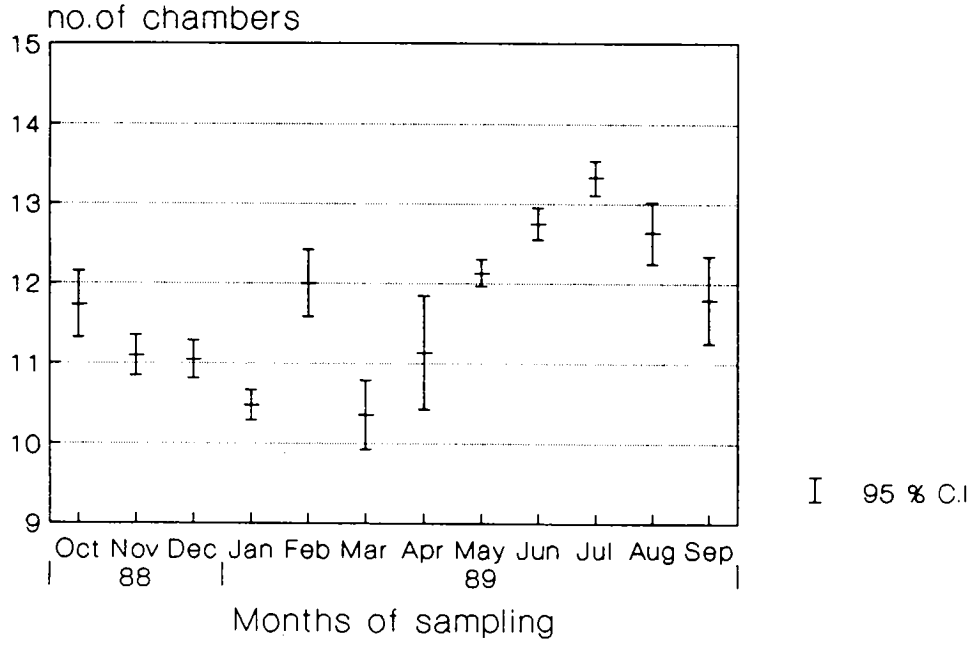

no.of chambers
15
14
13
12
11
10
9
Oct Nov Dec Jan Feb Mar Apr May Jun Jul Aug Sep
88
89
Months of sampling
95 % C.I

Figure 71: Fortnightly number of chambers of megalospheric specimens collected from Experiment 1, Site 1 of the recolonization study.

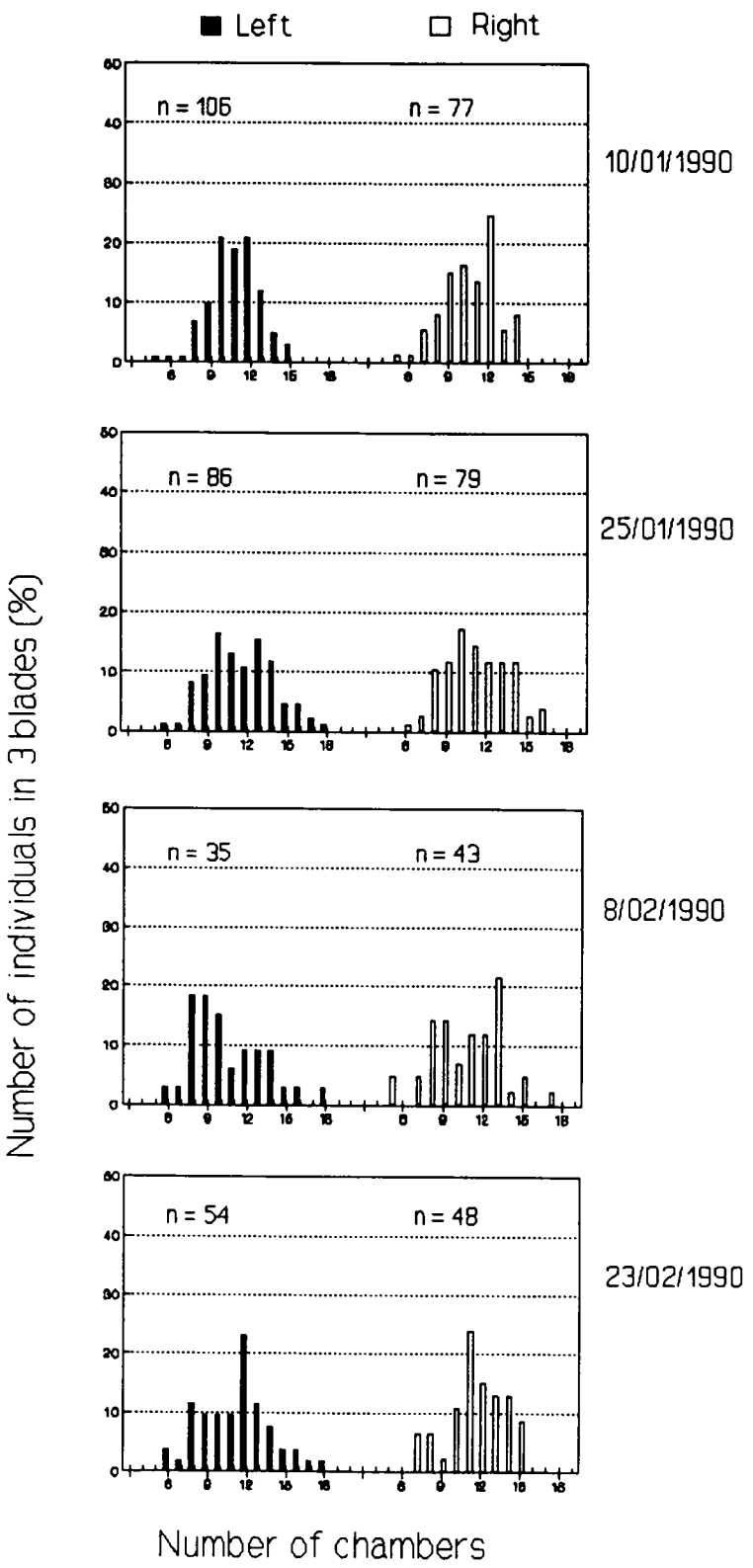

■ Left
□ Right
n = 106
n = 77
10/01/1990
n = 86
n = 79
25/01/1990
n = 35
n = 43
8/02/1990
n = 54
n = 48
23/02/1990
Number of individuals in 3 blades (%)
Number of chambers

Figure 72: Fortnightly number of chambers of megalospheric specimens collected from Experiment 2, Site 1 of the recolonization study.

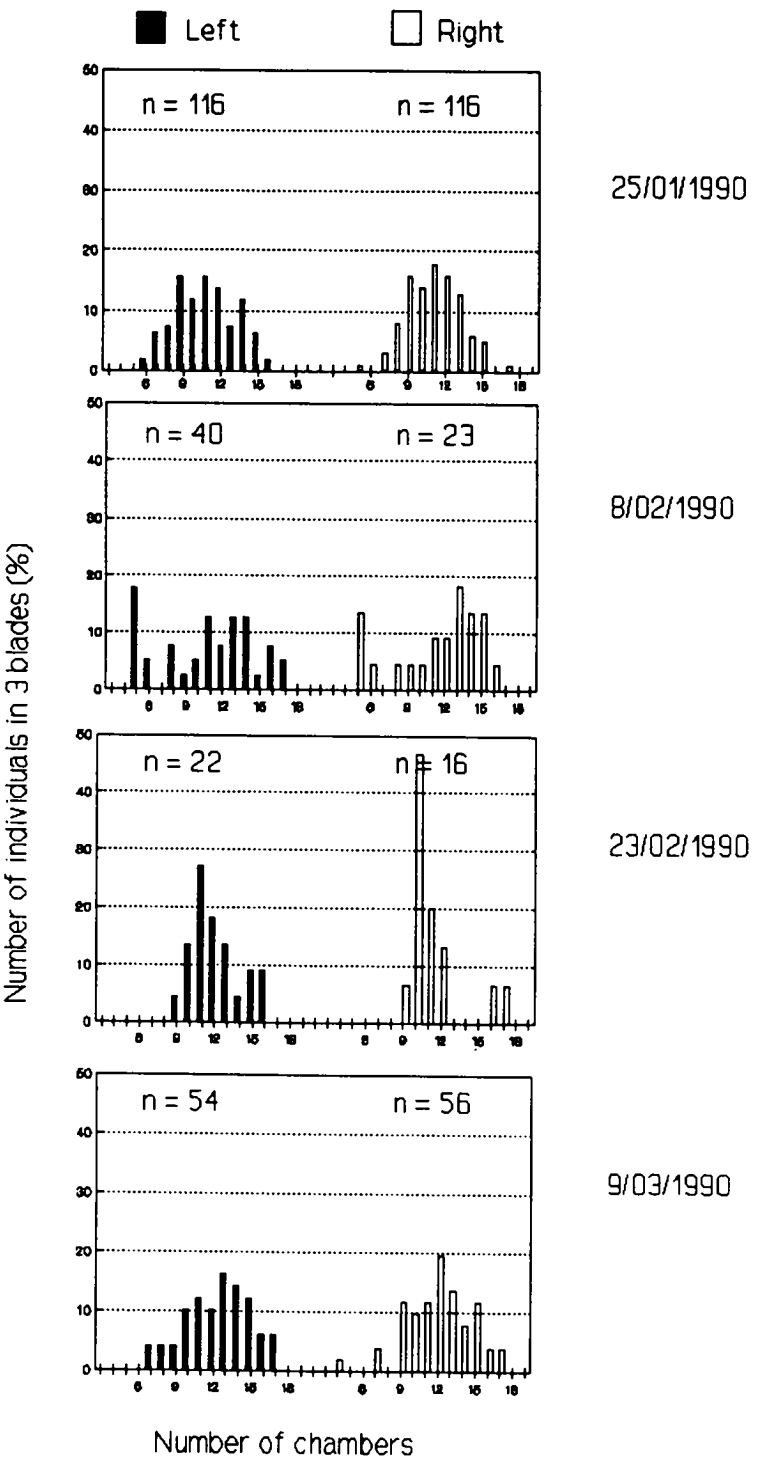

Left
Right
n = 116
n = 116
25/01/1990
n = 40
n = 23
8/02/1990
n = 22
n = 16
23/02/1990
n = 54
n = 56
9/03/1990
Number of individuals in 3 blades (%)
Number of chambers

Figure 73: Fortnightly number of chambers of megalospheric specimens collected from Experiment 3, Site 1 of the recolonization study.

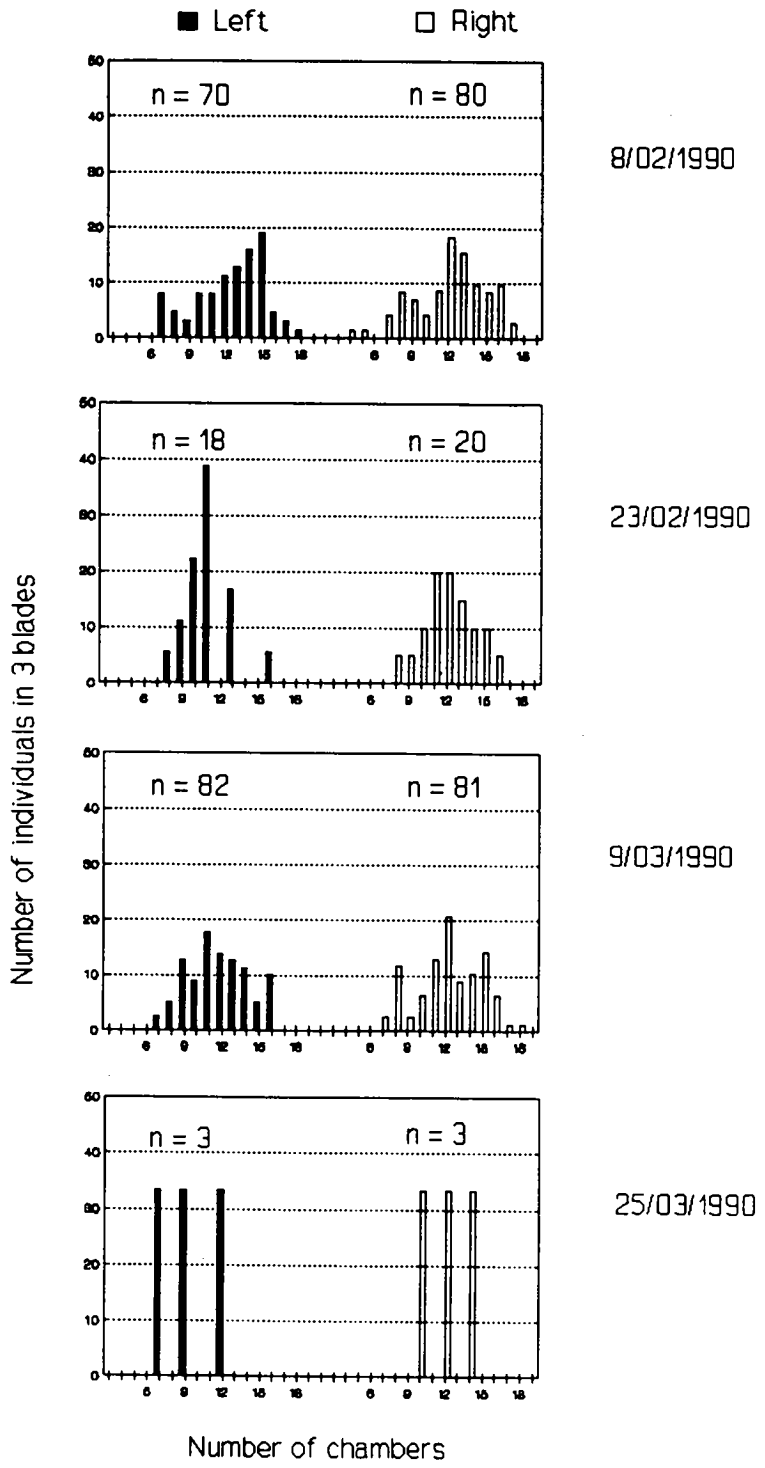

■ Left
□ Right
n = 70
n = 80
8/02/1990
n = 18
n = 20
23/02/1990
n = 82
n = 81
9/03/1990
n = 3
n = 3
25/03/1990
Number of individuals in 3 blades
Number of chambers

Figure 74: Fortnightly number of chambers of megalospheric specimens collected from Experiment 1, Site 2 of the recolonization study.

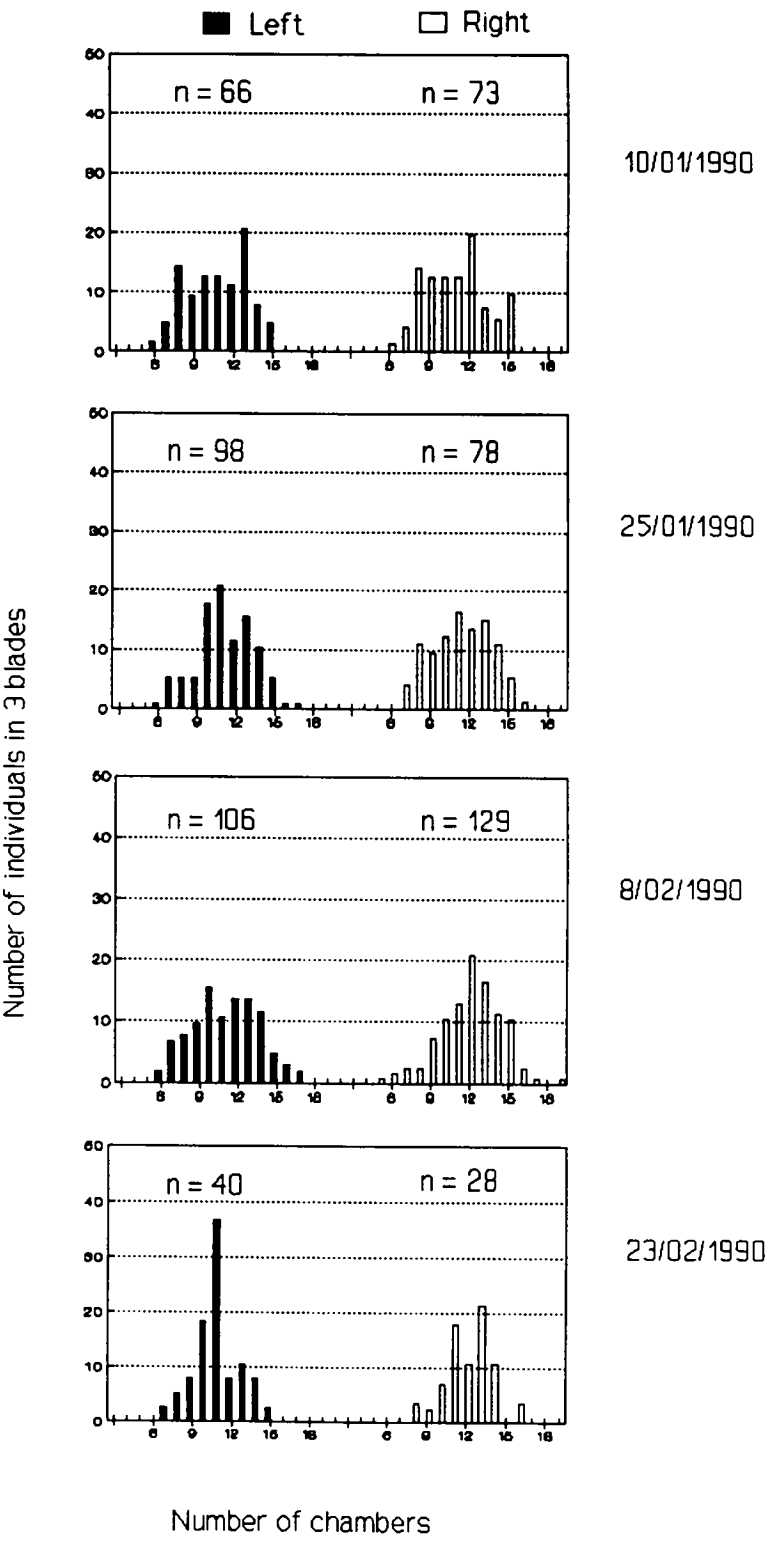

Left
Right
n = 66
n = 73
10/01/1990
n = 98
n = 78
25/01/1990
n = 106
n = 129
8/02/1990
n = 40
n = 28
23/02/1990
Number of individuals in 3 blades
Number of chambers

Figure 75: Fortnightly number of chambers of megalospheric specimens collected from Experiment 2, Site 2 of the recolonization study.

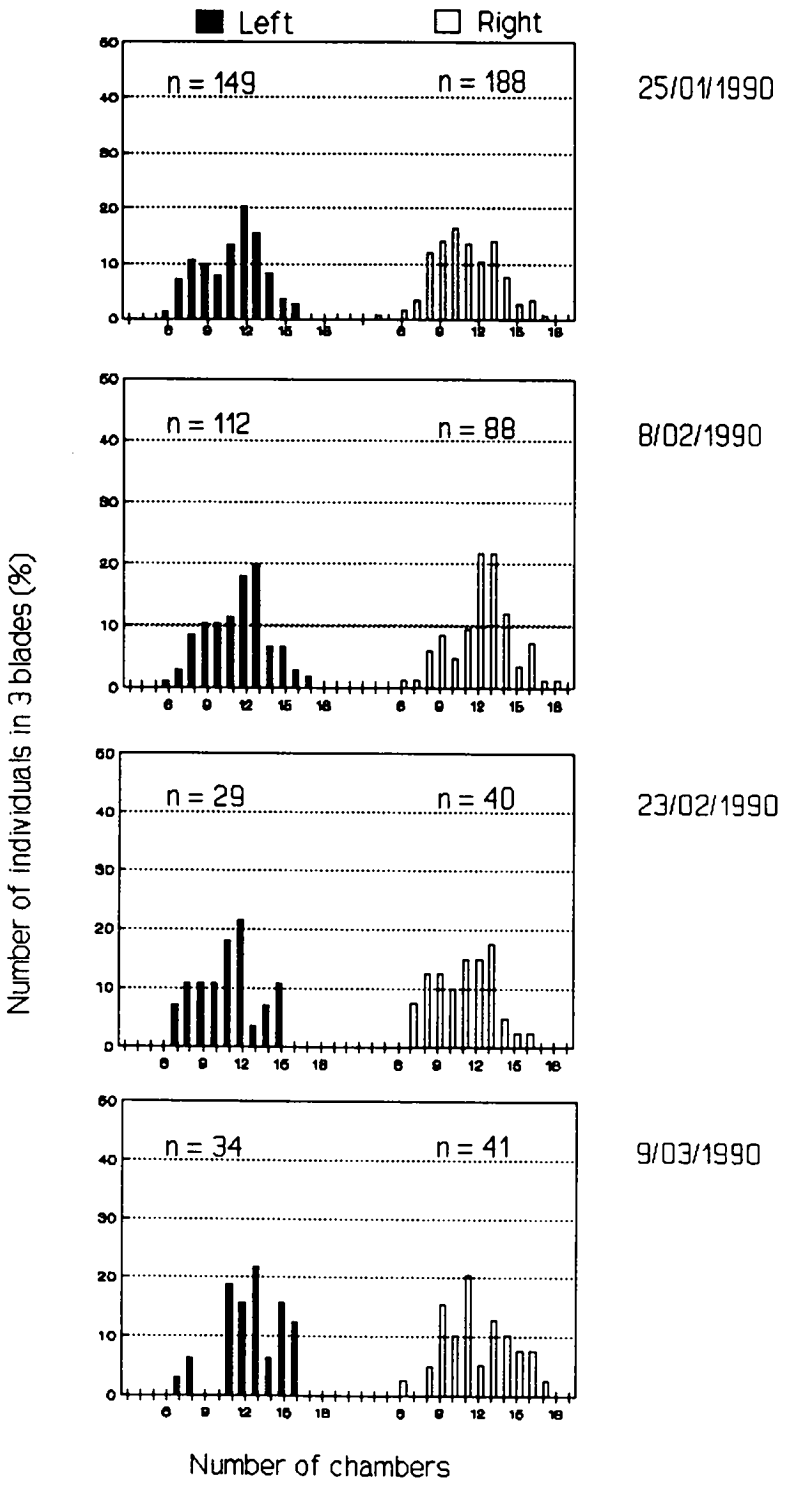
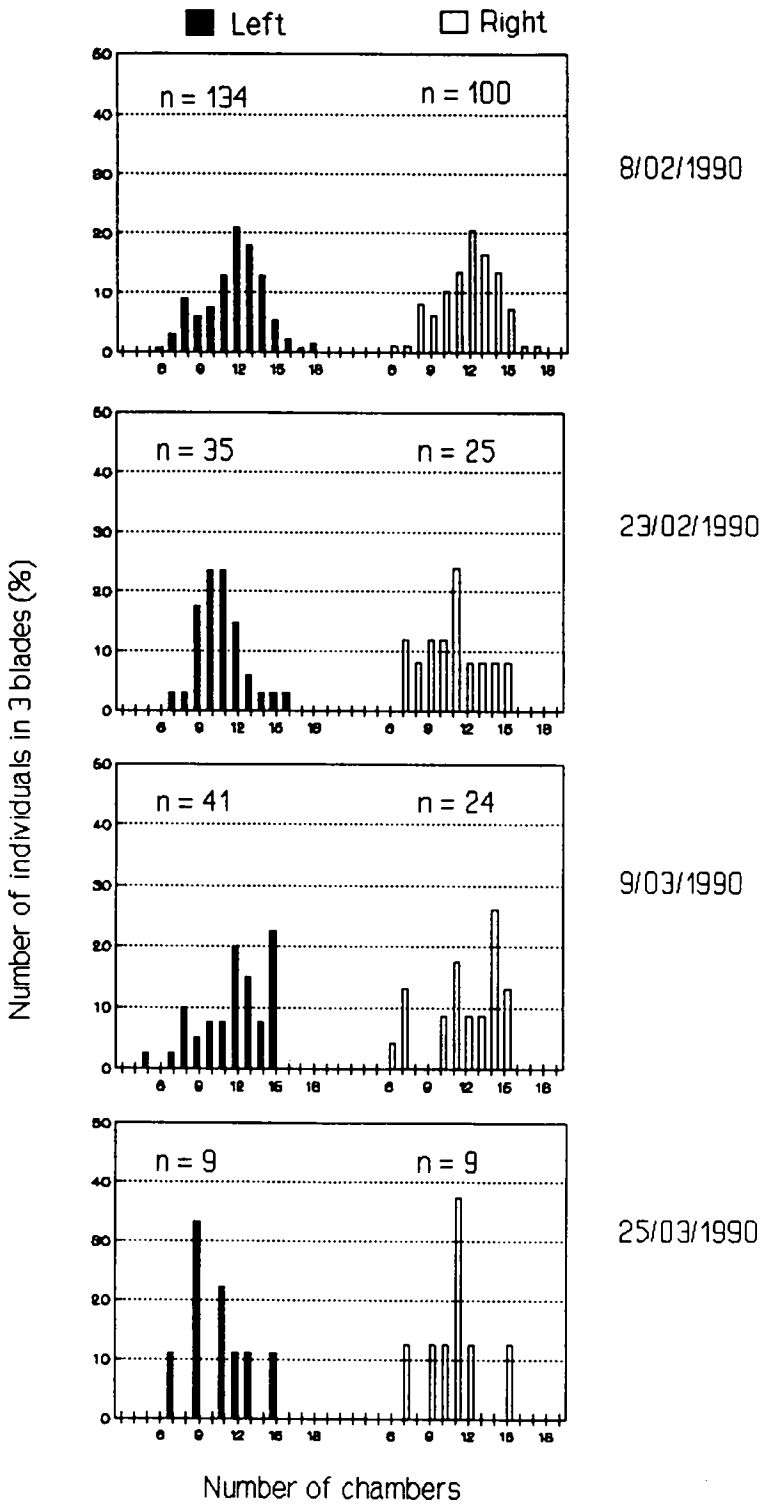

Left
Right
n = 149
n = 188
25/01/1990
n = 112
n = 88
8/02/1990
n = 29
n = 40
23/02/1990
n = 34
n = 41
9/03/1990
Number of individuals in 3 blades (%)
Number of chambers

Figure 76: Fortnightly number of chambers of megalospheric specimens collected from Experiment 3, Site 2 of the recolonization study.


Left
Right
n = 134
n = 100
8/02/1990
n = 35
n = 25
23/02/1990
n = 41
n = 24
9/03/1990
n = 9
n = 9
25/03/1990
Number of individuals in 3 blades (%)
Number of chambers

be obtained.

The observations on the temporal patterns of the mean number of chambers, also show no definite biweekly seasonal trends (see figures 77 to 80). In addition, these figures show that no significant increase in the mean number of chambers occurred during the study period. Thus, no growth rate information can be obtained from this short term study.

The monthly temporal distribution of the microspheric mature form is presented in figure 81. It shows that, both monthly experiments (experiment 1 and 2) give relatively similar seasonal patterns in the percentages of microspheric mature forms in the population. This form reaches its peak percentage in late winter or early summer (September and November).

Figure 82 shows the temporal percentage of microspheric mature forms in relation to the abundance of O.cf.venusta. It shows that there were some changes in the percentages of microspheric mature forms, as well as changes in the overall abundance of O.cf.venusta. The percentage of the microspheric mature form in the fortnightly study are presented in tables 17 and 18 They ranged from 0.42 to 2.41 %. The data in these tables, however, did not show any clear seasonal pattern in terms of microspheric mature occurrence in relation to

Figure 77: Trends of the mean number of chambers of left coiled megalospheric individuals collected from Site 1 of the recolonization study.

Experiment 1 = Recolonization study started on December 27th 1989;
Experiment 2 = Recolonization study started on January 10th 1990;
Experiment 3 = Recolonization study started on January 25th 1989;

Period 1 = 15 days after the study started;
Period 2 = 30 days after the study started;
Period 3 = 45 days after the study started;
Period 4 = 60 days after tge study started;

n = Number of Q.cf.venusta specimens observed.

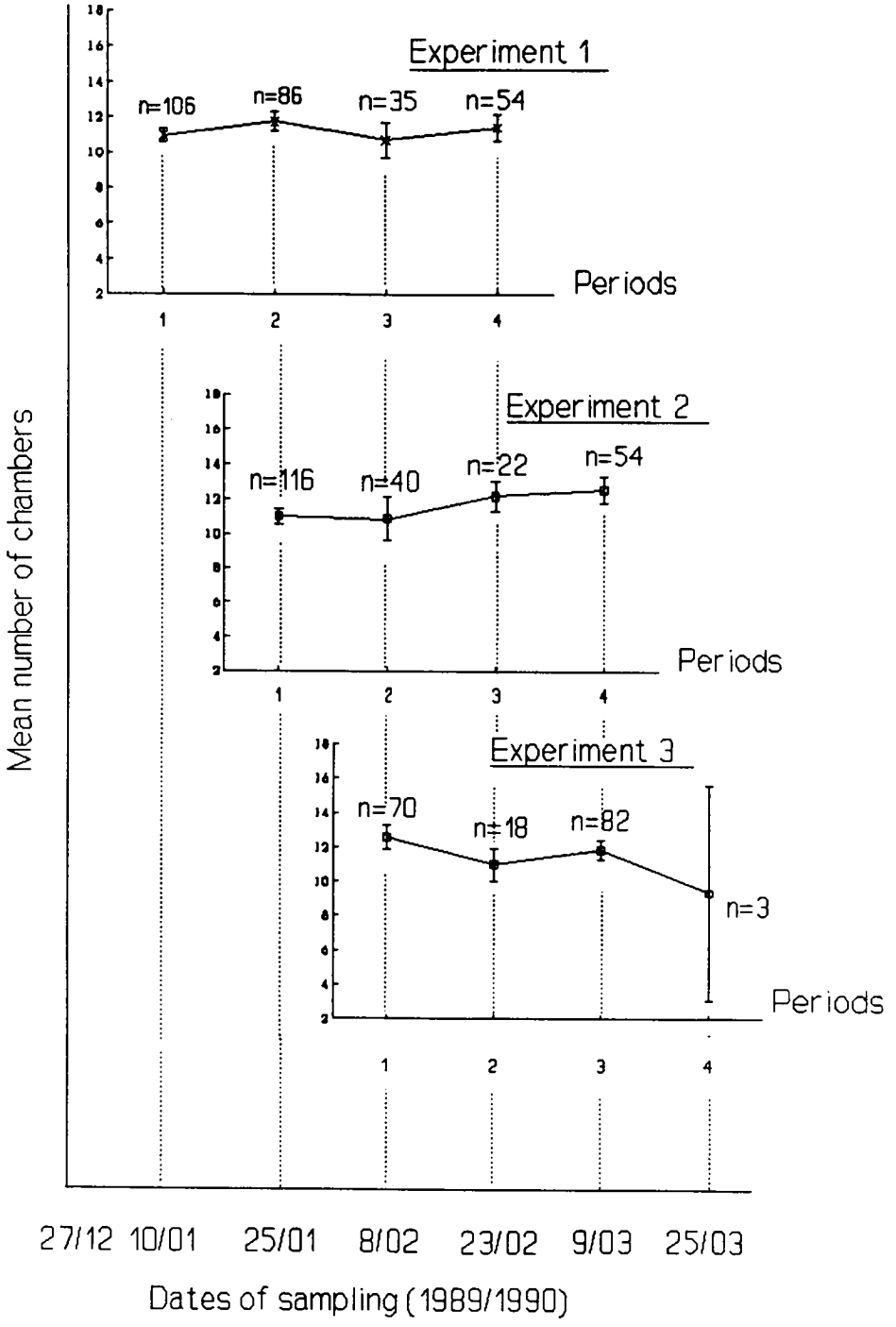

Experiment 1
n=106
n=86
n=35
n=54
Periods
Experiment 2
n=116
n=40
n=22
n=54
Periods
Experiment 3
n=70
n=18
n=82
n=3
Periods
Mean number of chambers
27/12 10/01 25/01 8/02 23/02 9/03 25/03
Dates of sampling (1989/1990)
I = 95% Confidence Interval

Figure 78: Trends of the mean number of chambers of right coiled megalospheric individuals collected from Site 1 of the recolonization study.

Experiment 1 = Recolonization study started on December 27th 1989;
Experiment 2 = Recolonization study started on January 10th 1990;
Experiment 3 = Recolonization study started on January 25th 1989;

Period 1 = 15 days after the study started;
Period 2 = 30 days after the study started;
Period 3 = 45 days after the study started;
Period 4 = 60 days after tge study started;

n = Number of O.cf.venusta specimens observed.

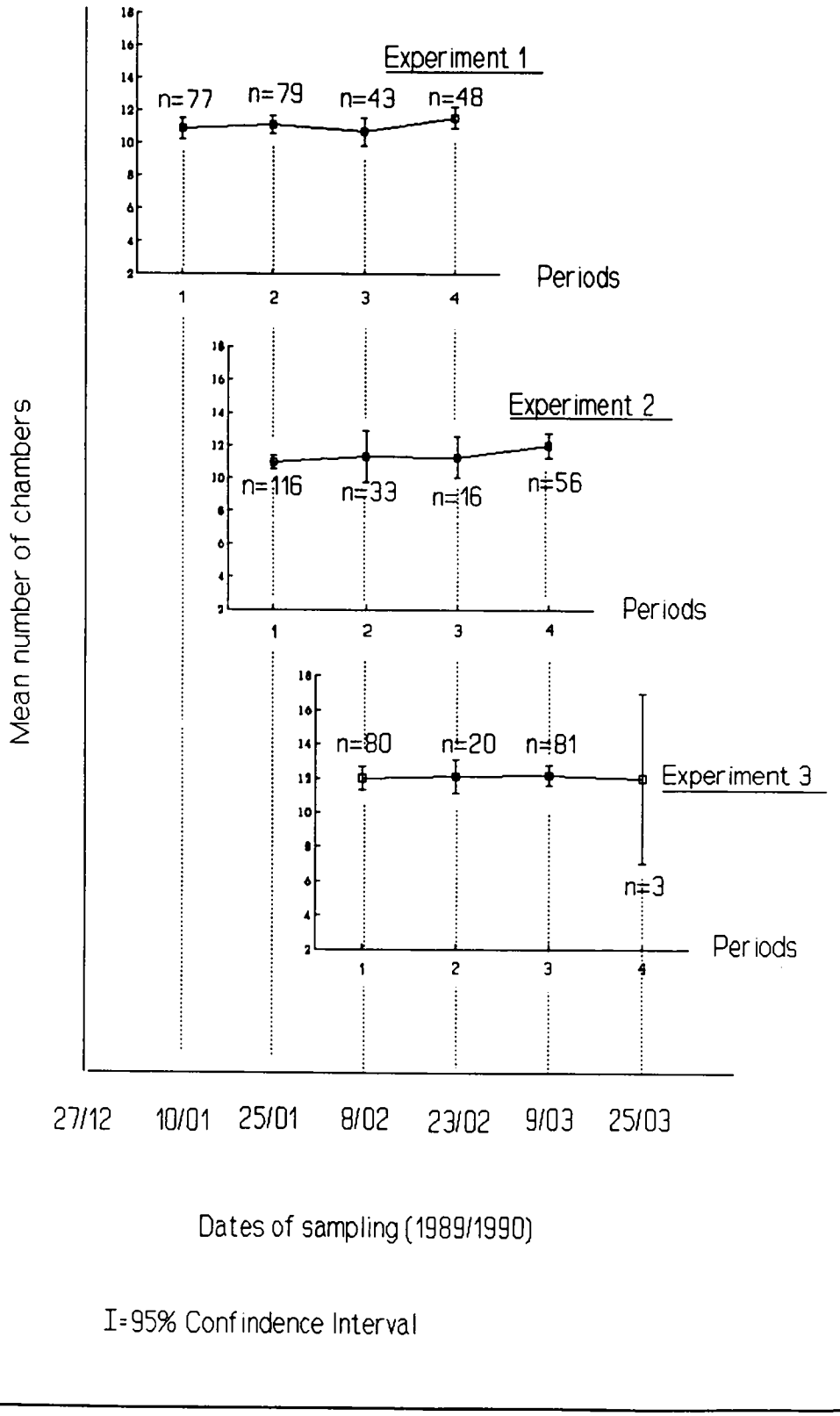

Experiment 1
n=77
n=79
n=43
n=48
Periods
Experiment 2
n=116
n=33
n=16
n=56
Periods
Experiment 3
n=80
n=20
n=81
n=3
Periods
Mean number of chambers
27/12
10/01
25/01
8/02
23/02
9/03
25/03
Dates of sampling (1989/1990)
I=95% Confindence Interval

Figure 79: Trends of the mean number of chambers of left coiled megalospheric individuals collected from Site 2 of the recolonization study.

Experiment 1 = Recolonization study started on December 27th 1989;
Experiment 2 = Recolonization study started on January 10th 1990;
Experiment 3 = Recolonization study started on January 25th 1989;

Period 1 = 15 days after the study started;
Period 2 = 30 days after the study started;
Period 3 = 45 days after the study started;
Period 4 = 60 days after tge study started;

n = Number of O.cf.venusta specimens observed.

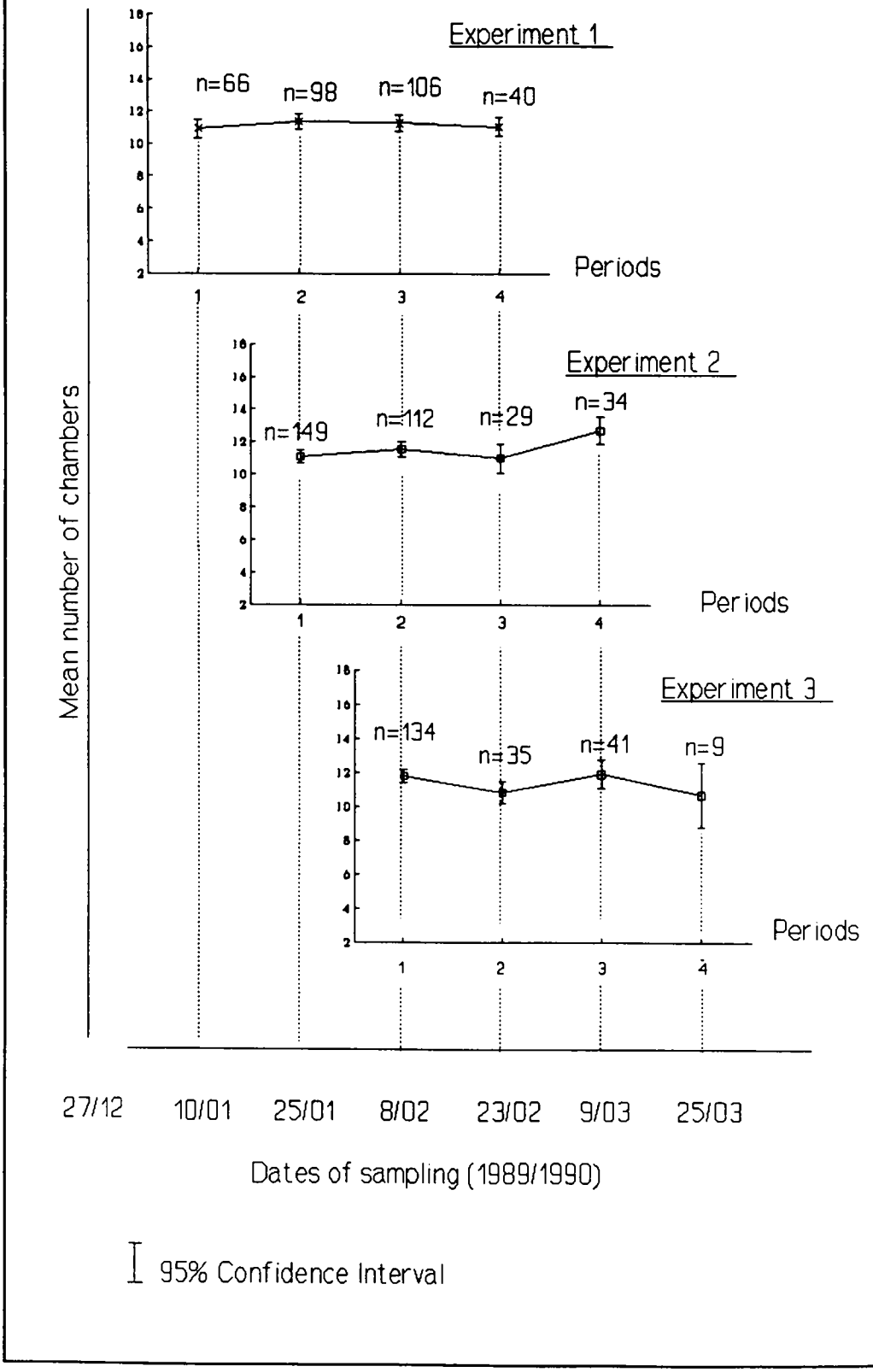

Experiment 1
n=66
n=98
n=106
n=40
Periods
Experiment 2
n=149
n=112
n=29
n=34
Periods
Experiment 3
n=134
n=35
n=41
n=9
Periods
Mean number of chambers
27/12
10/01
25/01
8/02
23/02
9/03
25/03
Dates of sampling (1989/1990)
95% Confidence Interval

Figure 80: Trends of the mean number of chambers of right coiled megalospheric individuals collected from Site 2 of the recolonization study.

Experiment 1 = Recolonization study started on December 27th 1989;
Experiment 2 = Recolonization study started on January 10th 1990;
Experiment 3 = Recolonization study started on January 25th 1989;

Period 1 = 15 days after the study started;
Period 2 = 30 days after the study started;
Period 3 = 45 days after the study started;
Period 4 = 60 days after tge study started;

n = Number of O.cf.venusta specimens observed.

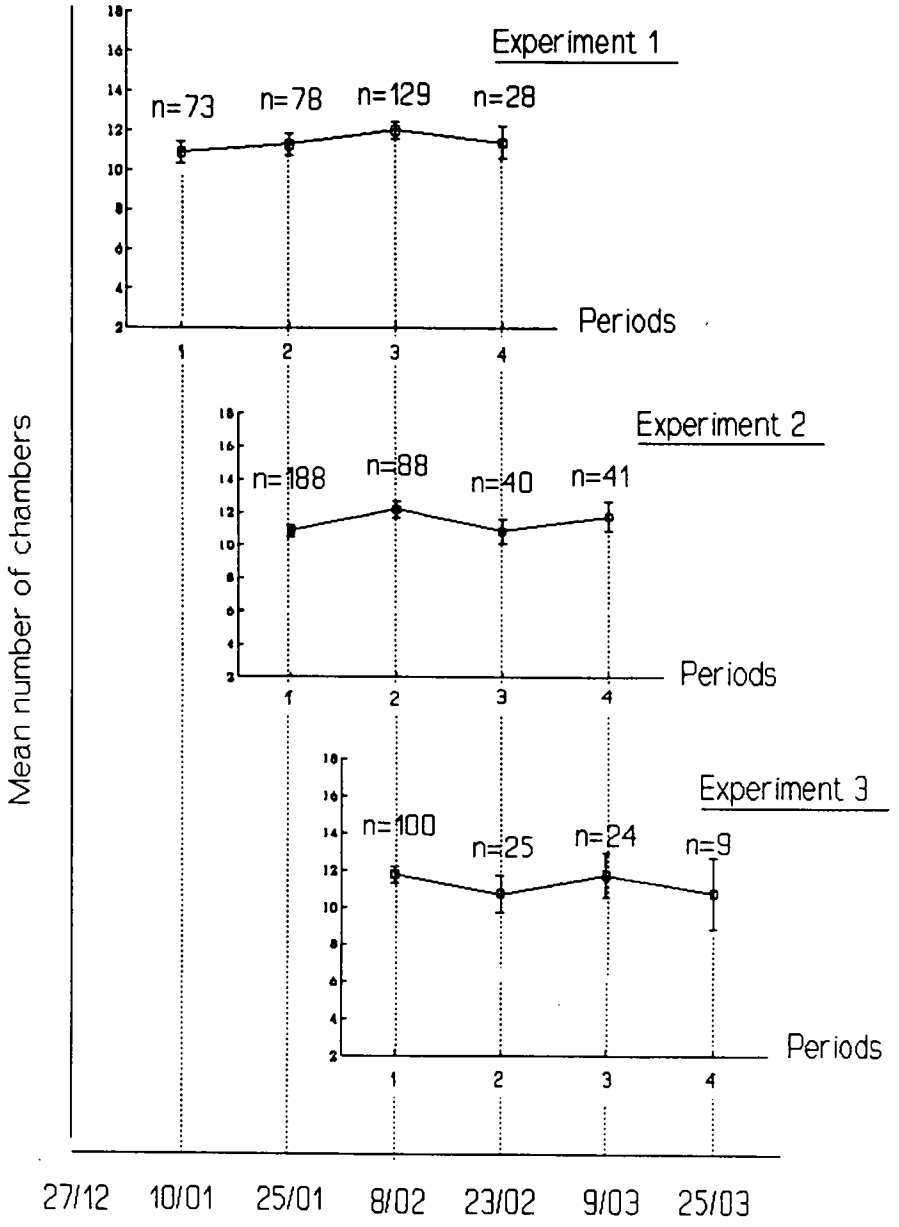
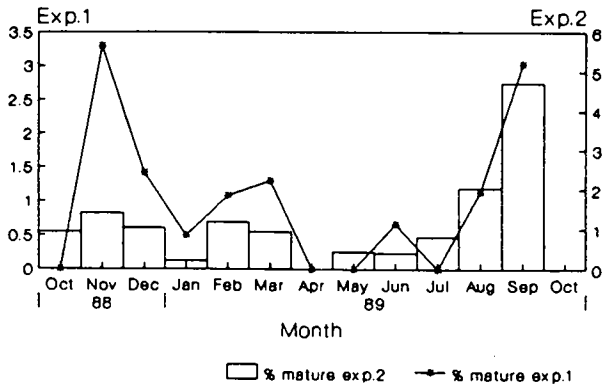
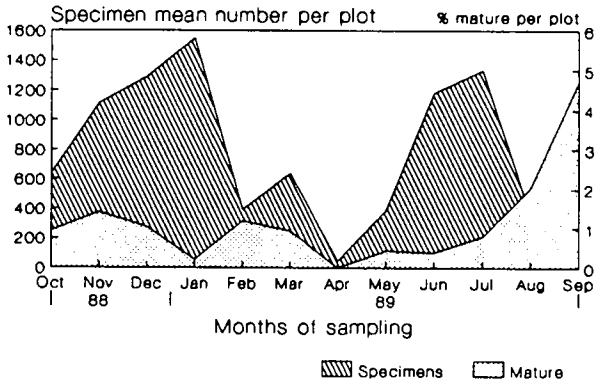

Experiment 1
n=73
n=78
n=129
n=28
Periods
Experiment 2
n=188
n=88
n=40
n=41
Periods
Experiment 3
n=100
n=25
n=24
n=9
Periods
Mean number of chambers
27/12
10/01
25/01
8/02
23/02
9/03
25/03
Dates of sampling (1989/1990)
95% Confidence Interval

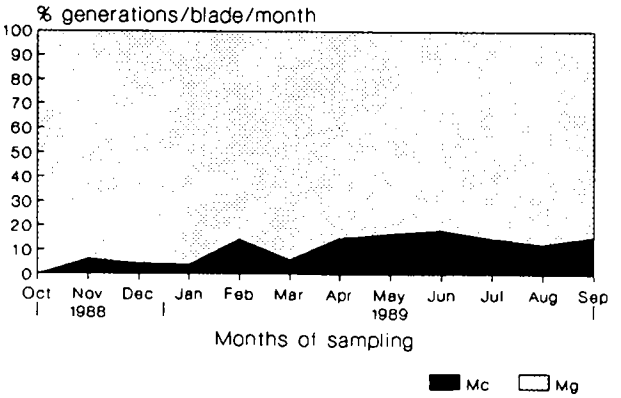
Figure 81: Percentages of microspheric mature specimens collected from Experiment 1 and 2 of the temporal distribution study (October 1988 - September 1989).

Figure 82: Percentages of microspheric mature specimens in relation to the number of O.cf.venusta per plot in Experiment 2 of the temporal distribution study.

Figure 83: Percentages of microspheric and megalospheric specimens in Experiment 1 of the temporal distribution study.


Exp.1
Exp.2
3.5
3
2.5
2
1.5
1
0.5
0
6
5
4
3
2
1
0
Oct
Nov
88
Dec
Jan
Feb
Mar
Apr
May
89
Jun
Jul
Aug
Sep
Oct
Month
% mature exp.2
% mature exp.1


Specimen mean number per plot
% mature per plot
1600
1400
1200
1000
800
600
400
200
0
6
5
4
3
2
1
0
Oct
Nov
88
Dec
Jan
Feb
Mar
Apr
May
89
Jun
Jul
Aug
Sep
Months of sampling
Specimens
Mature


% generations/blade/month
100
90
80
70
60
50
40
30
20
10
0
Oct
Nov
1988
Dec
Jan
Feb
Mar
Apr
May
1989
Jun
Jul
Aug
Sep
Months of sampling
Mc
Mg

the temporal abundance of O.cf.venusta.

5.1.4. Discussion

Most workers have relied on the size or diameter of specimens (Murray, 1967; Erskian & Lipps, 1987; Murray, 1983; Hallock et.all, 1986; Muller, 1974; Wefer, 1976; Sakai and Nishihara, 1981) in order to study the population dynamics and growth rate of foraminifera. The size of individual foraminifera, however, has been reported to be influenced by factors such as water temperature, salinity, the availability of calcium carbonate and food (Bradshaw, 1957; Bandy, 1963, Lewis and Jenkins, 1969; Corliss, 1979; Caralp, 1989; Bijma et.all, 1990;). Variations in such factors could lead to different results in a study of the population dynamics and growth of certain species. Size and age are not necessarily related.

The microspheric and megalospheric generations of foraminifera could also contribute to a misleading interpretation of size distribution. As revealed in this investigation, even though they had the same number of chambers, the microspheric generations tended to be smaller then their megalospheric counterparts. If

Dates	Experiment 1		Experiment 2		Experiment 3	
1990	M (%)	Total	M (%)	Total	M (%)	Total
09/Jan	1.04	192				
25/Jan	0.59	169	0.78	254		
08/Feb	0	81	0	65	2.41	166
23/Feb	0	106	0	39	0	38
09/Mar			0	120	0	170
25/Mar					0	6

Table 17: The percentages of micropsheric mature form in relation to the total specimens in six seagrass blades at Site 1 (M %= percentage of micropsheric mature form in the population).

Dates	Experiment 1		Experiment 2		Experiment 3	
1990	M (%)	Total	M (%)	Total	M (%)	Total
09/Jan	0.69	144				
25/Jan	0.55	183	0	347		
08/Feb	0.42	241	1.43	211	0	237
23/Feb	0	70	0	70	0	61
09/Mar			0	79	0	67
25/Mar					0	19

Table 18: The percentages of micropsheric mature form in relation to the total specimens in six seagrass blades at Site 2 (M %= percentage of microspheric mature form in the population).

environmental factors and reproductive stages can influence the size of individuals, then regularly sampled specimens could be comprised of individuals with very different histories, even though there were sampled on the same dates. The environmental history of each individual in the sample would have to be considered before constructing the "age" distribution based on the size or diameter of specimens. Each individual could have experienced different environmental factors and fluctuations that depend on their "real age" . Further confusion could result if adult microspheric forms were treated as juveniles because of their smaller size.

The use of number of chambers is thus considered to be a better option in dealing with population dynamics and population growth rate investigations, because the number of chambers is a genuine reflection of individual growth and maybe "age".

In spite of considerable effort, I was unable to detect the individual growth rate of O.cf.venusta. The population growth rate study, however, provides some information on the population growth behaviour of this species, especially when the observations were based on the temporal patterns of the mean number of chambers.

In the previous investigation, Jepps (1956, in Boltovskoy and Wright, 1976) reported that in Elphidium the juveniles grew at the rate of two chambers per day initially, but decreased with time. Myers (1943, in Boltovskoy and Wright, 1976) reported that Tretomphalus

needs 42 days to reach its adult size of 13 to 17 chambers. In this study the "growth rate" of O.cf.venusta ranged from 0.58 to 0.99 chamber/month and, it seems too slow compare to those two species above. The most probable explanation of this is because this growth rate data was derived from population data of O.cf.venusta thus it might not represent the accurate individual growth rate of O.cf.venusta

The problem in following the pattern of modal progression for the number of chambers (the "age structure" of the population) is presumably because either the sampling dates were not always matched with the time of growing or because the sampling designs were not frequent enough to detect individuals that contribute to the pattern of the "age structure" in the population on the blades. In other words, the "age structure" of O.cf.venusta on the blades could either be the result of the growth of local individuals or the migration of individuals from other blades (as will be described in section 5.3).

It is also suspected that living epiphytically on the blades of the seagrass Halodule uninervis in the intertidal zone, could also contribute in shaping the "age structure" of O.cf.venusta. The abrupt changes of environmental conditions in the intertidal zone, in conjunction with the continuous disturbances by waves and currents are assumed to strongly influence the

survival and "length of attachment" of each individual on the seagrass blades.

The lack of recent information on the population growth rate of intertidal epiphytic foraminiferal species with respect to the rate of chamber addition, and the fact that no definite growth rate could be deduced from the present study, lead to some difficulties in answering the question of how fast does O.cf.venusta really grow ?

The results of this investigation also suggest that, there might be seasonal reproduction (asexual or sexual) in the O.cf.venusta population. Other foraminifera have been reported to reproduce seasonally, e.g. two to four times a year (Wefer, 1976; Zohary, 1980, in Reiss and Hottinger, 1984; and Sakai and Nishihara, 1981), or even eight to nine times a year (Murray, 1983).

In O.cf.venusta, microspheric mature forms flourished twice a year i.e. in summer and late winter. The high percentages of this form were followed by peaks in abundance of individuals (in January and July). In addition, it is also noted that, in summer O.cf.venusta individuals tend to have fewer chambers compared with the individuals that were found in winter. Thus, the O.cf.venusta population in summer (October to March) was probably comprised of young megalospheric individuals that were produced by their microspheric parents during the late winter in the previous year. These young

megalospheric individuals continue their growth and attained their adult stage in July when they reached their maximum number of chambers. Overall, the O.cf.venusta population reached the second peak of its abundance at this time. Thus, it can be speculated that the O.cf.venusta population during winter is dominated mostly by adult and mature megalospheric individuals.

Based on the above findings, it is believed that late winter is the most favourable time for microspheric form of O.cf.venusta to reproduce. However, the persistence of microspheric mature individuals as well as the fact that megalospheric juveniles were found in several separate months, indicate that, O.cf.venusta is also able to reproduce asexually at any time during the year.

Late winter is the time megalospheric individuals reach their adult stage and start to reproduce sexually, as the maximum number of chambers of the megalospheric form is attained in July (mid winter), and therefore, sexual reproduction might start to occur in late winter. However, this period is not the only time for the megalospheric individuals to reproduce. The percentage of the microspheric form was surprisingly low in summer, but persisted and bloomed in winter. This situation was presumably, either because the microspheric juveniles have a low capability of survival in summer or because there were megalospheric individuals that start to reproduce later and not in the late winter.

5.2. Recolonization study.

5.2.1. Introduction

McCall (1977), with reference to the infaunal soft bottom benthos, stated that disturbances, such as storms, that either increased sedimentation or caused destabilisation of substratum, can trigger the colonisation sequence process. He also mentioned that spatial differences in abundance could be the result of different stages of community recovery from a previous disaster. Ellison and Peck (1983) stated that by observing the pattern of succession of a community as it recovered from a disturbance, that the dynamics and stages can be followed.

Several workers have studied the effect of disturbance on the development of foraminiferal communities (Buzas, 1978; Ellison and Peck, 1983; Buzas,et.al, 1989). They concluded that the process of colonisation or recolonization was always initiated with pioneering species that grow and reproduce rapidly. Later when the resources were less abundant, the more biotically competent species became dominant. Ellison and Peck (1983) reported that the greatest number of species were found in the early stages of recolonization. They emphasised that experimentally produced disturbance will increase diversity by reducing competition. The less efficient species will initially

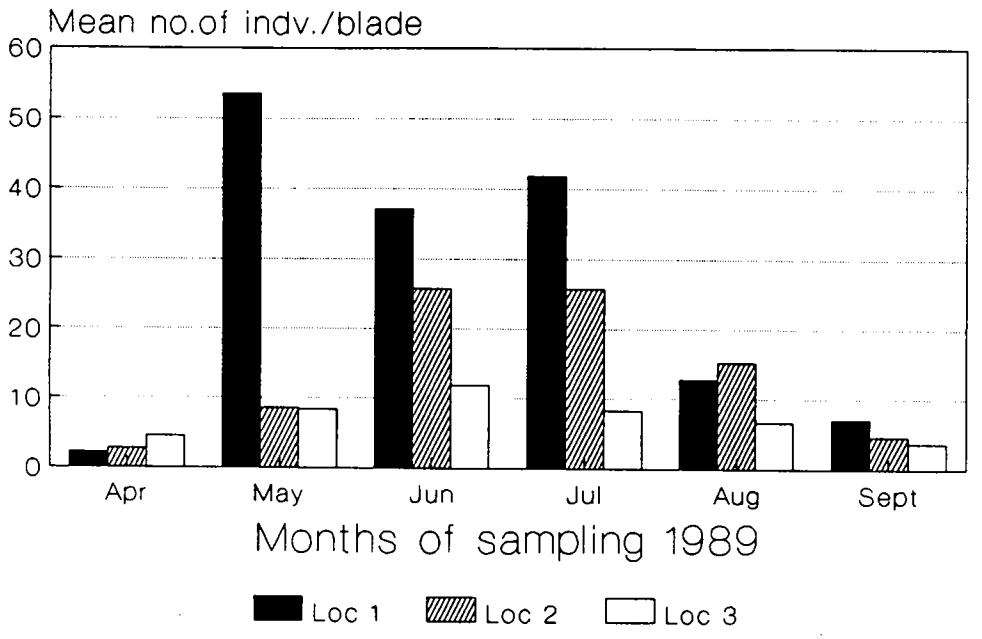
dominate the community. This domination will be challenged by the biotically more competent species and the diversity will decline if no further disturbance occurred.

Shelly Bay situated in the tropical area of North Queensland (± 9.5 kms northwest of Townsville Harbour), is typical of the north coast areas of Queensland, where cyclone induced waves or rainfall might be experienced at least once a year, with direct cyclone impact every 12 to 15 years.

The records of the monthly temporal study (see fig. 84 and Chapter III) show the need for a study of the effect of an abrupt disturbance on the population of O.cf.venusta. As shown in fig.84, the samples on April 1989 contained only a small number of O.cf.venusta. These samples were collected just one day after cyclone "Aivu" hit areas adjacent to Townsville. Based on this natural experience an artificial physical disturbance was set up by cleaning the H.uninervis blades of any foraminifera, and the process of recolonization and population redevelopment was monitored for 60 days.

Figure 84: Mean number of individuals per blade of the samples collected from Experiment 1 of the temporal distribution study (April 1989 to September 1989).

Loc. 1: Location 1
Loc. 2: Location 2
Loc. 3: Location 3.


Mean no.of indv./blade
60
50
40
30
20
10
0
Apr
May
Jun
Jul
Aug
Sept
Months of sampling 1989
Loc 1
Loc 2
Loc 3

5.2.2. Materials and methods

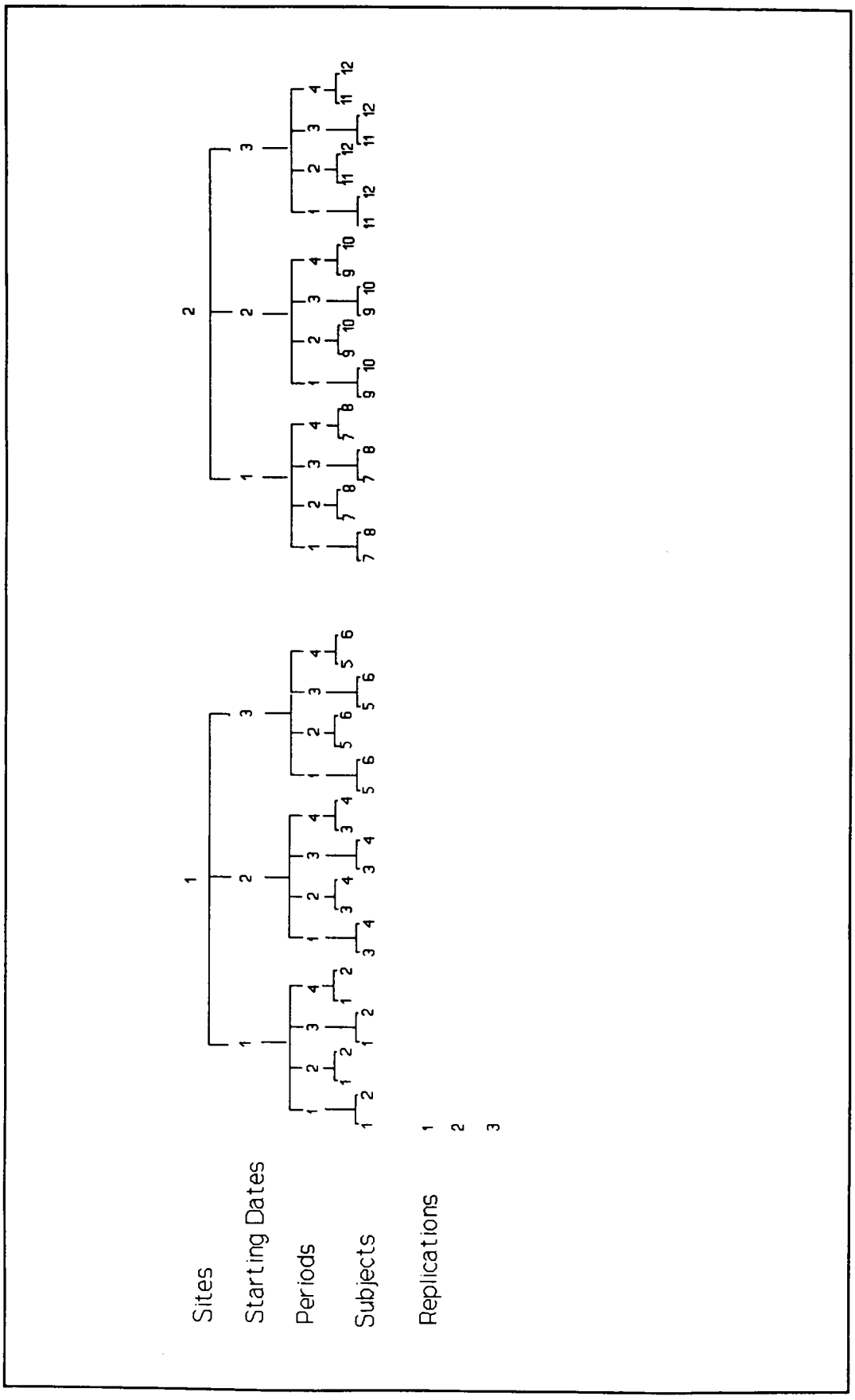
5.2.2.1. Field work

Living seagrasses with the sediment in which they live were transferred into plastic containers (11x16x5 cm^3). Whilst most of the work was done during the low tide, the used of plastic containers became necessary to manipulate the seagrass during the removal of foraminifera from the blades.

Three sets of experiments were conducted at three different times. The sampling design is presented in fig.85. Two study sites (150 metres apart) were set up in Shelly Bay. Site 1 was located near location 1 and site 2 was located near location 3 (see fig.2, Chapter III). In the beginning of each experiment, two plastic containers (with living "clean" seagrass) were placed in 5 cm deep holes dug on the natural sediment, at each study site. The sediment in the plastic containers was made level with the natural sediment surface. The plastic containers were then secured with galvanised mesh (2.5 x 2.5 cm) and iron bars.

Within each experiment, after a period of 15 days (P1), 30 days (P2), 45 days (P3), and 60 days (P4), five seagrass blades were picked haphazardly and placed in plastic vials filled with seawater for transporting to the laboratory.

Figure 85: Sampling design for the recolonization study.


Sites
Starting Dates
Periods
Subjects
Replications
1
2
3

5.2.2.2. Laboratory work

As soon as the field work was completed, the seawater was replaced with 70 % ethanol so the living O.cf.venusta were fixed in their natural position. Three blades were selected randomly, by using random numbers, and treated as replicate samples. The number of foraminifera was recorded by using a stereo microscope.

5.2.3. Results

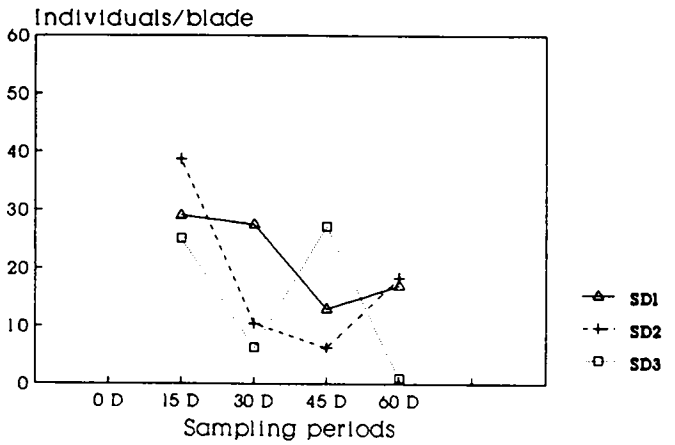
Figures 86 and 87 indicate that the "artificially cleaned" seagrass blades were already recolonized by O.cf.venusta after a 15 day period. The mean number of O.cf.venusta per blade in the first 15 days varied from 23.17 to 56.33 individuals depending on the site and experiment starting time .

The pattern of mean numbers of foraminifera for the three experiments showed a general decline in numbers after the initial 15 day period. If the three experiments are plotted in real time there is a suggestion of a background seasonal trend, with higher numbers in late January (see figs.88 and 89).

The test for sphericity of the data showed that the Mauchly's criterion = 0.93 and the Chisquare

Figure 86: Mean number of individuals per blade in Site 1 during 60 days study period.
0 D : starting day of experiment
15 D: 15 days period,
30 D: 30 days period,
45 D: 45 days period,
60 D: 60 days period.

Figure 87: Mean number of individuals per blade in Site 2 during 60 days study period.
0 D : starting day of experiment
15 D: 15 days period,
30 D: 30 days period,
45 D: 45 days period,
60 D: 60 days period.


Individuals/blade
60
50
40
30
20
10
0
0 D
15 D
30 D
45 D
60 D
Sampling periods
SD1
SD2
SD3

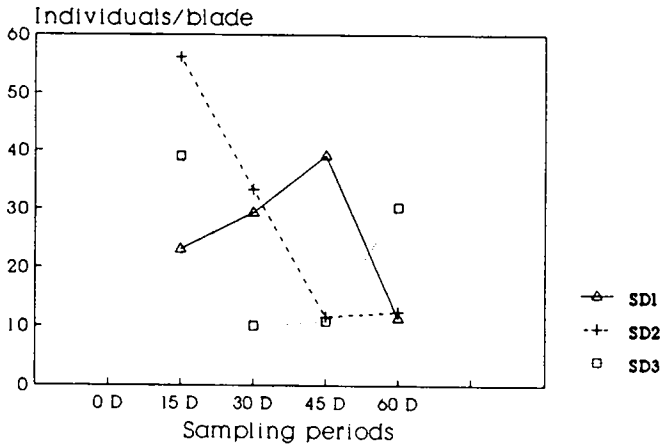
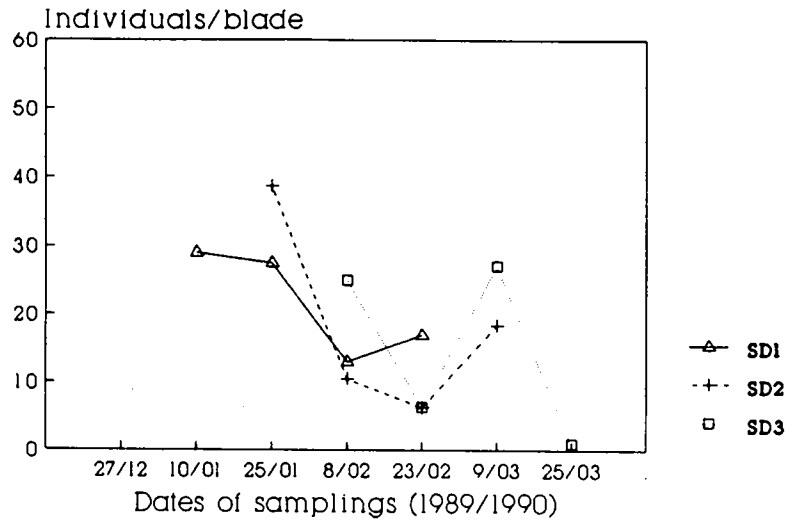
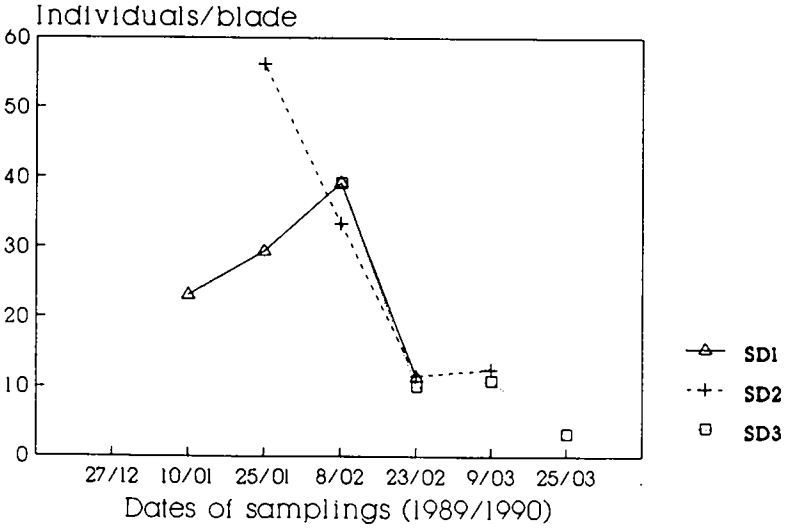

Individuals/blade
60
50
40
30
20
10
0
0 D
15 D
30 D
45 D
60 D
Sampling periods
SD1
SD2
SD3

Figure 88: Temporal mean number of individuals per blade in Site 1.
SD 1: Experiment 1, started on 27/12/1989,
SD 2: Experiment 2, started on 10/01/1990,
SD 3: Experiment 3, started on 25/01/1990.

Figure 89: Temporal mean number of individuals per blade in Site 2.
SD 1: Experiment 1, started on 27/12/1989,
SD 2: Experiment 2, started on 10/01/1990,
SD 3: Experiment 3, started on 25/01/1990.


Individuals/blade
60
50
40
30
20
10
0
27/12 10/01 25/01 8/02 23/02 9/03 25/03
Dates of samplings (1989/1990)
SD1
SD2
SD3


Individuals/blade
60
50
40
30
20
10
0
27/12 10/01 25/01 8/02 23/02 9/03 25/03
Dates of samplings (1989/1990)
SD1
SD2
SD3

approximation = 1.53 . Consequently, the test of the Null hypothesis in the analysis of variance was carried out by employing "The Univariate test approach" rather than "Multivariate approach" (Dea'th, 1991 pers. comm; SAS, 1987). The Anova (see table 19) indicated that there was a significance difference ($p<0.05$) between the two sites (150 metres apart in Shelly Bay). The experiment starting dates and the subsequent periods showed foraminiferal numbers that were significantly different. The interaction of the experiment starting dates with period was also significant ($p<0.05$). There was no significant difference among Period 1's (Period 1 experiment 1, Period 1 experiment 2 and Period 1 experiment 3) in the two different sites. There were, however, strong significant differences among other periods .

The Orthogonal Polynomial Contrast Analysis that was employed to test the trend of the mean number of O.cf.venusta on the blades during the 60 days of experiment showed that there was significant ($p<0.01$) support for a linear trend with periods (see table 20).

5.2.4 Discussion

Ellison and Peck (1982) in their recolonization study reported that foraminifera reached peak densities

between 10 and 43 weeks. According to Buzas (1978) foraminifera are able to grow exponentially on experimentally disturbed areas. The present study shows that O.cf.venusta recolonized very quickly (< 15 days). In the first 15 day period the "empty" H.uninervis blades seemed to be recolonized at the same rate (there was no evidence of a significant difference among Period 1's as shown in table 21). However, there is a strong suggestion of a different mean number of individuals of O.cf.venusta among Period 2's(30 days period), Period 3's (45 days period) and Period 4's (60 days period). Since the experiments were started at different dates, significant differences for the comparison among Period 2's, Period 3's and Period 4's indicate the possible existence of a biweekly and may be tidally driven seasonality pattern of the mean O.cf.venusta number on the blades. Such a hypothesis might be supported by the results from the repeated measurements anova (see table 19) that shows the significant effect of the interaction between experiment starting date and periods on the mean number of O.cf.venusta per blade. According to Buzas (1969, 1978, 1982) foraminifera always demonstrate seasonal periodicity . It is indicated in this work that, even though the mean number of O.cf.venusta at the early stage of recolonization (Period 1's) was the

Source	df	MS	F	P
Between group				
Sites (SI)	1	1.0341	14.32	0.0091 **
St.Date(SD)	2	1.2931	17.91	0.0030 **
SIxSD	2	1.7916E-01	2.48	0.1640
Subject (sub) subxSIxSD	6	7.2207E-02		
Within group				
Period (P)	3	2.0565	8.75	0.0009 **
SDxP	6	1.0592	4.51	0.0059 **
SIxP	3	5.6802E-02	0.24	0.8662
SIxSDxP	6	4.2387E-01	1.80	0.1551
SIxSDxPxsub	18	2.3509E-01		
SIxSDxPxsubxrep	96	1.3468E-01		

Table 19: Result of the ANOVA testing the effect of Sites, Starting Dates of experiment and Periods of sampling on the number of individual per blade (df= degree of freedom; MS= Mean Square; F= ratio of variances; P= probability of having Fisher's sampling distribution).

Degree	SS	F	P
1	5.6426	24.00	0.0001 **
2	4.4306E-02	0.19	0.6694
3	4.8257E-01	2.05	0.1691

Table 20: Polynomial Contrast for testing the trends of mean number of individuals during the Periods of sampling.

Degree 1 = linear trend (** highly significant)
2 = quadratic trend (non significant)
3 = cubic trend (non significant).

Source	df	MS	F ratio		F (2,6;0.05)
among P1's (Site 1)	2	1.3488E-01	1.8678	ns	5.1433
among P 1's (Site 2)	2	3.0911E-01	4.2807	ns	5.1433
among P 2's (Site 1)	2	6.9108E-01	9.5704		5.1433
among P 2's (Site 2)	2	8.8787E-01	12.2956		5.1433
among P 3's (Site 1)	2	1.2005	16.6252		5.1433
among P 3's (Site 2)	2	7.2269E-01	10.008		5.1433
among P 4's (Site 1)	2	1.4073	19.4889		5.1433
among P 4's (Site 2)	2	5.6785E-01	7.8638		5.1433
error term	6	7.2207E-02			

Table 21: Summary of the Anova testing the different among Periods at different experiment Starting dates.

Note.

The MS values were originally calculated at each Period for each Sites by using an ANOVA model of

Y = u + SD + Sub(SD) + Residuals.

with Y = number of individuals per blade
SD = Starting Dates of the experiments
Sub = The subject (containers) that were sampled repeatedly

The ANOVA table is :

Source of variance	df	MS
SD	2	
Sub (SD)	2	
SD x Sub x Rep	4	

The MS value of the SD factor drawn from this calculation was then treated as source of variances among Periods and was devided by the MS value of the error term of the "Between group" at table 19 that is 7.2207E-02 to create the F ratio value (De'ath, 1991 pers.comm). This F ratio were then compared with the F distribution table at the df of 2 and 6 with 0.05 level of significance.

same, the population developed to a significantly different mean number of individuals per blade in the following periods. This study also suggests that instead of following the common foraminiferal exponential growth model as reported by Buzas (1978) and Ellison and Peck (1983), O.cf.venusta individuals number decreased rapidly after the early stage of recolonization.

Because the average area of the seagrass blades were more or less the same, the density of O.cf.venusta is strongly expected to follow the same patterns as the number of individuals. This, also suggests that the rapid decrease of O.cf.venusta population is most likely not driven by the finite carrying capacity of the blades or the intraspecific competition for space.

By living epiphytically on the blades of the intertidal seagrass H.uninervis, O.cf.venusta populations could became a target of continuous disturbance by waves, diurnal tidal exposure or predators. These continuous disturbances, might contribute to the pattern of population decline found during the study time. The relationship between number of O.cf.venusta and environment parameters could be the subject of a more intensive study in the future.

5.3. The role of movements and migration in shaping the population of O.cf.venusta on the blades of Halodule uninervis.

5.3.1.Introduction.

Bock (1969) stated that some selected benthic foraminifera were dispersed by means of floating seagrass blades (broken or dead blades) and carried for a long distance by currents. In that way some species could become cosmopolitan.

In his work on Cibicides lobatulus, Rosalina floridana and Spirillina vivipara, Walker (1976) recognised the pattern of migration of microspheric juveniles. He discovered that only microspheric individuals can be found in the intertidal zone and suggested that sexual reproduction probably occurred in the deeper water, and microspheric juveniles then migrated to the intertidal zone with the help of tides.

The migration issues addressed by both Bock (1968) and Walker (1976) gave some idea of the passive dispersal of both epiphytic and benthic foraminifera. Kitazato (1988) showed clearly that some benthic foraminifera could actively move in or on the bottom sediment. He studied 22 species of coastal benthic foraminifera and reported that the average velocity of those species ranged from 8.0 to 82.3 um/minute or 11 to 118 mm/day. He also showed that Pseudorotalia gaimardii

formed a conical cavity in the sediment filled with bundles of pseudopodia in front of the test in order to move "forward". The term "forward" here referred to the direction of the aperture position of the test. Kitazato (1988) pointed out that the position of the aperture was highly correlated with the direction of movement, especially for species that move in the sediment. Individuals that move on the sediment surface, according to Kitazato (1988) move in any direction and not related to the position of the aperture.

Weinberg (1991) in his study of the rate of movement of deep-sea soft bottom foraminifera Laticarinina pauperata from the northwest Atlantic, found that the average velocity was 12-16 mm/day on the sediment surface, and 5 mm/day below the surface. He concluded that, compared with the coastal species studied by Kitazato (1988), L.pauperta move as slow as the slowest rate of movement of the coastal foraminiferal species.

As pointed out in the previous section (section 5.2) O.cf. venusta seems to have a high capability of recolonizing disturbed (cleaned) seagrass blades in less than 15 days. In addition, as mentioned in section 5.1, the variation in the number of chambers of the individuals that recolonized the blades and their frequency distributions may reflect the probability of individual migration from one blade to the other.

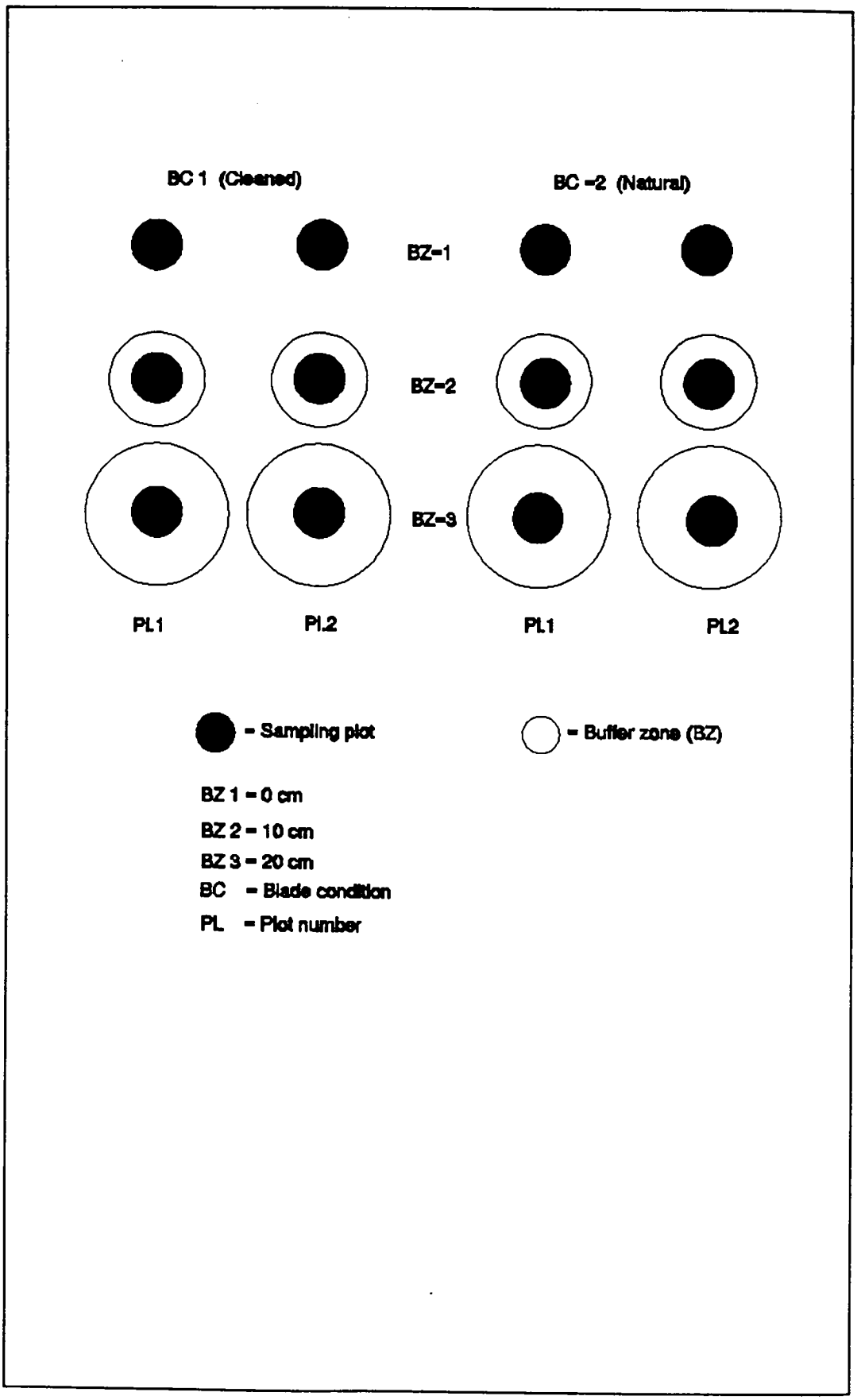
To investigate the possibility of Q.cf.venusta migration, two different experiments were carried out, one in the field, and the other one in the laboratory. The field investigation was designed to detect the migration of Q.cf.venusta from blade to blade and the second was carried out to observe movements of individual foraminifera on seagrass blades.

5.3.2. Materials and Methods.

5.3.2.1. Field investigation.

An experimental site was set up in a location near to site 1 of the recolonization study. Two blade conditions were established i.e. cleaned blades and natural blades. The cleaned blades were hand scraped free of any foraminifera one day prior to the sampling time and the natural blades were left in an untouched condition. For each blade condition three buffer zones of 0 cm , 10 cm and 20 cm radius were set up by removing or destroying the seagrass adjacent and outside the sampling plots. There were 2 circular sampling plots of 20 cm diameter in every buffer zone and for each blade condition. Figure 90 shows the diagram of the sampling design.

Figure 90: Field experimental design for studying the effect of blade conditions and space barrier on the epiphytic foraminiferal population.


BC 1 (Cleaned)
BC -2 (Natural)
BZ-1
BZ-2
BZ-3
PL1
PL2
PL1
PL2
= Sampling plot
= Buffer zone (BZ)
BZ 1 = 0 cm
BZ 2 = 10 cm
BZ 3 = 20 cm
BC = Blade condition
PL = Plot number

Five seagrass blades were picked randomly from each plot every day for five days periods in August (1990) and for four days in September (1990). The one day difference in September sampling was because at day 5, the tide was too high (> 0.5 m) and therefore no seagrass samples could be collected.

Each seagrass blade was put in a plastic vial filled with seawater and transferred to the laboratory. In addition, during August study period, a 4x4x1 cm^3 surface sediment sample was scrapped daily from each sampling plot to determine the abundance of living O.cf.venusta on the sediment.

5.3.2.2. Laboratory work.

Seagrass blade samples and sediment samples were fixed and stored in 70 % ethanol, to await further observation.

After at least 2 days in the 70 % ethanol the sediments were sieved through a 64 micron sieve, oven dried and subsampled by using a microsplitter. The subsampled sediment (± 1 gram/plot) was then observed under a stereo microscope and the number of "live" and dead O.cf.venusta were recorded. The ratio of the number of living to dead O.cf.venusta was calculated.

Three of the five seagrass blades were selected at random from each plot sample by using a random number

generated by a hand calculator, and the number of O.cf.venusta per blade was recorded

5.3.2.3. Data analysis.

A three way repeated measurements analysis of variance was performed (Winer, 1974). A repeated measurement analysis was used as each seagrass blade at each sampling plot had the same initial blade condition (natural or cleaned). The five replicate blades taken from the same plot, therefore, were not completely independent at each other. De'ath (pers.comm) and Mapstone (pers comm) suggested that the use of repeated measurement analysis was appropriate in dealing with such replicates. There is, however, one main requirement that should be satisfied in order to use the less complicated analysis such as the univariate analysis of variance. This requirement is the equality of covariances, that can be tested by employing the sphericity test (Winer, 1971; SAS/STAT Guide, 1987).

To use the repeated measurements analysis of variance, the sampling plots were treated as the Subjects, that were repeatedly sampled over five days periods in August and for four days periods in September. The sampling design is presented in figure 91 and the Null hypothesis are showed in table 22 and 23.

Polynomial contrasts test (Zar, 1984; Winer, 1974; Rowell and Walters, 1976; Statistix 3.5 User Manual,

1991), were used to recognise the trend of the average number of individuals on the blades trough time.

5.3.2.4. Laboratory investigations.

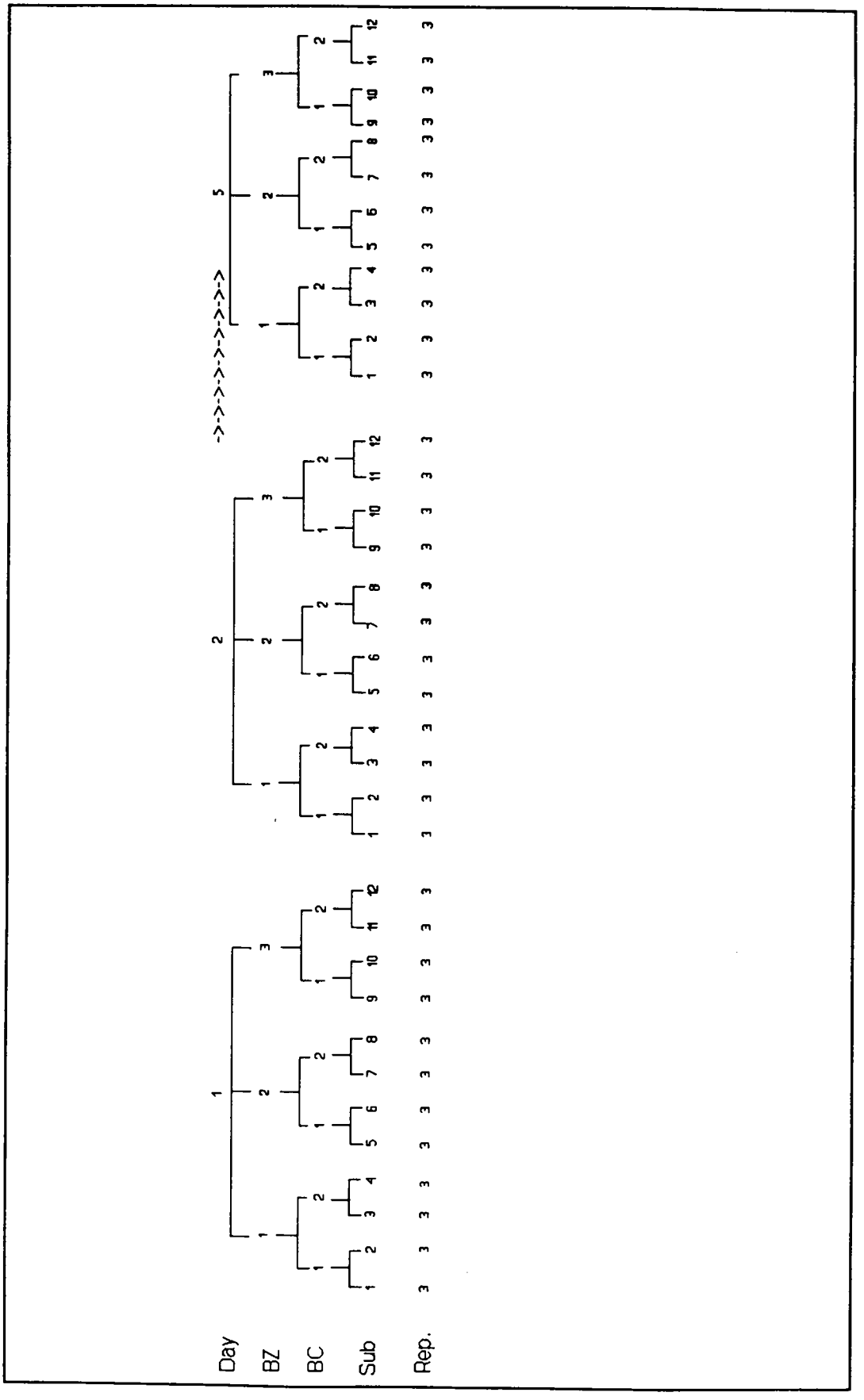
Samples of living seagrass, with the sediments they lived on, were taken from their natural habitat and transplant into 4 plastic containers (11x16x5 cm^3). The surface of the sediment was made level with the hight of the container. These containers were then kept in an aquarium with flowing seawater. These samples were used for observation and video recording.

Prior to the video recording time, one plastic container with the living seagrass in it was submerged into a slightly bigger plastic container filled with seawater ($\pm$ 1 cm above the sediment). The seagrass blade and individuals O.cf.venusta were recorded using a JVC CCD colour video camera mounted on microscope.

The seagrass blade was positioned so that it was on the top of a white head pin, used as a contrast background, so that the O.cf.venusta was in the centre of the field of observation with its dorsal or ventral side facing the camera.

A combination of a National Time Lapse video cassette recorder series AG 6010, and a fibre optic light source, were used to record the behaviour and

Figure 91: Sampling design for studying the effect of blade conditions and space barrier on the number of Q.cf.venusta in August 1990.


Day
BZ
BC
Sub
Rep.

Source	DF	MS	F	P
Between Subjects				
BZ	2	1.4159	5.02	> 0.05
BC	1	1.0426	3.70	> 0.05
BZ x BC	2	8.2326E-01	2.92	> 0.05
Subject (S) BZ x BC x S	6	2.8200E-01		
Within Subjects				
Day (D)	4	2.2509E-01	3.00	< 0.05 *
BZ x D	8	1.1789E-01	1.57	> 0.05
BC x D	4	1.4068E-01	1.87	> 0.05
BZ x BC x D	8	9.8582E-02	1.31	> 0.05
BZ x BC x S x D	24	7.5109E-02		
Replication (Rep) BZxBCxSxDxRep	120	7.2163E-02		

Table 22: Result of the ANOVA on the daily O.cf.venusta mean abundance in August 1990, testing the Null Hypothesis :

Ho_1: There is no significant difference among Buffer zones (BZ)

Ho_2: There is no significant difference between Blade conditions (BC)

Ho_3: There is no interaction effect between Buffer Zone and Blade conditions

Ho_4: There is no significant difference among Days

Ho_5: There is no interaction effect between Buffer Zones and Days

Ho_6: There is no interaction effect between Blade conditions and Days

Ho_7: There is no interaction effect among Buffer Zones, Blade conditions and Days

Ho_8: There is no interaction effect among Buffer Zones, Blade conditions, Days, and Subjects (sampling plots)

Data were transformed to Log (x + 1)

* : significant .

Source	DF	MS	F	P
Between Subjects				
BZ	2	2.8623E-01	4.57	> 0.05
BC	1	3.6479E-01	5.82	> 0.05
BZ x BC	2	1.7865E-01	2.85	> 0.05
Subject (S) BZ x BC x S	6	6.2688E-02		
Within Subjects				
Day (D)	3	2.8606E-01	8.6	< 0.05 *
BZ x D	6	4.2980E-02	1.29	> 0.05
BC x D	3	2.8884E-02	0.87	> 0.05
BZ x BC x D	6	3.7856E-02	1.14	> 0.05
BZ x BC x S x D	18	3.3252E-02		
Replication (Rep) BZxBCxSxDxRep	96	5.7202E-02		

Table 23: Result of the ANOVA on the daily O.cf.venusta mean abundance in September 1990, testing the Null Hypothesis :

Ho_1: There is no significant difference among Buffer zones (BZ)

Ho_2: There is no significant difference between Blade conditions (BC)

Ho_3: There is no interaction effect between Buffer Zone and Blade conditions

Ho_4: There is no significant difference among Days

Ho_5: There is no interaction effect between Buffer Zones and Days

Ho_6: There is no interaction effect between Blade conditions and Days

Ho_7: There is no interaction effect among Buffer Zones, Blade conditions and Days

Ho_8: There is no interaction effect among Buffer Zones, Blade conditions, Days, and Subjects (sampling plots)

Data were transformed to Log (x + 1)
* : significant

movements of O.cf.venusta for a three day period.

5.3.3. Results

5.3.3.1. Field investigations.

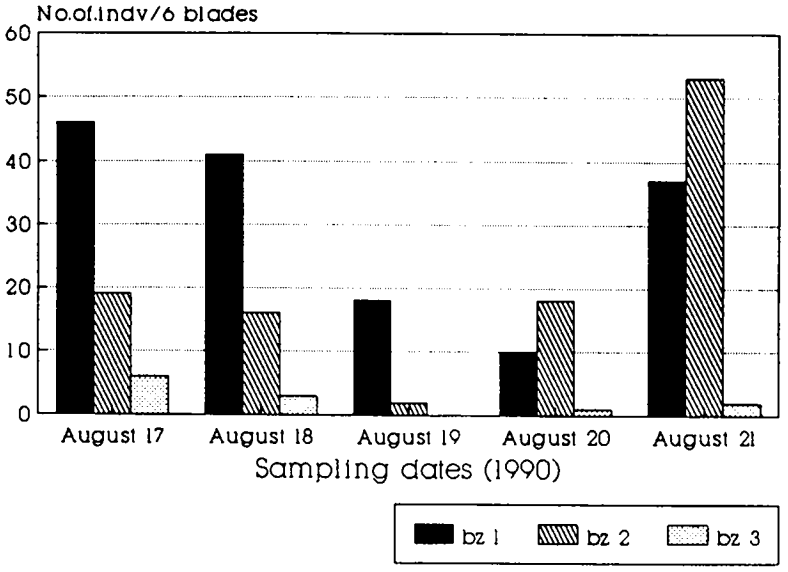
In the course of investigation it was revealed that O.cf.venusta needed less than one day to recolonize "cleaned" seagrass blades. In order to observe the general pattern of the number of individuals per blade, data from plot 1 and plot 2 were pooled. This revealed that the daily number of individuals on the "cleaned blades " (Blade condition 1) ranged from 0 to 2.5 in August, and from 0.166 to 1.17 per blade in September 1990 . During this time the daily number of individuals on the "natural blades" (Blade condition 2) ranged from 0 to 8.83 in August and from 0.16 to 3.83 in September.

Figures 92 to 95 show that, in general, the number of individuals per blade on the cleaned blade seagrass appears to be slightly lower than their natural blade counterparts.

The number of individuals O.cf.venusta found in the sediment is presented in figures 96 and 98. The percentages of live individuals in the sediments are shown in figures 97 and 99.

Figure 92: Daily number of individuals of O.cf.venusta per six "natural" seagrass blades in August 1990.
bz 1: buffer zone 1 or 0 cm,
bz 2: buffer zone 2 or 10 cm,
bz 3: buffer zone 3 or 20 cm.

Figure 93: Daily number of individuals of O.cf.venusta per six "cleaned" seagrass blades in August 1990.
bz 1: buffer zone 1 or 0 cm,
bz 2: buffer zone 2 or 10 cm,
bz 3: buffer zone 3 or 20 cm.


No.of.indv/6 blades
60
50
40
30
20
10
0
August 17
August 18
August 19
August 20
August 21
Sampling dates (1990)
bz 1
bz 2
bz 3

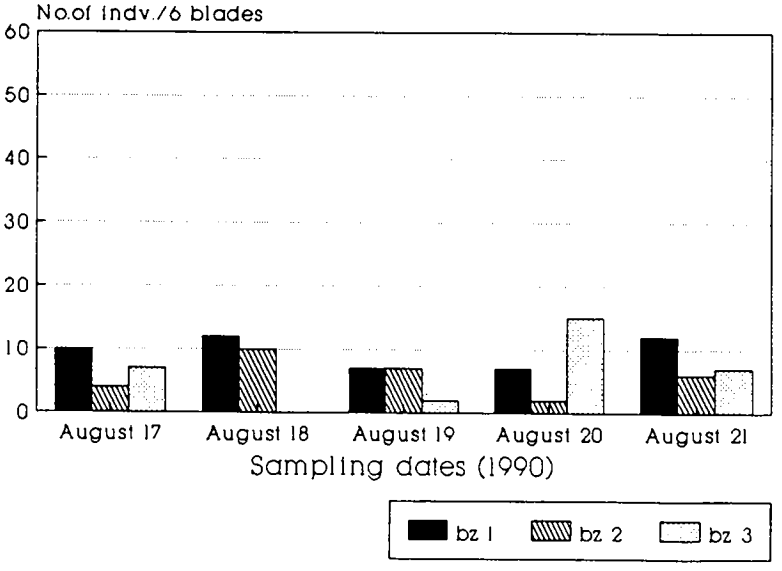
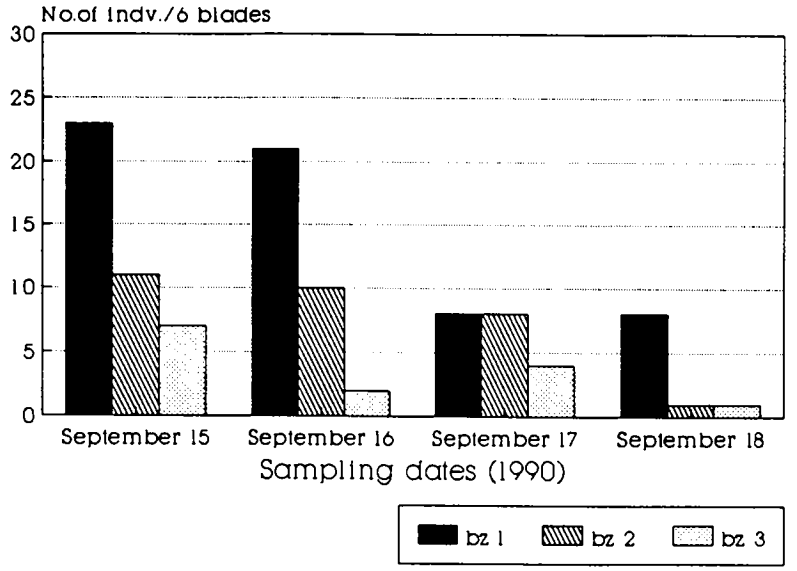

No.of indv./6 blades
60
50
40
30
20
10
0
August 17
August 18
August 19
August 20
August 21
Sampling dates (1990)
bz 1
bz 2
bz 3

Figure 94: Daily number of individuals of O.cf.venusta per six "natural" seagrass blades in September 1990.
bz 1: buffer zone 1 or 0 cm,
bz 2: buffer zone 2 or 10 cm,
bz 3: buffer zone 3 or 20 cm.

Figure 95: Daily number of individuals of O.cf.venusta per six "cleaned" seagrass blades in September 1990.
bz 1: buffer zone 1 or 0 cm,
bz 2: buffer zone 2 or 10 cm,
bz 3: buffer zone 3 or 20 cm.


No.of Indv./6 blades
30
25
20
15
10
5
0
September 15
September 16
September 17
September 18
Sampling dates (1990)
bz 1
bz 2
bz 3

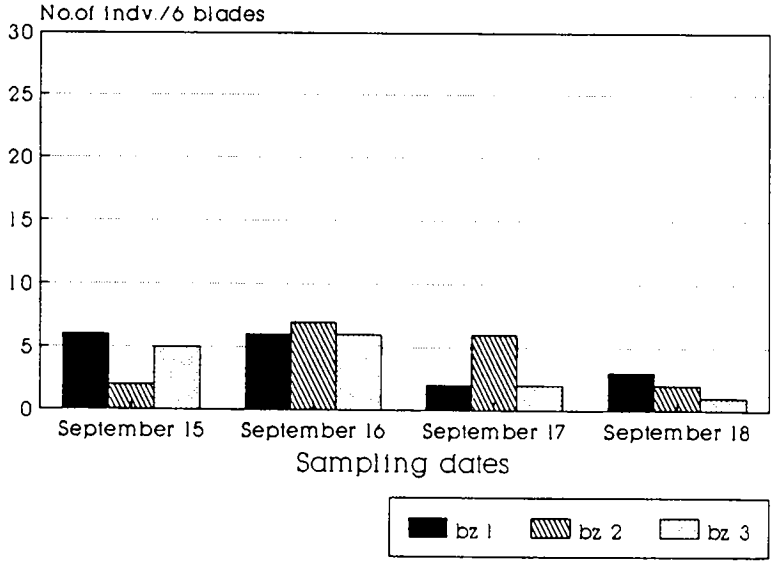
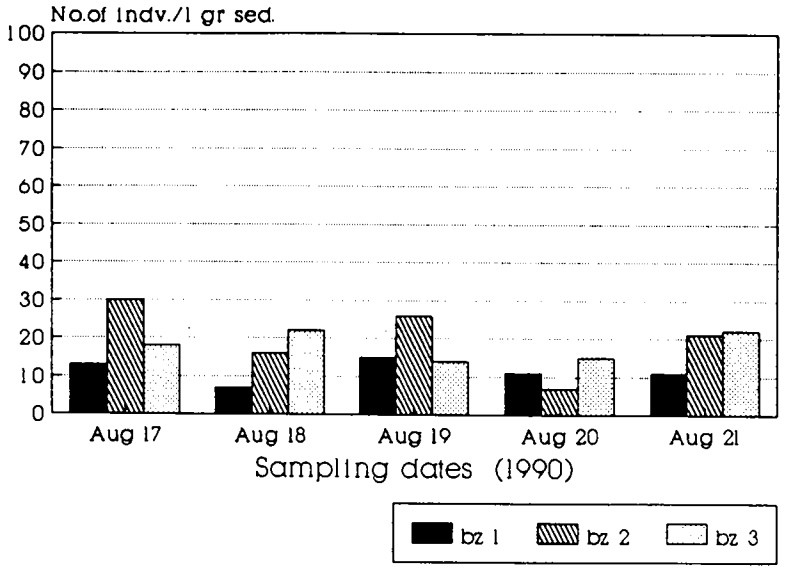

No.of Indv./6 blades
30
25
20
15
10
5
0
September 15
September 16
September 17
September 18
Sampling dates
bz 1
bz 2
bz 3

Figure 96: Daily number of individuals of Q.cf.venusta per one gram of sediment beneath the "natural" seagrass blades condition, in August 1990.
bz 1: buffer zone 1 or 0 cm,
bz 2: buffer zone 2 or 10 cm,
bz 3: buffer zone 3 or 20 cm.

Figure 97: Daily number of live Q.cf.venusta per one gram of sediment beneath the "natural" seagrass blades condition, in August 1990.
bz 1: buffer zone 1 or 0 cm,
bz 2: buffer zone 2 or 10 cm,
bz 3: buffer zone 3 or 20 cm.


No.of Indv./1 gr sed.
100
90
80
70
60
50
40
30
20
10
0
Aug 17
Aug 18
Aug 19
Aug 20
Aug 21
Sampling dates (1990)
bz 1
bz 2
bz 3

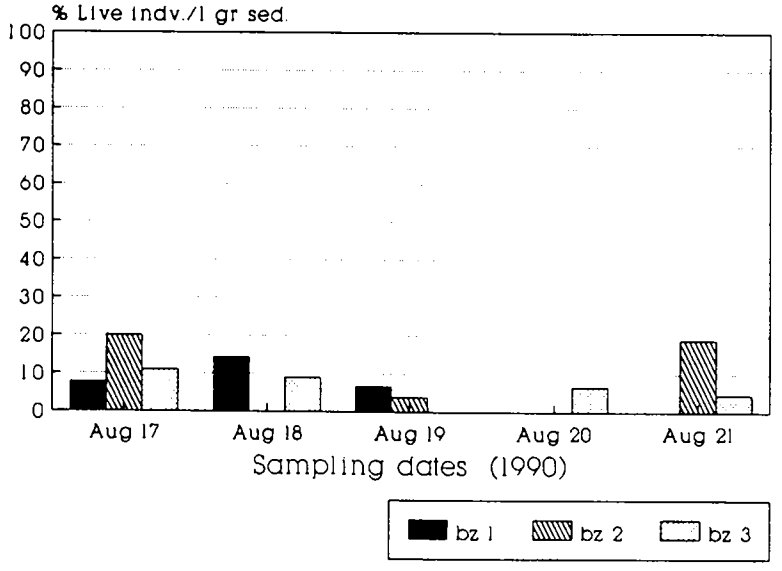
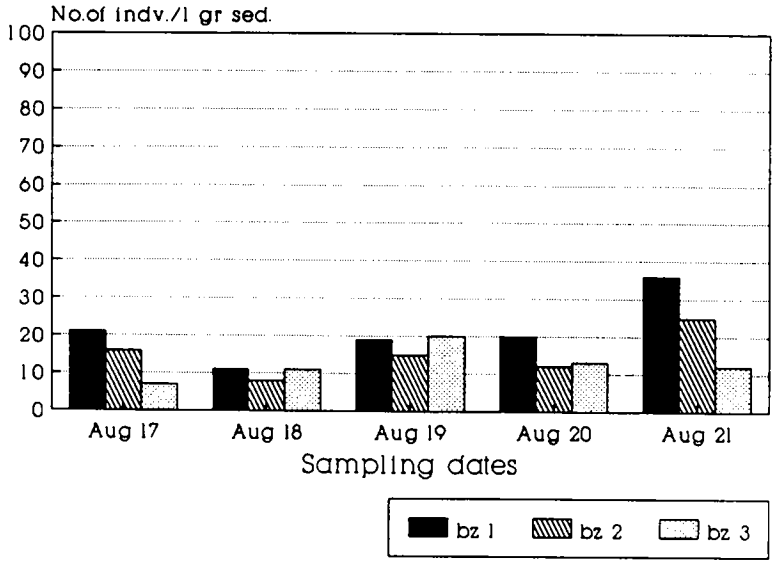
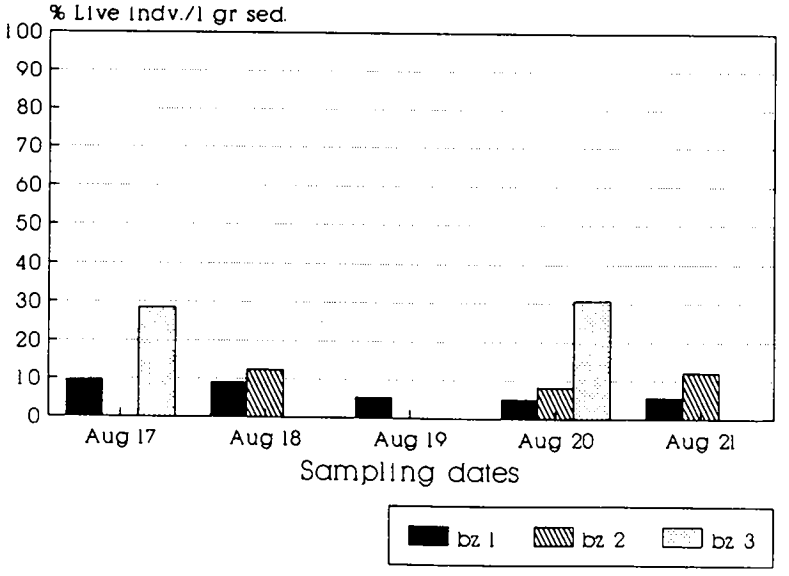

% Live Indv./1 gr sed.
100
90
80
70
60
50
40
30
20
10
0
Aug 17
Aug 18
Aug 19
Aug 20
Aug 21
Sampling dates (1990)
bz 1
bz 2
bz 3

Figure 98: Daily number of individuals of Q.cf.venusta per one gram of sediment beneath the "cleaned" seagrass blades condition, in August 1990.
bz 1: buffer zone 1 or 0 cm,
bz 2: buffer zone 2 or 10 cm,
bz 3: buffer zone 3 or 20 cm.

Figure 99: Daily number of live individuals of Q.cf.venusta per one gram of sediment beneath the "cleaned" seagrass blades condition, in August 1990.
bz 1: buffer zone 1 or 0 cm,
bz 2: buffer zone 2 or 10 cm,
bz 3: buffer zone 3 or 20 cm.


No.of indv./1 gr sed.
100
90
80
70
60
50
40
30
20
10
0
Aug 17
Aug 18
Aug 19
Aug 20
Aug 21
Sampling dates
bz 1
bz 2
bz 3


% Live indv./1 gr sed.
100
90
80
70
60
50
40
30
20
10
0
Aug 17
Aug 18
Aug 19
Aug 20
Aug 21
Sampling dates
bz 1
bz 2
bz 3

The test for sphericity on the data of the number of individuals on the blades in August and September gave the Mauchly's criterion of 0.836 ($p>0.05$) and 0.777 ($p>0.05$) respectively. The equality of covariances requirements over days was satisfied and, therefore the univariate repeated measurements analysis of variance could be used.

The analysis of variance for both sampling months (August and September) as presented in tables 22 and 23 show that there were no significant differences in number of individuals between "Blade conditions" and among "Buffer zones". The latter tables also show that the "Day" factor contributed significantly in influencing the average number of individuals on the blades.

The polynomial contrasts test on the August data, to recognise the trend of the number of individuals on the blades during the five day sampling period of observations strongly suggested the existence of a quadratic trend with Day factor (see table 24).
The same test applied on the September data showed a significant support for linear trend with Day factor (see table 25).

Degree	SS	F	P
1	1.8603E-02	0.25	0.6232
2	5.9967E-01	7.98**	0.0094
3	2.1087E-01	2.81	0.1068
4	7.1217E-02	0.95	0.3399

Table 24: Result of polynomial contrast of mean abundance of O.cf.venusta by Day in August 1990.

** = highly significant

Degree 1 = linear trend.
Degree 2 = quadratic trend.
Degree 3 = cubic trend.
Degree 4 = quartic trend.

Degree	SS	F	P
1	7.4738E-01	22.48 **	0.0002
2	9.2334E-02	2.78	0.1129
3	1.8467E-02	0.56	0.4658

Table 25: Result of polynomial contrast of mean abundance of O.cf.venusta by Day in September 1990.

** = highly significant

Degree 1 = linear trend.
Degree 2 = quadratic trend.
Degree 3 = cubic trend.

5.3.3.2. Laboratory video investigation

The investigation of the behaviour of individuals O.cf.venusta in the laboratory was carried out during the period May to July 1990. Most of the time, however, the results were very discouraging because the individuals could not be observed clearly, or detached themselves from the blades before any observation of movements could be made.

Some individual movements were recorded on the 29th and 30th of May and on the 29th and 30th of July, 1990.

It was observed that, in relation to their substratum (seagrass blades), the individual was always found attached either in a standing or clinging position, and positioned on the periphery of the last five or six chambers.

O.cf.venusta was observed to move along the edge and across the seagrass blade. It moved over small distances ranging from 0.83 mm to 3.24 mm, at a speed of 0.17 mm/min (with ± 0.08 mm standard deviation) either in same direction or opposite direction to the aperture. Besides its movements along and across the seagrass leaf, the individual was also seen to move off and onto the leaf. In addition, it was clearly noted that individuals O.cf.venusta tend to have a long period of quiescence in their clinging position.

Two individuals were seen to approach each other and made aperture contact. There were four aperture contacts made during the 7 hours and 42 minutes recording period,

recording period, lasting for about seven minutes to 2 hours and 39 minutes. Among these aperture contact periods there were periods of individuals separation, that ranged from six to twenty minutes.

A snail was observed to graze on the seagrass blade and dislodge the foraminifera from the blade.

5.3.4. Discussion.

The body of the results confirms the hypothesis that Q.cf.venusta does not live permanently on the blades of the seagrass H.uninervis. However, only a small proportion of the Q.cf.venusta population found on the sediment consisted of live specimens. This shows that Q.cf.venusta is mainly epiphytic on the seagrass blades. Some of the live specimens found on the sediments may have been dislodged during blade cleaning. It is also strongly possible that other factors such as snails that graze on the seagrass blades and water motions are responsible in contributing the number of live Q.cf.venusta on the sediments.

The video observations highlighted the capability of Q.cf.venusta to move along and across seagrass blades as well as move off and onto the blades. This suggests that Q.cf.venusta can actually move on a substratum other than the seagrass blades, as its living habitat. It is, therefore, believed that the live specimens on

the sediments are probably temporary sediment residents, still on their way to find a new blade to be colonized.

The average number of individuals on a blade was not significantly influenced by the initial condition of the blade (i.e. cleaned or natural). This indicates the rapid colonisation of the seagrass blades by Q.cf.venusta and that these colonizations are not solely by juveniles.

The three different buffer zones (0 cm, 10 cm and 20 cm) did not significantly affect the average number of individuals on the blades. This supports the finding that there is active movement of Q.cf.venusta across the sediment surface to colonize the blades.

Based on the above findings, it can be speculated that the populations of Q.cf.venusta on the seagrass blades change through time. The individuals that live on the blade can either move freely on the same blade, or move temporarily to the sediment to move to other blades.

The observations that Q.cf.venusta can move at the rate of 0.17 $\pm$ 0.08 mm per minute in the laboratory in still water could also explain why the 10 or 20 cm space barrier did not present a barrier to colonisation. If the individuals that colonized the blade originated from the seagrass blades outside the 20 cm buffer zone they would only need 13 hours and 20 minutes to reach the blades inside the plots. This neglects the effect of

water motion which may considerably aid foraminiferal movements.

The rate of movements of O.cf.venusta appears to be much higher than the rate of movement of benthic species observed by Kitazato (1988) and Weinberg (1991).

Kitazato (1988) reported that the apertural position and orientation was highly correlated with the direction of movements on the species, especially the ones that move in the sediment. He observed that when the specimens move on the sediment surface, their movements did not correlate with the position of the aperture. The present study suggests that, even though O.cf.venusta moves on a substratum, the direction of its movement is dictated by the apertural position

Plastogamy has been observed in several foraminifera (Boltovskoy and Wright, 1976). It was defined by Lipps and Erskian (1969) as " two (or rarely more) individuals join together by their apertural sides to mutually exchange gametes". They reported that, in Glabratella ornatissima (Cushman), individuals that undergo plastogamy formed a joining monolamellar membrane, less than 1 u thick. A large brood chamber was then constructed by the two or more adult individuals that joined together. The brood chamber was built by dissolving their apertural sides and internal septa.

This study observed two individuals that made several apertural contacts. These contacts did not occur over a regular time interval and the length of the

contact period also varied. The video observations in this study could not show clearly whether the apertural contacts made by O.cf.venusta were actually a sign of plastogamy or if it was only a situation in which two O.cf.venusta happened to come across one another. The fact that the two individuals moved away from one another after they met, supports the idea that there was no evidence of intraspecific competition for space in the O.cf.venusta population as has already mentioned in section 5.2.4. Further study needs to be undertaken to clarify this phenomenon.

Chapter VI

Concluding Discussion.

The body of the present study points out the characteristics of the epiphytic foraminifera, Osangularia cf.venusta. This species, that lives by clinging on the blades of the intertidal seagrass Halodule uninervis shows remarkably survival capabilities in coping with the harsh intertidal environment.

Apart from being a target of continuous physical disturbances caused by tides and waves as well as biological disturbance such as grazing snails, O.cf.venusta was observed to be able to survive, colonize and quickly recolonize the seagrass blades during the study period.

The test structure of O.cf.venusta, which has a thick wall and highly dense formation of pustules on the exterior surface, suggests that its function is to protect the individual and the juveniles from the abrupt environmental changes, water movements and abrasion by entrained sand particles in the intertidal zone. These features are in accordance with the statement made by Boltovskoy et.al. (1991) which highlighted that test

reinforcement is a common response of foraminifera that live in the high-energy environment. In addition, the way Q.cf.venusta lives by clinging on the blades of the seagrass seems also to be a method of species adaptation to survive in the intertidal habitat. By clinging on the seagrass blades, Q.cf.venusta reduces the chance of being washed about by currents and waves and also enables the individuals to minimise the abrasion by entrained sediment particles as well as the risk of being completely covered by sediment particles. These characteristics of adaptation, in conjunction with the ability of the individuals to tolerate variations in the environmental parameters such as temperature, and twice daily exposure, seems to facilitate Q.cf.venusta to maintain its existence and dominance in the intertidal seagrass habitat of Shelly Bay.

Another aspect of Q.cf.venusta that needs to be highlighted, is the ability of this epiphytic species to move freely along the seagrass blades as well as move off and onto the blades. This ability is especially beneficial for the individuals to disperse, colonize and recolonize seagrass blades.

The ability of Q.cf.venusta to move freely might also help the individuals to return and cling on the seagrass blades if they happened to be dislodged from the leaves by some unexpected factor, such as water movements or grazing animals.

Individuals dislodging from the seagrass blades, and active movements by O.cf.venusta, are probably the main factors that affect the temporal and spatial O.cf.venusta abundance. This will also have an affect on the density and the "age" distribution of the population on the seagrass blades. The observation that O.cf.venusta can move at speeds of 0.17 mm per minute in the laboratory, also emphasises the effect individual movements might have in governing colonisation, temporal and spatial abundance and the density of O.cf venusta. A similar conclusion was reached by Severin (1987) in his study on Marginopora vertebralis where he found it attached to six species of seagrass include Halodule uninervis and Halophila ovalis in Papua New Guinea. He stated that the size distribution of Marginopora vertebralis at each station might be the result of the movements of a large number of individuals.

It is highly probable that other factors, including seagrass condition and the natural population growth of O.cf.venusta, will play a role in determining the variations in temporal and spatial abundance, density and size or "age" distribution of this epiphytic species. The present study, however, could not successfully separate, or define, which factors might have the greatest influence on the temporal and spatial patterns of the abundance, density and "age" distribution of O.cf.venusta in Shelly Bay.

The observation that the abundance of Q.cf.venusta was significantly related to the area and abundance of seagrass blades, suggests that the seagrass is extremely important to Q.cf.venusta. Any interference with the Halodule uninervis population will strongly affect, directly or indirectly, the population of Q.cf.venusta.

Temporal and spatial variability was found in the proportion of micropsheric and megalospheric forms in the population. This is not surprising, since the whole Q.cf.venusta population clearly varied with time and space.

The microspheric form, even though it was only present as a small proportion, has the capability to produce a large number of megalospheric juveniles. Most of the microspheric forms seem to prefer late winter to reach maturity and produce juveniles. Late winter also seems to be the most favoured time for megalospheric forms of Q.cf.venusta to reach maturity and start reproducing. However, late winter is not the only time that Q.cf.venusta reaches its mature stage and starts reproducing. The present study also shows that the juvenile megalospheric and mature microspheric form can be observed in almost all the months of study. It is thus believed that individuals Q.cf.venusta were able to reach mature stages and start reproducing at any time during the study period, but late winter is definitely the preferred time for Q.cf.venusta to reproduce.

The observed temporal persistence of a left coiling direction preference in O.cf.venusta could not be correlated with variations in the temperature of the surrounding environment as suggested by many workers (Bandy, 1960; Cifelli, 1971; Hallock and Larsen, 1979).

The test abnormality phenomenon that was found in O.cf.venusta specimens collected during the study period, suggests a possible explanation other than those proposed by Boltovskoy and Wright (1976) and Boltovskoy (1982). Even though the present study could not determine the cause of the "twinned" phenomenon, it does show that this phenomenon is initiated at the very early stage of the individuals development. This study shows clearly that the whole process of being a "twinned" O.cf.venusta is started by the creation of a second aperture whilst the individual had only one chamber. The two apertures were then used to guide the developing two rows of the later chambers. In this way, the individual will have an appearance of a "twinned" specimen, with two tests that are attached one another via their dorsal side.

Further investigations.

The present study has clarified some aspects of the biology and ecology of the epiphytic foraminifera Osangularia cf.venusta in Shelly Bay. However, this study also generates some questions, especially on the

population dynamics and taxonomic issues of this intertidal epiphytic foraminifera.

The questions are:

1) How fast do individual Q.cf.venusta actually grow ?,

2) Do microspheric and megalospheric individuals grow at the same rate ?,

3) How long does an individual Q.cf.venusta live ?,

4) Are they any differences between the microspheric and megalospheric form in terms of their life span ?,

5) How much is the population biology of Q.cf.venusta affected by individuals dislodging and active movement ?

5) Are they any other environmental parameters that might influence Q.cf.venusta, to explain the abundance of left coiled individuals in the population ?,

6) What is the tropical distribution of Q.cf.venusta ?

7) Does this species always associate with Halodule uninervis in other areas, and dominate the epiphytic foraminiferal population ?

8) What kinds of factors promote the existence of the "twinned" individuals ?,

9) What is the correct name of the specimens that is called Osangularia cf.venusta in the present study ?

To answer those questions, future investigations therefore need to be undertaken. The investigations

should be broadened in order to obtain more data on the role of O.cf.venusta in the intertidal ecosystem. The information gathered could then be used to facilitate the interpretation of the paleobiological and paleoecological data of the intertidal area, especially the "history" of the intertidal seagrass distribution and the changing of the sea level.

References.

Aktürk, S.E., 1976, Traumatic variation in the Globorotalia menardii D'Orbigny group in late quaternary sediments from the Caribbean. **Jour. For. Res.**, v.6, no.3, p.186-192.

Alexander, S.D., and Banner, F.T., 1984, The functional relationship between skeleton and cytoplasm in Haynesina germanica (Ehrenberg). **Jour. For. Res.**, v.14, no.3, p.59-70.

Alve, E., 1991, Benthic foraminifera in sediment cores reflecting heavy metal pollution in Sørfjord, Western Norway. **Jour. For. Res.**, v.21, no.1, p.1-19.

Anderson, O.R., and Bé, A.W.H.,1978, Recent advances in foraminiferal fine structure research. In Hedley, R.H.,and Adams, C.G. (eds.), **Foraminifera**, vol.3, Academic Press, London, New York, San Fransisco, pp.121-202.

Angell, R.W. 1990. Observation on the reproduction and juvenile test building in the foraminifer Trochammina inflata. **Jour. For. Res.**, v. 20, no. 3,p. 246-247.

Bandy, O.L., 1963, Larger living foraminifera of the continental borderland of southern California. **Cush. Found. For. Res. Contr.**, v.14, no.4, p.121-126.

Bandy, O.L., 1960. The geologic significance of coiling ratios in the foraminifer Globigerina pachyderma (Ehrenberg). **Jour.of Paleontol.**, v. 34, no. 4, p.671- 681.

Barker, R.W., 1960, Taxonomic notes on the species figured by H.B. Brady in his report on the foraminifera dredged by H.M.S. Challenger during the years 1873-1876. **Society of Economic Paleontologists and Mineralogists**, special publication, no.9, Tulsa, Oklahoma, U.S.A, p.222-223.

Bates, J.M. and Spencer, R.S., 1979, Modification of foraminiferal trends by the Chesapeake-Elizabeth sewage outfall, Virginia Beach, Virginia. **Jour. For. Res.**, v.9, no.2, p.125-140.

Bé, A.W.H., and Spero, H.J., 1981, Shell regeneration and biological recovery of planktonic foraminifera after physical injury induced in the laboratory

culture. **Micropaleontology**, v.27, no.3, p.305-316,pls.1-4.

Bé, A.W.H., 1960, Ecology of recent planktonic foraminifera: Part 2- Bathymetric and seasonal distributions in the Sargasso Sea off Bermuda. **Micropaleontology**, v. 6, no.4, p.373-392.

Berger, W.H., 1971, Planktonic foraminifera sediment production in an oceanic front. **Jour. For. Res.**, v.1, no.3, p.95-118.

Bernhard, J.M., 1988, Postmortem vital staining in benthic foraminifera : Duration and importence in population and distributional studies. **Jour. For. Res.**, v.18, no.2, p.143-146.

Bijma, J., Faber, W.W.,Jr., and Hemleben, C., 1990, Temperature and salinity limits for growth and survival of some planktonic foraminifers in laboratory cultures. **Jour. For. Res.**, v.20, no.2, p.95-116, pl.1-2.

Billman, H., Hottinger, L., and Osterle, H., 1980, Neogene to recent rotaliid foraminifera from the Indopacific ocean; their canal system, their classification and their stratigraphic use. **Schweizerische Palaontologische Abhandlungen**, volumen 101, pp. 71 -113.

Bock, W.D., 1969, Thalssia testudinum, a habitat and means of dispersal for shallow water benthonic foraminifera. **Gulf Coast Assoc.of Geol.Soc.Trans.**, v.xix, p.337-340.

Bock, W.D., 1967, Monthly variation in the foraminiferal biofacies on the Thalassia and sediment in the Big Pine Key Area, Florida. **Unpublished Ph.D. thesis**, University of Miami.

Boersma, A., 1978, Foraminifera. In Haq, B.U., and Boersma, A., (eds), **Introduction to marine micropaleontology**. Elsevier North-Holland Inc, New York, Oxford, p.19-77.

Bolli, H. 1951. Notes on the direction of coiling of Rotaliid foraminifera . **Cushman Found. Foram. Res.,Contr.**, v. 2, p. 139 - 143.

Bolli, H.M., 1971. The direction of coiling in planktonic foraminifera . In Funnell, B.M.,and Riedel, W.R., (eds). **The micropaleontology of oceans**: Cambridge University Press, p.639 - 648.

Bolli, H.M., 1950. The direction of coiling in the evolution of some Globorotaliidae . **Cush. Found. For. Res.,Contr.**, v. 1, p. 82 - 89.

Boltovskoy, E., 1982, Twinned and flattened tests in planktonic foraminifera. **Jour. For. Res.**, v.12, no.1, p.79-82, pl.1.

Boltovskoy, E., and Lena, H., 1970, Additional note on unrecorded foraminifera from littoral of Puerto Deseado (Patagonia, Argentina). **Cushman Found. Foram. Res., Contr.**, v.21, no.4, p.148-155

Boltovskoy, E., and Wright, R., 1976, Recent foraminifera, Junk, The Hague, 515 p.

Boltovskoy , E., and Lena, H., 1969, Seasonal occurences, standing crop and production in benthic foraminifera of Puerto Deseado. **Cushman Found. Foram. Res. Contr.**, v.XX, part 3, p.87-95.

Boltovskoy, E., Scott, D.B., and Medioli, F.S., 1991, Morphological variations of benthic foraminiferal test in response to changes in ecological parameters: a review. **Jour.of Paleont.**, 65(2), p.175-185.

Boltovskoy, E.,1963, The littoral foraminifera 1 biocoenosis of Puerto Deseado (Patagonia, Argentina). **Cushman Found. Foram. Res., Contr.**, v.14, no.2, p.58-70.

Boltovskoy, E., and Lena, H., 1966, Unrecorded foraminifera from the littoral of Puerto Deseado. **Cushman Found. Foram. Res.,Contr.**, v.17, no.4, p.144-149.

Bradshaw, J.S., 1957, Laboratory study on the rate of growth of the foraminifer, "Streblus becarii (Linné) var. tepida (Cushman)". **Jour. of Paleont., v.31, no.6**, p.1138-1147.

Brady, H.B., 1884, Report on the foraminifera dredged by H.M.S. Challenger, during the years 1873-1876. Report on the Scientific Results of the Voyage of H.M.S. Challenger, **Zoology**, v. IX.

Brasier, M.D., 1975a, An outline history of seagrass communities. **Paleontology**, v.18, part 4, p.681-702.

Brasier, M.D., 1980, Microfossils, George Allen & Unwin Ltd, London Boston Sydney, pp. 91-121.

Brasier, M.D., 1975b, Ecology of recent sediment-dwelling and phytal foraminifera from the Lagoons

of Barbuda, West Indies. **Jour. For. Res.**, v.5, no. 1, p.42-62.

Buzas, M.A., 1978, Foraminifera as prey for benthic deposit feeders: results of predator exclusion experiments. **Jour. of Marine Res.**, v.36, no.4, p.617-625.

Buzas, M.A., Collins, L.S., Richardson, S.L. and Severin, K.P., 1989. Experiments on predation, substrate preference, and colonization of benthic foraminifera at the shelfbreak off the Ft.Pierce inlet, Florida. **Jour. For. Res.**, v. 19, no.2,p. 146-152.

Buzas, M.A., 1982. Regulation of foraminiferal densities by predation in the indian river, Florida. **Jour. For. Res.**, v. 12, no. 1, p. 66-71.

Buzas, M.A., 1969, Foraminiferal species densities and environmental variables. **Limnol. Oceanogr.** v.14, p.411-423.

Caralp, M.H., 1989, Size and morphology of the benthic foraminifer Melonis barleeanum: relationship with marine organic matter. **Jour. For. Res.**, v.19, no.3, p.235-245, pl.1-3.

Cifelli, R., 1971. On the temperature relationships of planktonic foraminifera. **Jour. For.Res.**, v.1, no. 4, p. 170 - 177.

Clayton, P.D., 1987, Aspects of the ecology of Actinoporus elongatus (Cnidaria: Actiniaria). **Unpublished BSc Hon.** thesis, James Cook University of North Queensland, 94 pp.

Coleman, A.R., 1979, Recent foraminifera from Bowling Green Bay, North Queensland. **Unpublished M.Sc. thesis,** James Cook University of North Queensland.

Cooper, W.C., 1961, Intertidal foraminifera of the California and Oregon Coast. **Cushman Found. Foram. Res.,Contr.**, v.12, no.2, p.47-63.

Corliss, B.H., 1979, Size variation in the deep-sea benthonic foraminifer Globocassidulina subglobosa (Brady) in the southeast Indian Ocean. **Jour. For. Res.**, v. 9, no.1, p.50-60, pl.1.

Davies, G.R., 1970, Carbonate bank sedimentation, Eastern Shark Bay, Western Australia. **Mem. Am. Ass. Petrol. Geol.**, 13, p.85-168.

Delaca, T.E., 1986, Determination of benthic rhizopod biomass using ATP analyses. **Jour. For. Res.**, v.16, no.4, p.285-292

Delaca, T.E., and Lipps, J.H., 1972, The mechanism and adaptive significance of attachment and substrate pitting in the foraminiferan Rosalina globularis D'Orbigny. **Jour. For. Res.**, v.2, no.2, p.68-72, pls.1 and 2.

Dobson, M., and Haynes, J., 1973, Association of foraminifera with hydroids on the deep shelf. **Micropaleontology**, v.19, no.1, p.78-90, pl.1.

Ellison, R.L., and Peck, G.E., 1983, Foraminiferal recolonization on the continental shelf. **Jour. For. Res.**, v.13, no.4, p.231-241.

Ericson,D.B., Wollin, G.,and Wollin, J. 1954. Coiling direction of Globorotalia truncatulinoides in deep sea cores . **Deep-Sea Research**, v. 2,p. 152-158.

Erskian, M.G., and Lipps, J.H., 1987, Population dynamics of the foraminiferan Glabratella ornatissima (Cushman) in Northern California.**Jour. For. Res.**, v.17, no.3, p.240-256.

Erskian, M.G., and Lipps, J.H., 1987, Population dynamics of the foraminiferan Glabratella ornatissima (Cushman) in Northern California. **Jour. For. Res.**, v.17, no.3, p.240-256, pl.1.

Faber, W.W. Jr., 1991, Distribution and substrate preference of Peneroplis planatus and P.arietinus from the Halophila meadow near Wadi Taba, Eilat, Israel. **Jour. For. Res.**, v. 21, no.3, p 218-221.

Finger, L.F.,and Lipps, J.H., 1981. Foraminifera decimation and repopulation in an active volcanic caldera, Deception Island, Antartica. **Micropaleontology**, vol. 27, no. 2,p. 111-139.

Finlay, H.J., 1939, New Zealand foraminifera: Key species in stratigraphy -No.1. **Trans. Roy. Soc. New Zealand.**, vol 68, p.504-533.

Goldstein, S.T., 1988, On the life cycle of Saccamina alba Hedley, 1962. **Jour. For. Res.**, v.18, no.4, p.311-325, pl.1-5.

Grell, K.G., 1988, The life-cycle of the monothalamous foraminifer Heterotheca lobata, n.gen.,n.sp. **Jour. For. Res.**, v.18, no.1, p.54-74, pl.1-14.

Hallock, P., and Larsen, A.R., 1979. Coiling direction in Amphistegina. **Marine Micropaleontol**, 4, p.33 - 44.

Hallock, P., Cottey, T.L., Forward, L.B., and Halas, J., 1986, Population biology and sediment production of Archaias angulatus (Foraminiferida) in Largo Sound, Florida. **Jour. For. Res.**, v.16, no.1, p.1-8.

Hallock, P., Cottey, T.L., Forward, L.B., and Halas, J., 1986, Population biology and sediment production of Archaias angulatus (Foraminiferida) in Largo Sound, Florida. **Jour. For. Res.**, v.16, no.1, p.1-8.

Hansen, H.J., and Reiss, Z., 1972, Scannning electron microscopy of some asterigerinid foraminiferida. **Jour. For. Res.**, v. 2, no. 4,pp. 191-199.

Hansen, H.J., and Lykke-Andersen, A.L., 1976, Wall structure and classification of fossil and recent elphidiid and nonionid foraminifera, Fossils and **Strata,** no. 10, pp. 1-37.

Haward, N.G.B., and Haynes, J.R., 1976, Chlamys opercularis (Linnaeus) as a mobile substrate for foraminifera. **Jour. For. Res**, v.6, no.1, p.30-38, pl.1.

Haynes, J.R., 1981, Foraminifera, Macmillan Publishers Ltd, London, pp. 40-59.

Heron-Allen, E., and Earland, A., 1914, The foraminifera of the Kerimba Archipelago (Portugues East Africa). **Trans. Zool. Soc. London**, v.XX, part XII, no.1.

Heron-Allen, E., and Earland, A., 1915, The foraminifera of the Kerimba Archipelago (Portugues East Africa). **Trans. Zool. Soc. London**, v.XX, part XVII, no.1.

Hofker, J., 1951, The foraminifera of the Siboga expedition : pt. III. Foraminifera dentata. **Siboga Reports.** IVa (III), pp. 333-336.

Hottinger, L., Halicz, E., and Reiss, Z., 1991, Architecture of Eponides and Pororeponides (foraminifera) reexamined. **Micropaleontology**, vol. 37, no. 1, pp. 60-75.

Hottinger, L., 1978, Comparative anatomy of elementary shell structure in selected larger foraminifera, In Hedley, R.H., and Adams, C.G. (eds.), Foraminifera, vol.3, Academic Press, London, New York, San Fransisco, pp. 203-266.

Hottinger, L., Halicz, E., and Reiss, Z., 1991, The foraminiferal genera Pararrotalia, Neorotalia, and

Calcarina: taxonomic revision: **Journal of Paleontology**, v. 65, no. 1, pp. 18-33.

Hyunh, H., and Feldt, L.S., 1970, Conditions under which mean square ratios in repeated measurements designs have exact F-distributions. **Jour. of the American Stat. Assoc.**, v.65, no. 332, p.1582-1589.

Jenkins, D.G., 1967. Recent distribution, origin, and coiling ratios changes in Globorotalia pachyderma (Ehrenberg). **Micropaleontol**, v.13, no. 2, p. 195 - 203.

Jenkins, D.G., 1971. New Zealand cenozoic planktonic foraminifera . **Bull.Geol.Surv. N.Z.** (Paleonto), v.42, p. 1-228.

Jennings, A.E., and Nelson, A.R., 1992, Foraminiferal assemblage zones in Oregon tidal marshes-relation to marsh floral zones and sea level. **Jour. For. Res.**, v.22, no.1, p.13-29.

Kalia, P., and Chowdhury, S., 1983. The coiling direction in Ceratobuliminid foraminifera as climatic index - a proposition . **Palaeogeo. palaeoclimat. palaeoeco**, 41, p. 165 - 170.

Kenny, R., 1974, Inshore surface sea temperature at Townsville. **Aust. J. Mar. Freshw. Res.**, v. 25, p.1-5.

Kitazato, H., 1988, Locomotion of some benthic foraminifera in and on sediments, **Jour. For. Res.**, v.18, no.4, p.344-349, pl.1.

Kloos, D.P., 1984, Parents and broods of Sorites orbiculus (Forskal), a biometric analysis.**Jour. For. Res.**, v.14, no.4, p.277-281.

Lee, J.J., Freudenthal, H., Kossoy, V., and Bé, A.W.H., 1965, Cytological observations on two planktonic foraminifera, Globigerina bulloides, d'Orbigny 1826 and Globigerina ruber, (d'Orbigny, 1839) Cushman 1927. **Jour.Paleont.**, v.12, no.4, p.531-542.

Lee, J.J., 1974, Towards understanding the niche of foraminifera. In Hedley, R.H., and Adams, C.G. (eds), Foraminifera. vol.1, p.207-260.

Lewis, K., and Jenkins, C., 1969, Geographic variation of Nonionellina flemingi. **Micropaleontology**, v.15, no.1, p.1-12.

Lipps, J.H. and Erskian, M.G., 1969. Plastogamy in foraminifera: Glabratella ornatissima (Cushman). **Journal of Protozoology**, v. 16, no. 3,p. 422-425.

Loeblich, A.R.,Jr., and Tappan, H., 1964, Sarcodina chiefly "Thecamoebians" and Foraminiferida, in R.C. Moore , (ed.), Treatise on invertebrate Paleontology, Part C, Protista 2. Lawrence: Geological Society of America and University of Kansas Press.

Loeblich, A.R., Jr., and Tappan, H., 1988, Foraminiferal genera and their classification, Van Nostrand Reinhold Company, New York, v. 1, 970 p., v. 2, 212 p.

Longinelli, A.,and Tongiorgi, E., 1964. Oxygen Isotopic Composition of some right- and left-coiled foraminifera. **Science**, v. 144, p. 1004 - 1005.

Lutze, G.F.,and Wefer,G., 1980. Habitat and asexual reproduction of Cyclorbiculina compressa (Orbigny), Soritidae. **Jour. For. Res.**, v. 10, no.4, p. 251-260.

Malmgren, B.A., 1989. Coiling patterns in Terminal Cretaceous planktonic foraminifera. **Jour. For. Res.**, v. 19, no. 4, p.311 - 323.

Marzalek, D.S., 1969, Observation on Iridia diaphana, a marine foraminifer. **Jour. Protozool.**, v.16, no.4, p.599-611.

McCall, P.L., 1977, Community patterns and adaptive startegies of the infaunal benthos of Long Island Sound. **Journal of Marine Research**, v.35, no. 2, p.221-266.

Michie, M.G., 1982, Aspects of recent benthic foraminifera from Port Darwin, Northern Territory. **Unpublished M.Sc.** thesis James Cook University of North Queensland.

Michie, M.G., 1987, Distribution of foraminifera in a macrotidal tropical estuary: Port Darwin, Northern Territory of Australia. **Aust. J. Mar. Freshw. Res.**, 38, p.249-259.

Moodley, L., 1990, Sothern North Sea seafloor and subsurface distribution of living benthic foraminifera. **Netherland, Jour. Sea Res.**, v.27, no.1, p.57-71.

Muller, P.H., 1974, Sediment production and population biology of the benthic foraminifer Amphistegina madagascariensis. **Limnology and oceanography, v.19, no.5**, p.802-809

Murray, J.W., 1967, Production in benthic foraminiferids. **Jour. Nat. Hist.**, 1, p.61-68.

Murray, J.W., 1973, Distribution and ecology of living benthic foraminiferids. Heinemann Educational Books Ltd, London, 274 pp.

Murray, J.W., 1983, Population dynamics of benthic foraminifera: results from the Exe Estuary, England. **Jour. For. Res.**, v.13, no.1, p.1-12.

Murray, J.W., 1991, Ecology and palaeoecology of benthic foraminifera, Longman Group UK Limited,Longman House, Burn Mill, Harlow, Essex CM20 2JE, England, 397 p.

Nagappa, Y., 1957. Direction of coiling in Globorotalia as an aid in correlation . **Micropaleontol**. v. 3, no. 4, p.393 - 398.

Olsson, R.K., 1974. Pleistocene paleoceanography and Globigerina pachyderma (Ehrenberg) in site 36, DSDP, Northeastern Pacific. **Jour. For. Res**, v.4, no. 2, p. 47 - 60.

Reiss, Z., and Hottinger, L., 1984, The Gulf of Aqaba, ecological micropaleontolgy. Springer-Verlag, Berlin, Heidelberg, 354 pp.

Reiter, M., 1959, Seasonal variations in intertidal foraminifera of Santa Monica Bay, California. **Jour. Paleont.**, 33, p.606-630.

Reynolds, L.A., and Thunnell, R.C., 1986, Seasonal production and morphologic variation of Neoglboquadrina pachyderma (Ehrenberg) in the northeast Pacific. **Micropaleontology**, v.32, no.1, p.1-18, pl.1-2.

Röttger, R., Fladung, M., Scmaljohann, R., Spindler, M., and Zacharias, H., 1986. A new hypothesis: The so-called megalospheric schizont of the larger foraminifer, Heterostegina depressa D'Orbigny, 1826, is a separte species. **Jour. For. Res.**, v. 16, no. 2, p. 141-149.

Röttger, R.,Kruger, R.and de Rijk, S.,1990. Trimorphism in foraminifera (Protozoa)- Verification of an old hypothesis: **Europ.J.Protistol.**,25,p.226-228.

Rowell, J.G., and Walters, D.E., 1976, Analysing data with repeated observations on each experimental unit. **J.Agric.Sci., Camb**. v.87,p.423-432.

Saito, T., 1976. Geologic significance of coiling direction in the planktonic foraminifgera Pulleniatina. **Geology**, v.4(5),p. 305 - 309.

Sakai, K., and Nishihara, M. 1981. Population study of the benthic foraminifer Baculogypsina sphaerulata on the Okinawan Reef flat and preliminary estimation of its annual production. **Proc. of the Fourth International Coral Reef Symposium, Manila**, v.2.

SAS/STAT Guide for Personal Computer, version 6 edition, 1987. SAS Institute Inc.

Sautter, L.R., and Thunell, R.C., 1989, Seasonal succession of planktonic foraminifera: results from a four-year time-series sediment trap experiment in the Northeast Pacific. **Jour. For. Res.** v.19, no.4, p.253-267.

Scott,G.H., 1976. Biometry of the foraminiferal shell: In HEDLEY,R.H.,and ADAMS, C.G., (eds). Foraminifera, II.Academic Press, London, New York, N.Y.,pp. 88 - 93.

Severin, K.P., 1983, The size-frequency distribution of the foraminifera Marginopora vertebralis on seagrass through time. **Science in New Guinea**, v.10, no.3, p.187-195.

Severin, K.P., 1987, Spatial and temporal variation of Marginopora vertebralis on seagrass in Papua New Guinea during a six week period. **Micropaleontology**, v.33, no.4, p.368-377.

Statistix version 3.5 , 1991, An interactive statistical analysis program for the IBM PC. Analytical Software, St.Paul MN.55113

Thiede, J., 1971, Variations in coiling ratios of Holocene planktonic foraminifera. **Deep-Sea Research.**, v.18, p.823-831.

Vella, P., 1974. Coiling ratios of Neogloboquadrina pachyderma (Ehrenberg). Variations in different size fraction. **American Bulletin.Geol.Soc.**,v.85,p. 1421 - 1424.

Walker, D.A., 1976, An insitu investigation of life cycles of benthonic midlittoral foraminifera. In Schafer, C.T. and Pelletier, B.R. (eds). First international symposium on benthonic foraminifera of continental margins. **Maritime Sediments Special Publication No.1, part A**, p.51-59.

Walker, D.A., Linton, A.E., and Schafer, C.T., 1974, Sudan Black B: a superior stain to rose bengal for dsitinguishing living from non-living foraminifera. **Jour. For. Res.**, v.4, no.4, p.205-215.

Walker, T.A., 1981, Annual temperature cycle in Cleveland Bay, Great Barrier Reef Province. **Aust. J. Mar. Freshw. Res.**, v.32, p.987-991.

Walton, W.R., 1952, Techniques fro recognition of living foraminifera. **Cushman Found. For. Res. Contr.**, v.3, part 2, p.56-64.

Wefer, J., 1976, Environmental effects on growth rates of benthic foraminifera (sahllow water, Baltic Sea). In Schafer, C.T. and Pelletier, B.R. (eds). First international symposium on benthonic foraminifera of continental margins. **Maritime Sediments Special Publication No.1, part A**, p.39-50.

Wienberg, J.R., 1991, Rates of movement and sedimentary traes of deep-sea foraminifera and mollusca in the laboratory. **Jour. For. Res.**, v.21, no.3, p.213-217.

Winer, B.J., 1971, Statistical principles in experimental design. 2nd edition. McGraw-Hill, New York, p.515-603.

Zar, J.H., 1984, Biostatistical analysis. 2nd edition, Prentice-Hall International, Inc, p.206-311.

Zumwalt, G.S., and Delaca, T.E., 1980, Utilization of brachiopod feeding currents by epizoic foraminifera. **Jour. Paleont.**, v.54, no.2, p.477-484.