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ASPECTS OF THE ECOLOGY, BEHAVIOUR AND PHYSIOLOGY OF THE GHOST CRAB *OCYPODE SARATAN* (FORSKÅL)

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A Thesis submitted for the degree of Doctor
of Philosophy in the Faculty of Science at
the University of Glasgow

University Marine Biological Station Millport
and
Department of Zoology, Glasgow University

November 1985

DECLARATION

I hereby declare that this thesis represents, except where a note is made to the contrary, work carried out by myself. It has not been previously submitted for any degree.

Ali Adnan Eshky

1st November 1985

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SUMMARY

The ghost crab, Ocypode saratan (Forskål) is the most conspicuous member of sandy beach communities in the Red Sea. The present studies were on populations occurring in the Jeddah region where the crabs burrow in moderately well sorted, mostly fine to medium grain sands above the tide level. The beaches experience small semi-diurnal tides which influence crab feeding behaviour and the level of mean sea level varies seasonally with higher levels (c. 1m) in winter which modify crab distribution since their zones move further up the shore. The crabs exhibited a clear cut zonation pattern with mature males constructing their burrows furthest from the sea, females occurring lower down the supralittoral shore and juveniles confined to a zone close to the water's edge. Most burrows opened towards the sea. Adult male crabs constructed complex burrows which in the breeding season had a sand pyramid at the entrance of a spiral burrow section from which there could be an extensive system of side branches. The burrows of female crabs were generally of a shallow U-shape but often with the landward shaft stopping just short of the sand surface. Most juvenile burrows were Y-shaped but again with the landward shaft often stopping just below the surface of the sand. The overall distribution of burrows was usually random but there was evidence of territorial spacing of male burrows in some months during the breeding season.

A comparison of ambient temperatures and relative humidities with the conditions within the crab burrows showed that the burrows provided protection from environmental extremes. Even in summer when air temperatures approached 40°C, temperatures within burrows remained below 30°C and at no time were in-burrow temperatures of less than 20°C measured. Relative humidity within burrows was always high.

Crabs were usually active away from their burrows around dawn and dusk and during the night. Various crab activities are discussed, especially feeding behaviour. *O. saratan* can be a deposit feeder, general herbivorous forager, scavenger or predator. Feeding behaviour is discussed in relation to stomach contents and mouthport morphology.

O. saratan avoided extreme environmental conditions by behavioural means but also showed physiological adaptation to its high temperature semiterrestrial environment. Branchial morphology, gill area, and branchial volume were examined in a size range of crabs and terrestrial adaptations demonstrated. The species had fewer gills and less gill area than aquatic crabs and had epibranchial 'lungs'. Cardiac and ventilatory activity were investigated. Heart rate varied with body size such that the smallest crabs had the highest heart rates and experiments at a range of temperatures showed adaptation to high temperature conditions. Ventilatory activity indicated different patterns in air and water with special patterns of scaphognathite activity responsible for ventilating the 'lungs' with air and for filling and flushing the gill chamber with water. Weight specific oxygen consumption was examined under aerial and aquatic conditions. This indicated that the smallest crabs had the highest weight specific oxygen consumption and that the rate of aquatic respiration was lower than that in air. Q_{10} data and information on blood characteristics again indicated both semiterrestrial adaptation and adaptation to a high temperature environment. This was also supported by data on desiccation which indicated that small crabs were more susceptible to water loss than large ones and that loss was greatest in conditions of low relative humidity.

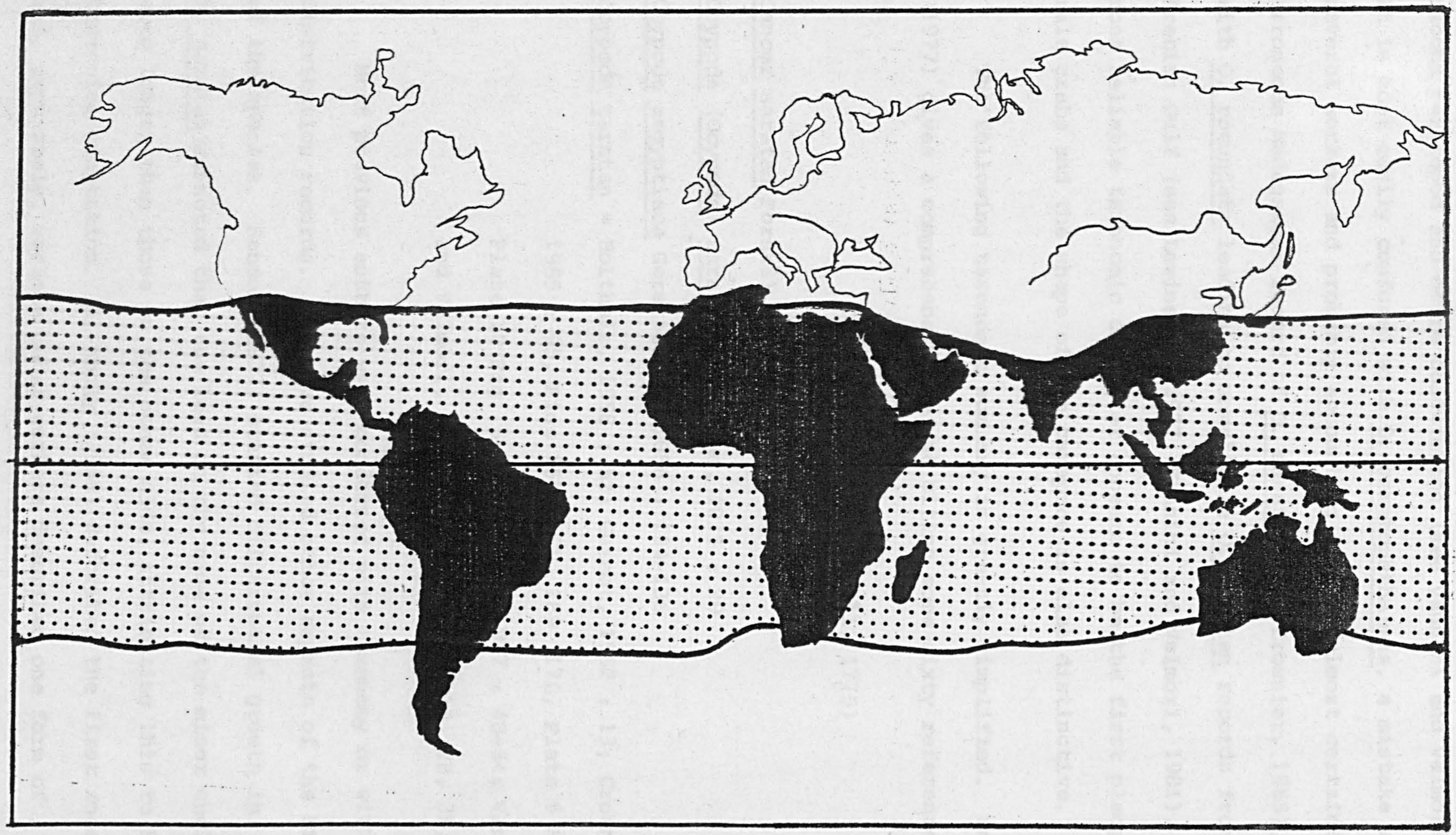
CHAPTER 1. GENERAL INTRODUCTION

The Brachyuran family Ocypodidae Rafinesque, 1815 is composed of brachygnathous, semiterrestrial, mostly amphibious burrowing crabs, largely confined to a variety of shore and estuarine habitats in the tropics (Crane, 1975; Abele and Felgenhauer, 1982). The Ocypodidae contain some 19 genera and 231 species (Abele and Felgenhauer, 1982). The best known genera include Macrophthalmus, Scopimera, Ilyoplax, Heloecius, Uca and Ocypode (Crane, 1975). Uca and Ocypode are members of the subfamily Ocypodinae Dana, 1851 and are the only cosmopolitan genera. Crabs of the genus Ocypode Weber, 1795 are amongst the most typical inhabitants of tropical sandy beaches (Dahl, 1953; Hedgpeth, 1957) and are commonly known as beach crabs, running crabs or ghost crabs. Fig. 1.1 illustrates their distribution throughout the world as given by Dahl (1953). The crabs are usually gregarious and occupy conspicuous burrows in sandy sediments.

The species which is the subject of this study is Ocypode saratan (Forskål, 1775) which populates Red Sea sandy beaches (see Fishelson, 1971; Eshky, 1980; Bemert and Ormond, 1981). The species seems to be present only in the Red Sea, Gulf of Aden and the upper eastern Somalian coast (Vannini and Valmori, 1981). An early record from Madagascar cannot be confirmed (Crosnier, 1965) and records from the Arabian Gulf are unreliable (Lewinsohn, 1977). The original description of Forskål (1775) is presented again by Holthuis (1958) who noted that the name O. aegyptiaca Gerstaecker, 1856 then in use was incorrect in that Forskål's specific name saratan was older and therefore had priority. The species is illustrated in Plate 1.1.

Good descriptions of the species are found in Crosnier (1965), Lewinsohn (1977) and Vannini and Valmori (1981). Its most obvious

Fig. 1.1. World distribution of the genus Ocypode (stippled region) according to Dahl (1953).



characteristic features are slender, sinuous styliform processes on the eyestalks, a single brush of hairs present on the propodus of the second pereiopod and ochre colouration (see Vannini and Valmori, 1981). It is most easily confused with *O. ceratophthalmus*, a mistake made by several workers and probably accounting for the almost certainly erroneous Madagascar record of *O. saratan* (see Crosnier, 1965), and with *O. rotundata* leading to unreliable *O. saratan* records from the Arabian Gulf (see Lewinsohn, 1977; Vannini and Valmori, 1981). The most reliable taxonomic character appears to be the first pleopod of male crabs and the shape of the carapace is also distinctive.

The following taxonomic summary is greatly simplified. Lewinsohn (1977) gives a comprehensive resumé citing some sixty references.

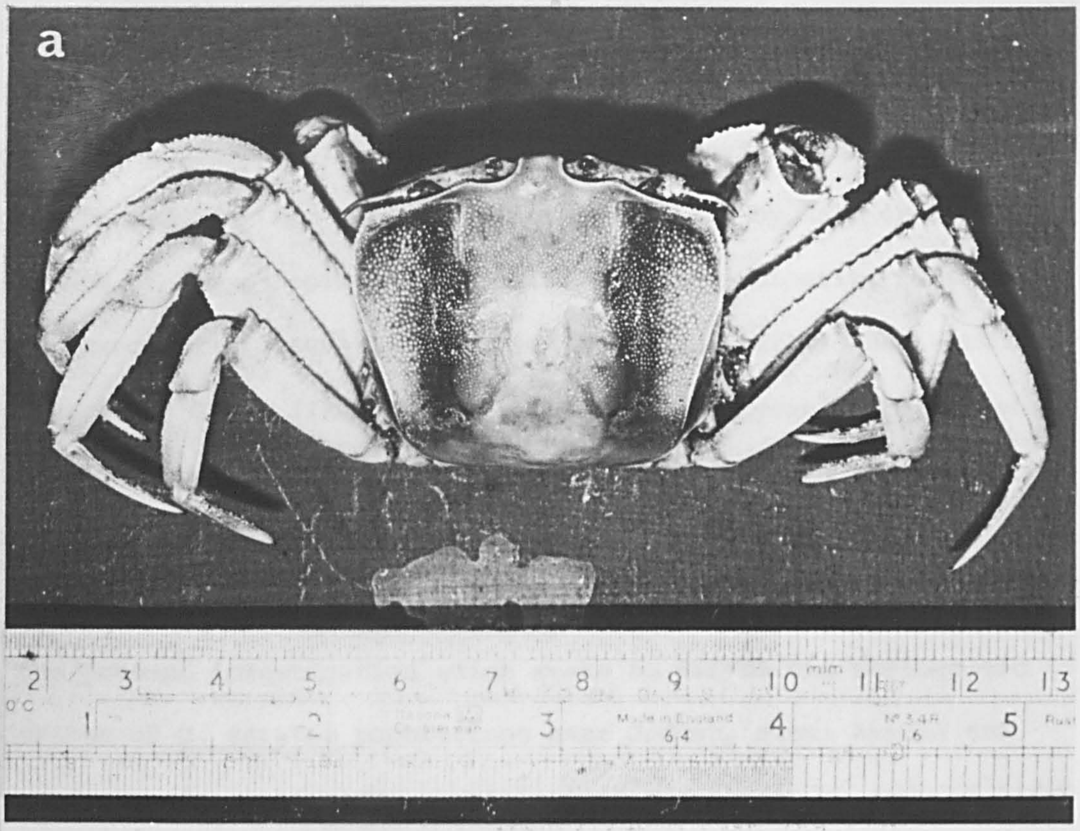
Ocypode saratan (Forskål, 1775)

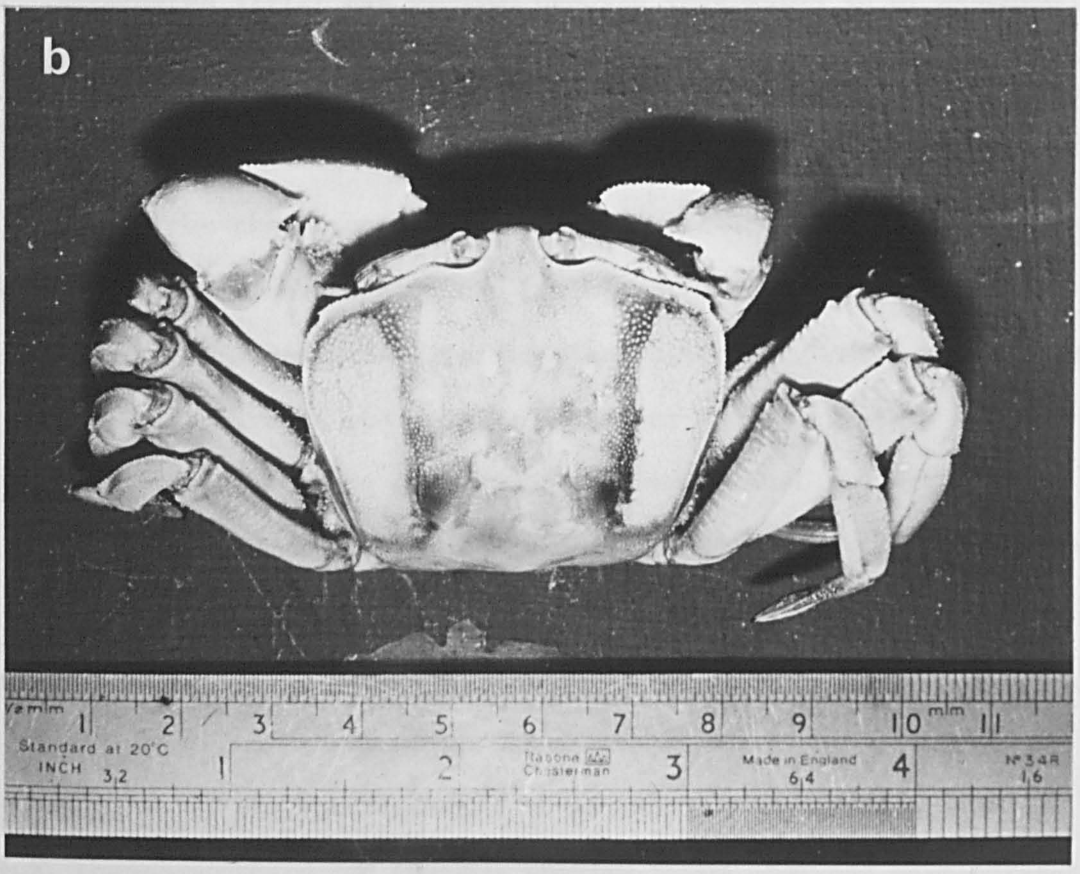
Cancer saratan Forskål, 1775 : 87, 88
Ocypode (Ocypode) saratan - de Haan, 1835 : 29
Ocypode aegyptiaca Gerstaecker, 1856 : 134-136
Ocypode saratan = Holthuis, 1958 : 52; Guinot, 1962 : 13; Crosnier, 1965 : 95, Figs 153, 161, 169, 170, Plate 8 Fig. 2, Plate 10 Fig. 5; Lewinsohn, 1977 : 48-54; Vannini and Valmori, 1981 : 205-206, Figs 1B, 2B, 3B, 4B.

Most previous authors were concerned with taxonomy or with distribution records. Few have studied other aspects of the biology of the species. Sandon (1937) studied differential growth in *O. saratan* and noted that the legs on the side of the minor cheliped were longer than those on the other side, attributing this to be a burrowing adaptation. Al-Kholy (1959) described the first zoea. He, and, separately, various other workers described one form of *O. saratan* burrow (Parenzan, 1931; Al-Kholy, 1959; Magnus, 1960;

Plate 1.1. Ocypode saratan (a, b, males)

NB The variation in carapace shape with size was noted by George and Knott (1965). The dark markings on the carapace are post-mortem artifacts.


a
2 3 4 5 6 7 8 9 10 m/m 11 12 13
0°C
1 2 3 4 5
Rabone Chesterman
Made in England
6,4
No 34R
1,6
Rust


b
½ m/m
1 2 3 4 5 6 7 8 9 10 m/m 11
Standard at 20°C
INCH 3,2
1 2 3 4
Rabone Chesterman
Made in England
6,4
No 34R
1,6

Linsenmair, 1964, 1965, 1967). This is the so-called 'spiral burrow' constructed by male crabs in the breeding season though only Linsenmair realised the significance of this burrow type, terming it the 'Kopulationshöhle'. Linsenmair (1967) described in detail the signal function of the sand pyramids constructed by male crabs at the entrances of these 'spiral' burrows, a pyramid indicating to females the presence of a mature male. There has been little other work on the species. Carli (1969) again noted the sand pyramids constructed by the male crabs and she speculated on ecological and physiological adaptations to the burrowing, semiterrestrial mode of life in a 'desk-top' exercise involving no experimentation. Similar ideas are pursued in the present investigation which seeks to define the ecology and behaviour of *O. saratan* populations near Jeddah, Saudi Arabia and investigate, in particular, physiological adaptation to mode of life.

Spaargaren (1977) has studied osmotic regulation in *O. saratan*. It maintains a very constant internal concentration when exposed to a wide range of salinities.

Apart from the extensive taxonomic literature, there is quite a large amount of literature on the biology of other *Ocypode* species, particularly concerning their ecology and behaviour. Much of this is concerned with burrows and digging behaviour and is reviewed by Vannini (1980a). *Ocypode* crabs construct individual semi-permanent burrows. Juvenile crab burrows are morphologically distinct from the burrows of adults and male burrows may differ from those of females, particularly so in *O. ceratophthalmus* and as seen in this study, in *O. saratan*. *O. ceratophthalmus* has received the greatest attention with records of its burrow structure dating from Borradaile (1903). It is the most widespread *Ocypode* species found from the east African coast to Hawaii and Australia (Vannini and Valmori, 1981) and this wide range is reflected in the numerous authors that have published on the species (see Vannini, 1980a). It is also evident that, apart from interspecific differences in burrow structure, there are intraspecific differences that might be specific to different populations (Fellows, 1973).

The spatial distribution of burrows has also received study (Lighter, 1976; Shuchman and Warburg, 1978; Fisher and Tevesz, 1979; Leber, 1981) and demonstrates, amongst other things, density dependent territoriality in male O. ceratophthalmus. Linsenmair (1967) described the establishment and maintenance of territories by male O. saratan but did not undertake a detailed spatial analysis.

The environmental factors influencing burrowing have been considered by some workers eg. the effect of temperature and beach geomorphology on O. ceratophthalmus (Chakrabarti, 1981) and soil moisture content on O. cursor (Shuchman and Warburg, 1978; Warburg and Shuchman, 1979). Vannini (1980a) notes that the burrow is a protection against predators, conspecifics, overheating, dehydration and possibly provides access to the water table. He presents evidence of the burrow providing thermal protection for O. ryderi but points out that the evidence for access to the water table is equivocal. He considers it unimportant in O. ryderi, O. cordimana, O. pallidula and O. africana. Utashiro and Horii (1965) did not find any correlation between burrow depth and water table depth in O. stimpsoni and neither did Fellows (1966) in O. ceratophthalmus from Hawaii in contrast to Takahasi (1932) who suggested a correlation for O. ceratophthalmus in Taiwan. Shuchman and Warburg (1978) and Warburg and Shuchman (1979) indicated that although O. cursor did not dig down to the water table, the moisture content of the sand was of great importance in determining distribution. Chakrabarti (1980) studied the influence of the biogenic activity of O. ceratophthalmus on the granulometry of beach sediments and noted dramatic deviations in the pattern of grain size distributions between burrowed and unburrowed sites.

Several authors have investigated the effects of human or natural disturbance of Ocypode populations. Fisher and Tevesz (1979) considered that O. quadrata from disturbed American beaches had a lower adult:juvenile ratio compared to undisturbed beaches, less probability of survival to reproductive age and, in the case of man-disturbed beaches reduced reproductive capacity. Leber (1981) showed these conclusions to be incorrect; the product of statistical error. Wolcott and Wolcott (1984), however, demonstrated dramatic human impact effects on an O. quadrata population when they investigated off-road vehicle effects. During the day, crabs remained in their burrows and were protected from injury but could be killed in large numbers while feeding on the foreshore at night. The Wolcotts collate information from a number of sources including the work of Steiner and Leatherman (1981) who suggested that disruption may be more extensive, including direct crushing, behavioural derangement and physiological stress resulting from sediment compaction and changes in water content. It will be noted in this thesis that human interference has had a dramatic effect on O. saratan populations in the region of Jeddah.

References to various aspects of the population biology of Ocypode species are numerous but usually brief and are often combined with investigations of burrows and burrowing. Notable amongst these studies are those of Fellows (1966) for O. ceratophthalmus and O. pallidula (= O. laevis) in Hawaii and Fellows (1973) for O. ceratophthalmus and O. cordimana at Fanning Atoll, Line Islands. No-one has yet comprehensively analysed the population biology of an

Ocypode species and it is clear from present studies that such an investigation would be time consuming and difficult.

Sexual behaviour has received attention from a number of workers and has led to a debate as to whether copulation occurs within the burrow or not. Linsenmair (1967) considered this to be in the burrow for O. saratan, by inference not observation. Hughes (1973) observed out-of-burrow copulation in O. quadrata and O. occidentalis though it was not seen in his observations on O. ceratophthalmus (Hughes, 1966). Both Fellows (1966) and Vannini (1976a) consider copulation to be principally an in-burrow activity. No instances of copulation were observed in the present studies for O. saratan.

The most comprehensive behavioural analysis of an Ocypode species is by Linsenmair (1967) for O. saratan. He was principally concerned with the sexual and territorial behaviour of male crabs. Most Ocypode papers contain some behavioural notes but the few detailed studies include those of Evans et al. (1976) who studied foraging and agonistic behaviour in O. ryderi and Vannini (1980b) who has recently followed this up with studies of agonistic behaviour, courtship, avoidance behaviour and cleaning behaviour in O. ryderi. Most Ocypode spp. are nocturnal (Vannini, 1976a). Also, Fellows (1966) studied burrowing behaviour in O. pallidula and O. ceratophthalmus in some detail. Both shared a common ethogram.

The larvae of several Ocypode species have been described. Crane (1940) described the first zoea and megalopa of O. gaudichaudii, the megalopa of O. quadrata (then O. albicans) and the megalopa of O. occidentalis. Raja Bai Naidu (1951, 1954) described the first zoea of O. platytarsis and the megalopae of O. platytarsis and O. cordimana. Al-Kholy (1959) described the first zoea of O. saratan which was also seen in the present studies. The complete larval development of *O. quadrata* is reported by Diaz and Costlow (1972). Also, Terada (1979) described the 5 zoeae of *O. stimpsoni* and compared them with zoeal information on *O. quadrata*, *O. platytarsis* and *O. gaudichaudii* and also with *Uca* spp. and members of the ocypodid subfamilies Macrophthalminae and Scopimerinae. He presented a key to the zoeae of 17 species from the family Ocypodidae.

Aspects of feeding (mouthparts, diet, feeding behaviour) have been studied in a number of *Ocypode* species (see Takahasi, 1935; Crane, 1941; Tweedie, 1950; Hughes, 1966; Jones, 1972; Rajabai, 1972; Wolcott, 1978). *Ocypode* feed in a number of ways, described as foraging, scavenging, sand pellet feeding and predatory feeding by Hughes (1966) for *O. ceratophthalmus* and this generalisation holds true for other species. The most detailed feeding behaviour investigation is by Wolcott (1978) for *O. quadrata* which was shown to be over 90% predatory and his inference is that the generalised scavenging rôle usually ascribed to *Ocypode* species (he cites Cowles, 1908; Cott, 1929; Phillips, 1940; Crane, 1941; Hedgpeth, 1957; Taylor, 1971) requires reassessment. Rajabai (1972), however, is emphatic that the *O. macrocera* he studied in India were not active predators but scavengers. The present work shows that *O. saratan* adopts a variety of feeding techniques, like *O. ceratophthalmus*.

Crane (1941) and Wolcott (1978) considered growth along with feeding, the latter author considering the crabs rôle in beach productivity. Rao (1966, 1968a) studied various aspects of growth and moulting in *O. macrocera* including the physiological control. Paulraj *et al.* (1982) have examined relative growth before and after sexual maturity in *O. platytarsis* and *O. cordimana* and one conclusion was that major chela length was a sexually dimorphic feature with an increase in the growth coefficient of males after the onset of sexual maturity. Growth in crabs has recently been viewed by Hartnoll (1982) and this highlights the sparsity of information on Ocypode.

Most physiological studies of Ocypode spp. have been concerned with adaptation to the semiterrestrial mode of life.

Pearse (1929a, b, 1950) noted a progressive reduction in gill volume associated with an increasingly terrestrial mode of life. He also noted that in O. quadrata the gill number was reduced from the normal 18 to 12. He noted that two gills were fused to form a 'great gill'. As shall be seen in this thesis this 'fusion' is really an interfoliation of adjacent lamellae, and the gills (the anterior and posterior arthrobranchs of the cheliped) are structurally separate. Concurrently, Greenaway and Farrelly (1984) have pointed this out for O. cordimana. The true number of gills is therefore 14. Nevertheless, the number of gills given by Pearse is continued in the subsequent literature even though Calman (1909) had defined it correctly for an unspecified Ocypode sp. in a table of branchial formulae. Gray (1957) showed a tendency towards reduction in gill area per unit of weight with increasingly terrestrial life. For both Pearse and Gray, O. quadrata was the most terrestrially adapted of the crabs they studied. The vaulted epibranchial chamber was seen to have an irregular lining - 'irregular rows of respiratory tufts' according to Pearse (1929b). The morphology of the branchial chamber in O. quadrata has subsequently been studied by Diaz and Rodriguez (1977) who clearly demonstrated its respiratory function. Oxygen uptake was demonstrated both at the gills and at the branchial wall folds. In fact, similar suggestions for the branchial wall had been made for O. saratan by Carli (1969) in her little known paper. Storch and Welsch (1975) investigated the structure and function of the gills of

O. ceratophthalmus and indicated that the ultrastructure of the gill epithelia suggested an osmoregulatory function. Greenaway and Farrelly (1984), considering Storch and Welsch's (1975) evidence along with their own, conclude that 'there is no reason to suppose that the gills of O. ceratophthalmus or O. cordimana are incapable of significant gas exchange'. Greenaway and Farrelly (1984) identified gas exchange sites in the gills and 'lungs'.

There have been a number of studies of oxygen consumption in Ocypode species, including those of Flemister and Flemister (1951) on O. quadrata who investigated the rate of O_2 consumption in air and in water where it was influenced by chloride regulation. McMahon and Wilkens (1983) have pointed out that the tendency towards increased standard levels of oxygen consumption with increases in terrestriality is well established and is also true for isolated tissues (see Pearse, 1929b; Ayers, 1938; Edney, 1960). Vernberg (1956) investigated O_2 consumption in excised tissue from the gills and mid gut gland of O. quadrata and 8 other crab species and indicated that the rate of O_2 uptake of gill tissue is highest in terrestrial species (the mid gut gland showed no such migratory adaptation). Vernberg (1956) had, in fact, extended the work of Ayers (1938) and came to similar conclusions. Veerannan (1974) investigated oxygen consumption in air and water in O. platytarsis and he also calculated its gill area. Aerial and aquatic respiration is investigated in O. saratan in this thesis as are some aspects of blood chemistry.

The question of water requirements is central to the research on terrestrial adaptation and is thoroughly examined by Bliss and her co-workers (Bliss, 1963, 1968; Bliss et al., 1966; Bliss and Mantel, 1968; Mantel et al., 1975; Powers and Bliss, 1983), Mantel (1979) and Mantel and Farmer (1983). The Ocypode species which receives most attention is *O. quadrata*. The problems of desiccation, water uptake and conservation, moulting, and osmotic and ionic regulation are examined in relation to the semiterrestrial mode of life. Wolcott (1984) has recently followed up his earlier work (Wolcott, 1976) on water uptake in *O. quadrata* and has described the rôle of the capillary tufts of setae between the 3rd and 4th pereiopods in water collection and the subsequent bulk uptake of water into the gill chamber. Certain aspects of this were investigated concurrently in the work reported here for *O. saratan*. Wolcott (1976, 1984) did not investigate the detailed action of the scaphognathite in contrast to the studies reported here for *O. saratan*, though he did measure the suction pressure generated by the scaphognathite, this being responsible for bulk intake of water from the setal tufts to the gill chamber. In addition there is passive osmotic water uptake (Wolcott, 1984). The osmotic problems faced by *O. saratan* are likely to be different from those experienced by *O. quadrata*. The soil water available to *O. saratan* is saline, not dilute as may occur for *O. quadrata*. *O. quadrata* voids excess salts in isosmotic urine with minimum energy cost (Wolcott, 1984). The present work examines water loss in *O. saratan* but not osmoregulation which has been studied by Spaargaren (1977).

Other physiological investigations in the literature include work on the physiology of reproduction, for example, seminal chemistry has been investigated in *O. platytarsis* and *O. ceratophthalmus* (see Adiyodi, 1985) and sexual differentiation in *O. quadrata* (see Charniaux-Cotton and Payen, 1985).

Slow morphological colour change (alteration in numbers of chromatophores) has been studied in *O. ceratophthalmus* (Green, 1964) and rapid physiological colour change (pigment movements) have been investigated in O. macrocera (see Rao, 1985).

A moult inhibiting hormone in O. macrocera was studied by Rao (1965) and further details are given in Kleinholz (1985).

There are also a few neurobiological studies including work on locomotion in O. ceratophthalmus (Hafemann and Hubbard, 1969; Burrows and Hoyle, 1973), which can travel at 2.1 $m.s.^{-1}$; work on auditory communication in O. ceratophthalmus, O. quadrata, O. gaudichaudii and O. cordimana (Horch and Salmon, 1969, 1972; Horch, 1971, 1975), the crabs stridulate using the larger cheliped and can detect airborne and ground transmitted vibrations; and work on eye structure on vision in O. cursor (Kunze, 1967, 1968; Kunze and Boschek, 1968) and O. ceratophthalmus (Horridge, 1978).

Comparative eye morphology in ocypodid crabs is discussed by von Hagen (1970) who mentions most Ocypode species. O. saratan is one of several species with stylophorous eyes, ie. the peduncle is projected beyond the cornea. The function of this is probably sensory but unclear. Whether stylophorous or not, the eyes of Ocypode species are large and elongated (von Hagen, 1970) with a large number of ommatidia (Nunnemacher, 1966) and almost all round vision with binocular overlap (Barnes, 1968; Horridge, 1978).

The geological record of the Ocypodidae appears to date from the Eocene and that of the genus Ocypode from the Miocene epoch (Glaessner, 1969). Burrows attributable to Ocypode have been described from Poland (Middle Miocene) (Radwanski, 1977), Kenya (Upper Pleistocene) (Stephenson, 1965), Georgia and Florida (Pleistocene) (Rathbun, 1935; Frey and Mayou, 1971) and Taiwan (Tertiary ? Miocene) (Hayasaka, 1935). Such traces may be used to reconstruct ancient environments (Frey, 1970; Hertweck, 1972) and according to Radwanski (1977) the evidence indicates 'a world-wide distribution of the *Ocypode* burrows along warm water seashores already at the Miocene time.'

Referring to 'Crane's monumental monograph on *Uca* (1975)', Vannini (1980a) states 'a taxonomic revision together with a larger and deeper study on the ecology and behaviour may lead to the drawing of an acceptable outline of the phylogenetic history of the *Ocypode* as well.' Some areas of taxonomic confusion have recently been clarified (Sakai and Türkay, 1976) and a new species has recently been described (George, 1982) but it is clear from reading the *Ocypode* literature that there is still a great deal to be learnt and clarified.

The following is a list of the *Ocypode* species referred to in this thesis.

O. africana de Man	W. Africa
O. ceratophthalmus (Pallas)	E. Africa to Australia and Hawaii
O. convexa Quoy and Gaimard	Australia
O. cordimana Desmarest	Red Sea, E. Africa to Japan and Tahiti
O. cursor (L.)	W. Africa, Mediterranean
O. fabricii H. Milne-Edwards	Australia, Oceania
O. gaudichaudii H. Milne-Edwards and Lucas	El Salvador to Chile, Galapagos
O. kuhlii de Haan	Indonesia
O. macrocera H. Milne-Edwards	India
O. madagascariensis Crosnier	Madagascar
O. mortoni George	Hong Kong
O. nobilii de Man	Borneo
O. occidentalis Stimpson	Lower California to Peru
O. pallidula Jaquinot (= *O. laevis*)	Madagascar, Pacific Islands

O. pauliani Crosnier	Madagascar
O. platytarsis H. Milne-Edwards	India
O. quadrata (Fabricius) (= *O. arenaria*, *O. albicans*)	Caribbean, temp. Atlantic USA
O. rotundata Miers	Arabian Gulf
O. ryderi Kingsley (= *O. kuhlii*, part)	E. Africa
O. saratan (Forskål) (= *O. aegyptiaca*)	Red Sea, Gulf of Aden, Somalia
O. stimpsoni Ortmann	Japan

There are numerous outdated synonyms and only the main ones recurring in the literature are shown above. Revisions have deposed *O. portonovoensis* Premkumar and *O. urvillei* Guerin (Sakai and Türkay, 1976) and *O. jousseaumei* Nobili is enigmatic apparently being known only from the holotype which was probably collected in the Red Sea (Crosnier, 1965; Lewinsohn, 1977). Undoubtedly further revisions and additions are necessary.

This review is not indended to be exhaustive and additional references are cited throughout the thesis. It does, however, indicate the background against which the present studies were undertaken.

There is an extensive literature on other genera within the Ocypodidae, again mostly ecological and physiological in nature; for example, investigations on *Uca* (see Crane, 1975), on *Dotilla* (Hartnoll, 1973; Fishelson, 1983), on *Heloecius* and *Hemiplax* (Griffin, 1971) and on *Macrophthalmus* (Hawkins and Jones, 1982). These and other ocypodids are not reviewed here but are included in the discussions of subsequent results when relevant.

The first part of this thesis deals with aspects of the ecology of *O. saratan* and is centred on its burrowing, semiterrestrial mode of life. This invites questions of behavioural and physiological adaptations to their environment and aspects of behaviour and physiology are examined in the second and third sections of the thesis, respectively. The greatest emphasis is placed upon respiratory physiology. Overall, the approach is one of balancing field studies with laboratory observation and experimentation such that laboratory studies are environmentally realistic: it is a blend of behavioural and physiological ecology.

The fieldwork reported in this thesis was conducted near Jeddah, Saudi Arabia, and experimental work was conducted both in Saudi Arabia using the facilities of the Marine Station of the Faculty of Marine Science, King Abdul-Aziz University, Jeddah, and in Scotland at the University Marine Biological Station Millport, Isle of Cumbrae (Universities of London and Glasgow) and the Zoology Department, University of Glasgow.

The importance of considering an animal's physiology in relation to its ecology rather than in isolation is now generally recognised (see Jørgensen, 1983) and this approach is followed here.

DIVISION 1. ECOLOGY

CHAPTER 2. THE ENVIRONMENT

2.1. Red Sea: general description

The Red Sea is comparatively young and is part of a rift system formed by the movement of the Arabian and African tectonic plates (Bemert and Ormond, 1981; Koenig, 1982). It is a long narrow basin about 1900km in length and its width varies from 305km near Massawa and Gizan to 27km at the Strait of Bab-el-Mandab. Sea surface area is c. $4.4 \times 10^5 km^2$, mean depth is c. 500m, and greatest recorded depth is 2920m in the central trough, contrasting with only 100m at the Bab-el-Mandab sill (Morley, 1975). The rift continues into the Gulf of Aqaba where water depth may exceed 1800m but the Gulf of Suez is a narrow basin of 40m mean depth and never in excess of 90m depth (Morley, 1975; Bemert and Ormond, 1981).

The rift movements apparently originated 70 million years ago and the Red Sea has in its geological history been connected with both the Mediterranean Sea and the Indian Ocean. The present link with the Indian Ocean is comparatively recent being some 300,000 years old and the present biota is related to that of the Indian Ocean (see Bemert and Ormond, 1981).

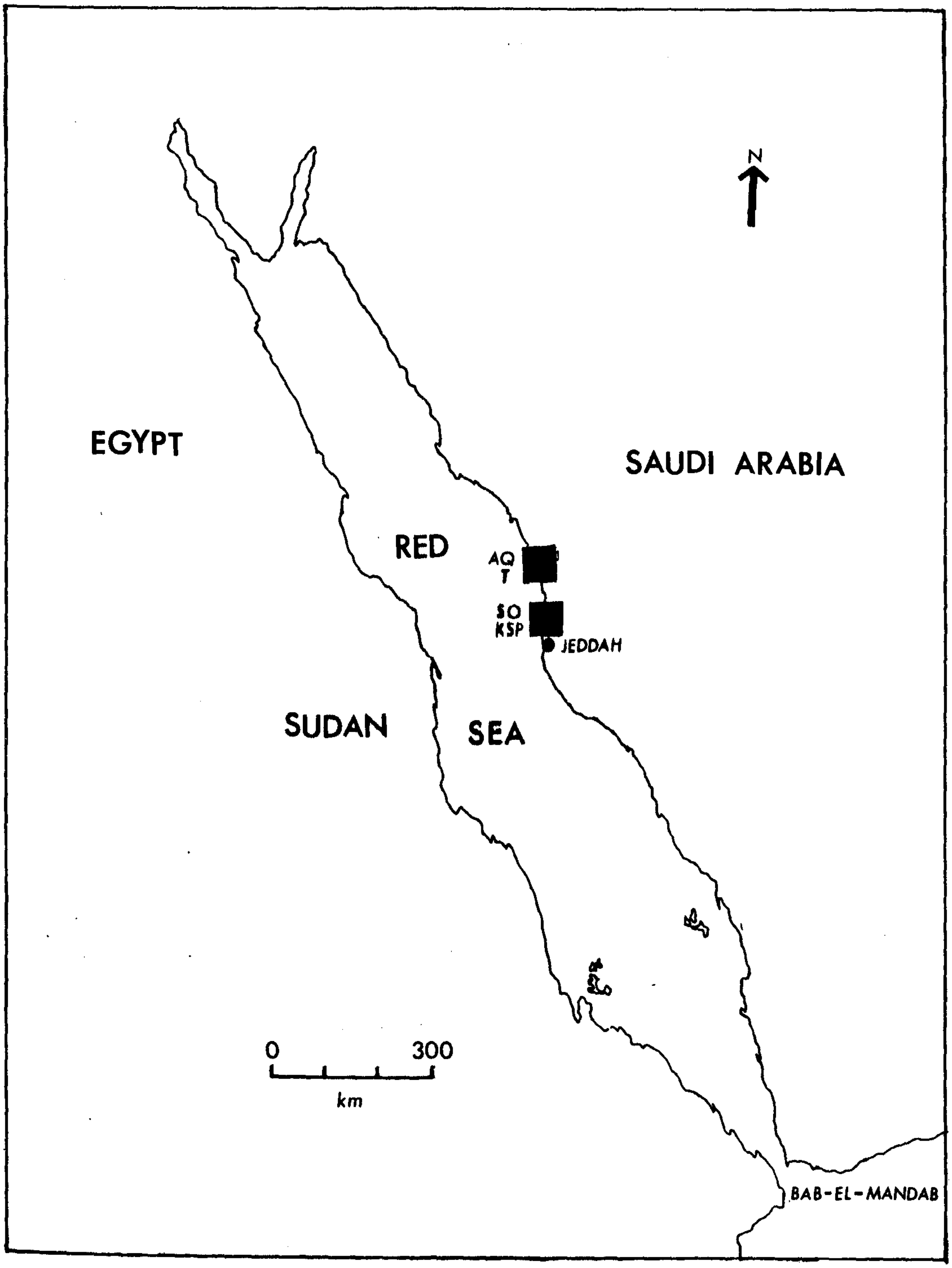
The Red Sea extends from latitudes 13°N to 30°N and below 18°N is one of the hottest regions in the world. Air and water circulation are influenced by the Indian Ocean monsoon winds which reverse seasonally in response to pressure changes over the continent of Asia. In the region of Jeddah (latitude 21°N), however, the prevailing winds are predominantly NNW throughout the year (see Morcos, 1970; Morley, 1975). Further detail of hydrology and climate are given later in this chapter.

Salinity is high in the Red Sea and so is water temperature. Salinity may reach nearly 41°/oo in the north (28°) and may exceed 40°/oo in reef-flat pools in the Jeddah region in July and August (Morley, 1975). Coastal sea surface salinity measured for the Jeddah region by Morley (1975) was between 37°/oo and 39°/oo. Sea surface temperature varies from 25°C to 31°C in the centre and south to 20°C to 26°C in the north (Bemert and Ormond, 1981). Morley (1975) gives coastal seawater temperatures for the Jeddah region of between 26°C and 29°C but reaching over 40°C in isolated reef-flat pools. Beyond 700m depth, temperature is a constant 21.5°C (Bemert and Ormond, 1981) but may reach 57°C and 320°/oo salinity at the sea bed in the rift (Saudi-Sudanese Red Sea Joint Commission, 1982).

The coastline of the Red Sea is bordered by extensive fringing reefs and these are well developed around Jeddah. Immediately north of Jeddah where the present study was based, the beach forms a long 'ribbon' of sand and behind the shoreline is desert or semi-desert. Offshore there are numerous patch reefs and, in places, small islands seemingly derived from reef systems. Extensive complexes of large offshore islands occur in the South of the Red Sea eg. Farazan Islands but not in the Jeddah region. Nevertheless, small islands do occur and Al-Quaid is one of such a group north of Jeddah. Further offshore a disjointed barrier reef system is present. The shoreline is periodically indented by creeks (sharms) and within these, although there is no developed fringing reef, there may be a moderately developed coral fringe as at Sharm Obhor which was central to the present investigations.

Wherever sand beaches are found along the coastline, in sharms

Fig. 2.1. Map of Red Sea showing study regions. AQ = Al-Quaid Island, T = Twwal, SO = Sharm Obhor, KSP = King Saud Palace.


N
EGYPT
SAUDI ARABIA
RED
AQ
T
SO
KSP
JEDDAH
SUDAN
SEA
0
300
km
BAB-EL-MANDAB

or on islands, these provide a habitat for the ghost crab O. saratan.

Fig. 2.1 illustrates the Red Sea and identifies the field sites used in this study. These sites are introduced in the following section.

2.2. Study sites

Most studies were carried out at two sites, one just North of King Saud Palace, 45km N of Jeddah and the other adjacent to the King Abdul-Aziz University, Faculty of Marine Science Marine Station at Obhor, 25km N of the centre of Jeddah. Further studies were conducted at Al-Quaid Island, 75km N of Jeddah and some 5km offshore (near Ras Hatiba), and at Twwal some 120km N of Jeddah.

Beach profiles were established using a theodolite (Sokkisha Model C3A) and fixed reference points were established at two shores to standardize subsequent surveying. Sea level was also measured and related to fixed reference points. The lowest tide experienced during the year at each main site was used to establish a tidal datum (TD) for each site, ie. TD = lowest tide measured during study.

2.2.1. King Saud Palace

This site is illustrated in Plate 2.1 and it is typical of much of the shoreline behind the fringing reefs. The site profile (Fig. 2.2) indicates a steep, narrow sandy shore with dunes at the top and a coral rock platform at the bottom. The seasonal change in sea level (see below) results in this rock platform being submerged in winter and exposed during part of the summer (July, August). The lagoon within the fringing reef is some 160m in width and only 0.5-1m in depth. The reef crest is largely submerged in winter but is exposed in July and August when the lagoon is sometimes reduced to a series

Plate 2.1. a) King Saud Palace beach, looking in a northerly direction. Tyre tracks can be seen in the sand.

b) Same beach, viewed from the dunes.

a

b

of shallow pools. At this time the O. saratan must travel some distance to reach the sea (see Fig. 2.2).

The site is in fact about 1km N of the abandoned coastal palace of King Saud which is the nearest reference point and which now serves as a popular picnic area. The study site is therefore subject to human disturbance (note tyre tracks on Plate 2.1a) and this is detailed later.

2.2.2. Sharm Obhor

The study site is illustrated in Plate 2.2 and Figs 2.3 and 2.4. It is situated on the S side of the sharm (= inlet) adjacent to the Marine Station of the Faculty of Marine Science, King Abdul-Aziz University, Jeddah. The sandy beach is flatter (Fig. 2.3) and therefore wider than at King Saud Palace. At its landward side is the cliff of the raised coral limestone beach while seaward is the narrow lagoon behind the coral fringe of the sharm. This lagoon is only 5-20m wide and less than 2m in depth and is superficially muddy. The coral fringe is never exposed to air, even in summer.

By good fortune the beach is privately owned and rarely used. It is therefore not subject to human disturbance and for this reason was chosen for the largest proportion of field studies. Its proximity to the Marine Station was also a significant logistic advantage when undertaking intensive field experiments, eg. television work.

2.2.3. Twwal

This site is very similar to that at King Saud Palace except that it is in an area of restricted access (near Naval Installations) and therefore not subject to human disturbance.

Plate 2.2. a) View of Sharm Obhor beach looking into the Sharm. The rubble bed of an abandoned section of the Al-Corniche coastal highway can be seen at the top of the picture. The pyramids constructed by male *O. saratan* can be seen in the foreground.

b) View of the same beach looking in the opposite direction.

a

b

Its distance from Jeddah, however, ruled out other than occasional visits.

2.2.4. Al-Quaid Island

There are hundreds of small patch reefs near Jeddah, some of which form distinct islands. Al-Quaid is one such island and is surrounded by a sandy beach subject to little human disturbance. The beach is shallow in profile and similar to that at the Sharm Obhor site.

This site was visited occasionally and provided a source of crabs for experimental purposes since it was considered unwise to remove many crabs from the main study sites at King Saud Palace and especially Sharm Obhor.

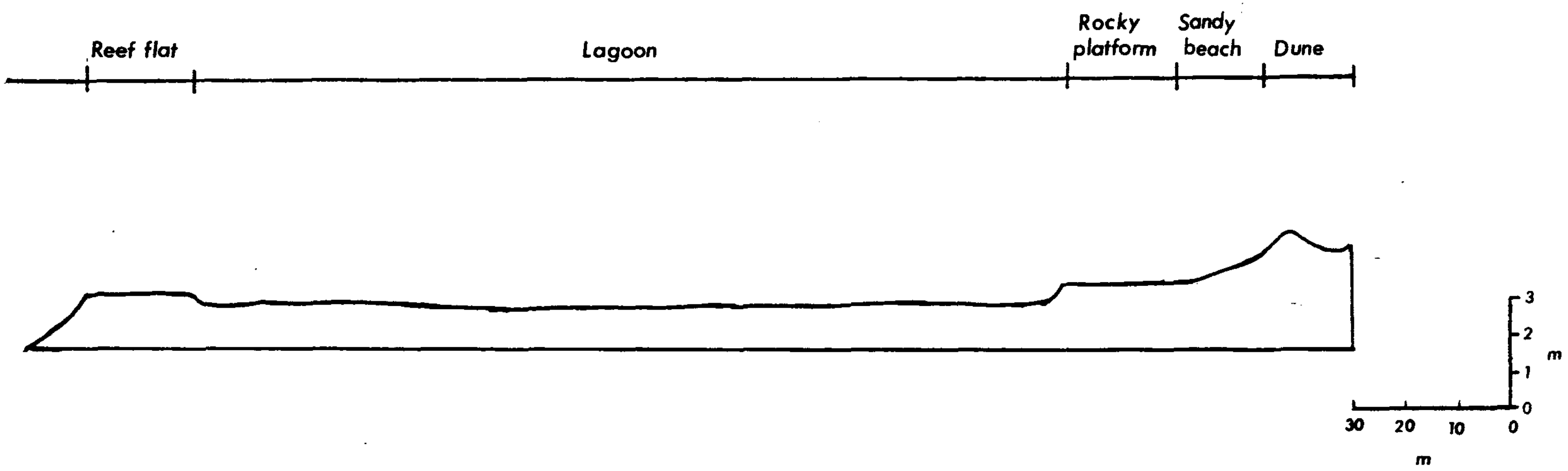
2.3. The local physical environment

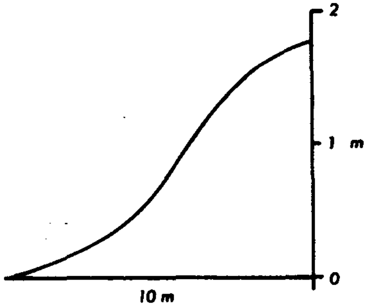
2.3.1. Geomorphology

The main difference between the main study sites, ie. King Saud Palace and Sharm Obhor is in the profile of the two shores. The study section at the King Saud Palace site is part of an extensive coastal strip of sand which is interrupted to the South by jetties and private buildings. The Sharm Obhor site is one of several discrete beaches in the Sharm, it is not extensive and is bounded by the low dead coral cliffs of the raised beach. The beach gradient at King Saud Palace is 1 in 7.5 while that at Sharm Obhor is much shallower, being 1 in 15 (see Figs 2.2 and 2.4). The maximum sand thickness at King Saud Palace is much greater than that at Sharm Obhor. At Sharm Obhor the area delineated at Zone 1 on Fig. 2.3 has a sand thickness which is shallower than Zone 2. Only in Zone 2 do the 'copulation burrows' (see Linsenmair, 1967) of male crabs develop.

Fig. 2.2. Shore profile and plan for King Saud Palace site.

The supralittoral beach profile in the region occupied by <u>O. saratan</u> is shown in the lower left corner.


Reef flat
Lagoon
Rocky platform
Sandy beach
Dune
3
2
1
0
m
30
20
10
0
m


2
1 m
0
10 m

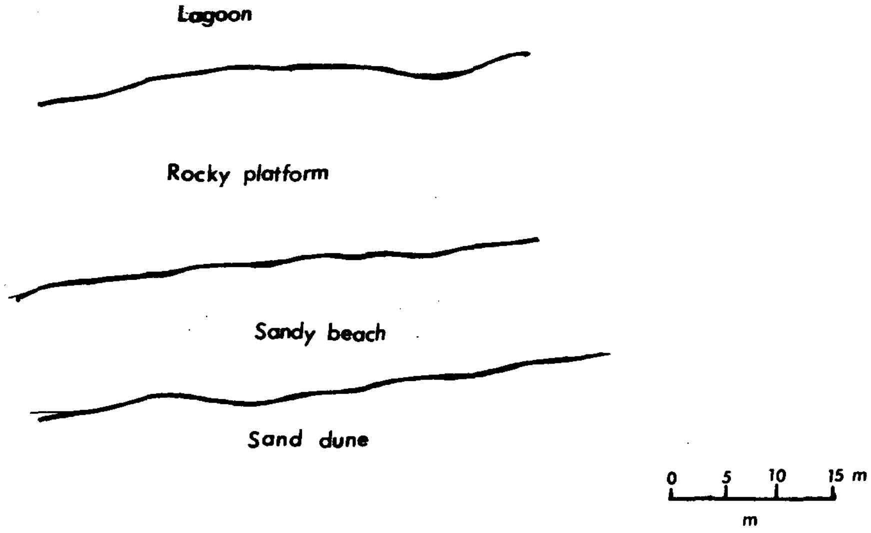

Lagoon
Rocky platform
Sandy beach
Sand dune
0
5
10
15 m
m

Fig. 2.3. Shore plan for Sharm Obhor site. In Zone 1 the sand is not deep enough for the development of spiral burrows (see Chapter 3). These are confined to Zone 2 where there is a greater depth of sand.

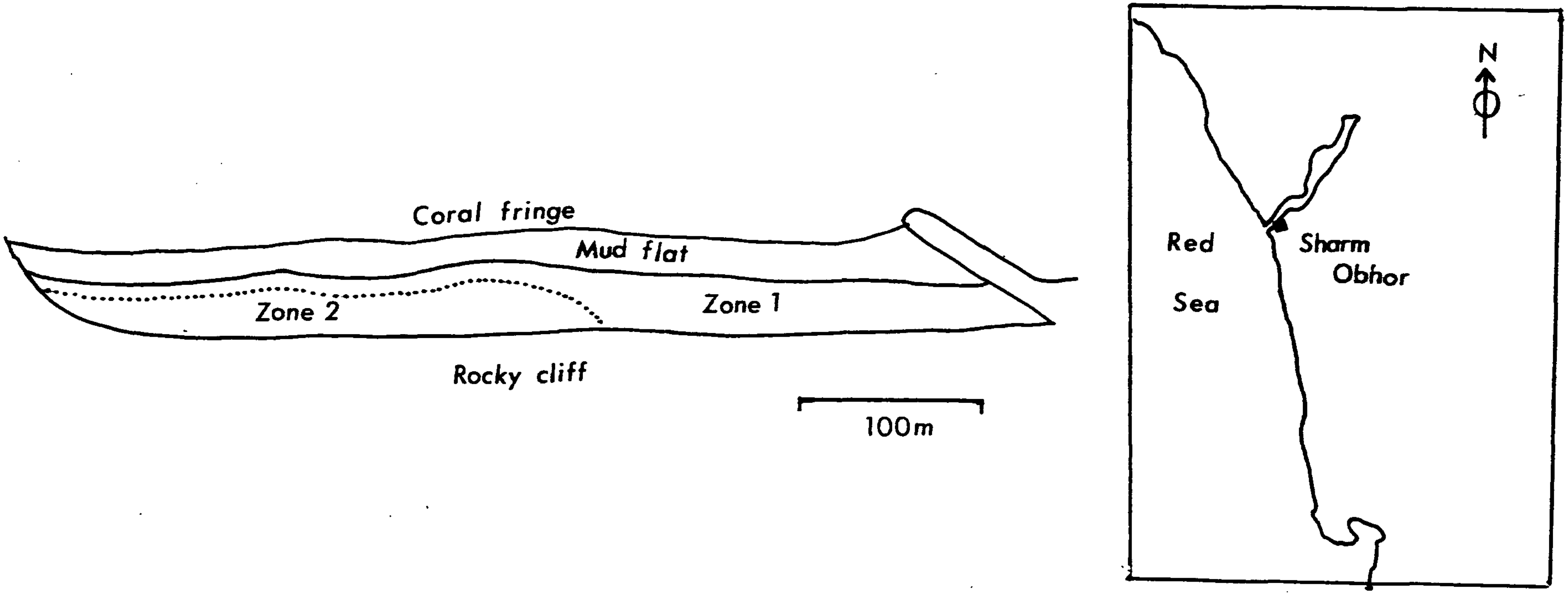
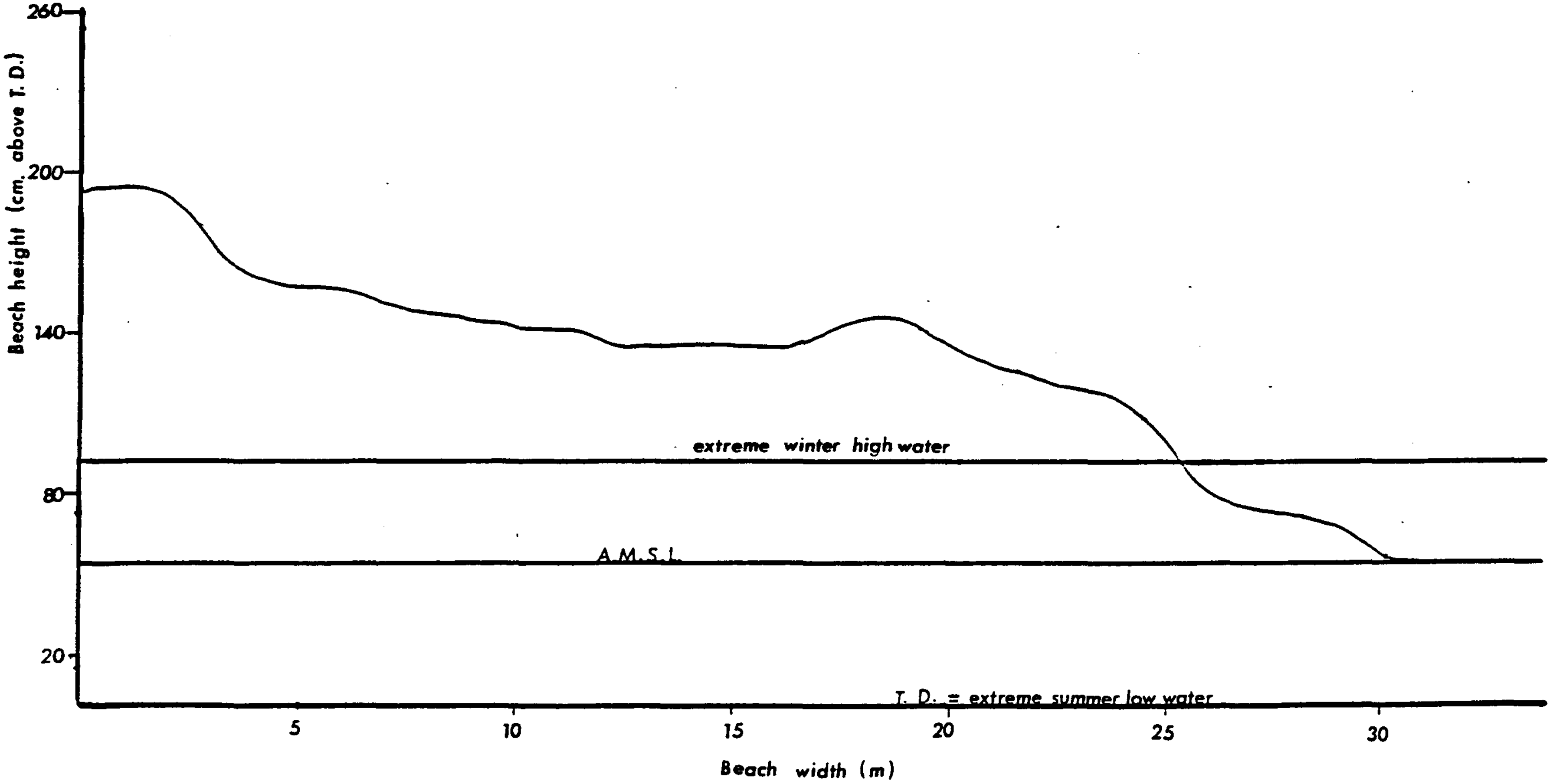

Coral fringe
Mud flat
Zone 2
Zone 1
Rocky cliff
100m
N
Red
Sea
Sharm
Obhor

Fig. 2.4. Shore profile for Sharm Obhor site (November 1983 - the profile varied slightly between surveys). ASML = Arbitrary Mean Sea Level (see text).


260
200
140
80
20
Beach height (cm. above T. D.)
extreme winter high water
A.M.S.L.
T. D. = extreme summer low water
5
10
15
20
25
30
Beach width (m)

Both beaches are to some extent protected from wave action; the King Saud Palace site by the fringing reef and the Sharm Obhor site by its sheltered inlet situation.

2.3.2. Substratum characteristics

Sediment cores were taken for granulometric analysis using standard mesh sieves. Where possible cores were vertically partitioned to indicate granulometric changes with depth. Cores were taken at the lowest edge of the *Ocypode* zone, in the middle of the zone and at the upper edge. Sediment analysis followed methods detailed by Folk (1974), Gray (1981) and Buchanan (1984) and were conducted with the assistance of the Marine Geology Department of the Faculty of Marine Science, King Abdul-Aziz University, Jeddah.

The granulometry of beach sands is given in Table 2.1 and representative cumulative log plots of particle sizes are given in Fig. 2.5.

To enable comparisons to be made with data on tropical beaches by other workers (eg. Fellows, 1966; McIntyre, 1968; Trevallion *et al.*, 1970; Jones, 1974; Messana *et al.*, 1977; Chakrabarti, 1980) data are tabulated in phi units and in µm. $\phi = {}^{-}\log_2$ of the particle diameters in millimeters and conversions were made using a computer program written for this purpose. Also, several sorting coefficients are given for the King Saud Palace site where data were more vigorously collected and analysed.

Median grain size data for Sharm Obhor and median grain size and sorting characteristics at King Saud Palace are reasonably comparable with similar tropical Indian beaches (McIntyre, 1968; Trevallion *et al.*, 1970) where *Ocypode* species (*O. macrocera*, *O. platytarsis*,

Table 2.1. Sediment Grain Characteristics

Site	Distance from sea	Depth of core (cm)	Graphic mean ϕ	Graphic mean µm	Description
Obhor	25m	0-10	2.14	227	fine sand
	25m	10-20	1.94	261	medium sand
	25m	20-30	-1	2000	very coarse sand
	13m	0-10	1.99	252	f/medium sand
	13m	10-20	1.55	342	medium sand
	13m	20-30	1.30	406	medium sand
	1m	0-10	2.21	216	fine sand
	1m	10-20	2.10	233	fine sand
King Saud Palace	15m	0-1	2.29	205	fine sand
	15m	1-4	2.28	206	fine sand
	15m	5-8	1.95	259	medium sand
	15m	9-12	c.-1	c2000	very coarse sand
	7m	0-18	2.08	236	fine sand
	7m	18-28	1.95	259	medium sand
	7m	28-33	1.80	287	medium sand
	1m	0-10	2.18	221	fine sand
	1m	10-30	2.30	203	fine sand
Twaal	10m	0-20	2.15	225	fine sand
	5m	0-20	1.71	306	medium sand
	1m	0-20	0.86	551	coarse sand

Site	Distance from Sea	Skewness Sk_I (Sk_G)	Sorting Q_D	Sorting σ_G	Sorting σ_I	Description
King Saud Palace	15m	-0.13	0.20	0.30	0.37	well sorted
	15m	-0.32	0.25	0.46	0.51	mod. well sorted
	15m	(-0.48)	0.50	0.80	-	mod. well sorted
	15m	-	-	-	-	-
	7m	-0.28	0.34	0.55	0.55	mod. well sorted
	7m	-0.23	0.70	0.45	0.77	moderately sorted
	7m	(-0.48)	0.64	1.15	-	poorly sorted
	1m	-0.16	0.42	0.42	0.65	mod. well sorted
	1m	-0.32	0.27	0.70	0.58	mod. well sorted

Inclusive Graphic Skewness $$Sk_I = \frac{\phi16 + \phi84 - 2\phi50}{2(\phi84 - \phi16)} + \frac{\phi5 + \phi95 - 2\phi50}{2(\phi95 - \phi5)}$$

Graphic Skewness $$Sk_G = \frac{\phi16 + \phi84 - 2\phi50}{(\phi84 - \phi16)}$$

Phi Quartile Deviation $$Q_D = \frac{\phi75 - \phi25}{2}$$

Graphic Standard Deviation $$\sigma_G = \frac{\phi84 - \phi16}{2}$$

Inclusive Graphic Standard Deviation $$\sigma_I = \frac{\phi84 - \phi16}{4} + \frac{\phi95 - \phi5}{6.6}$$

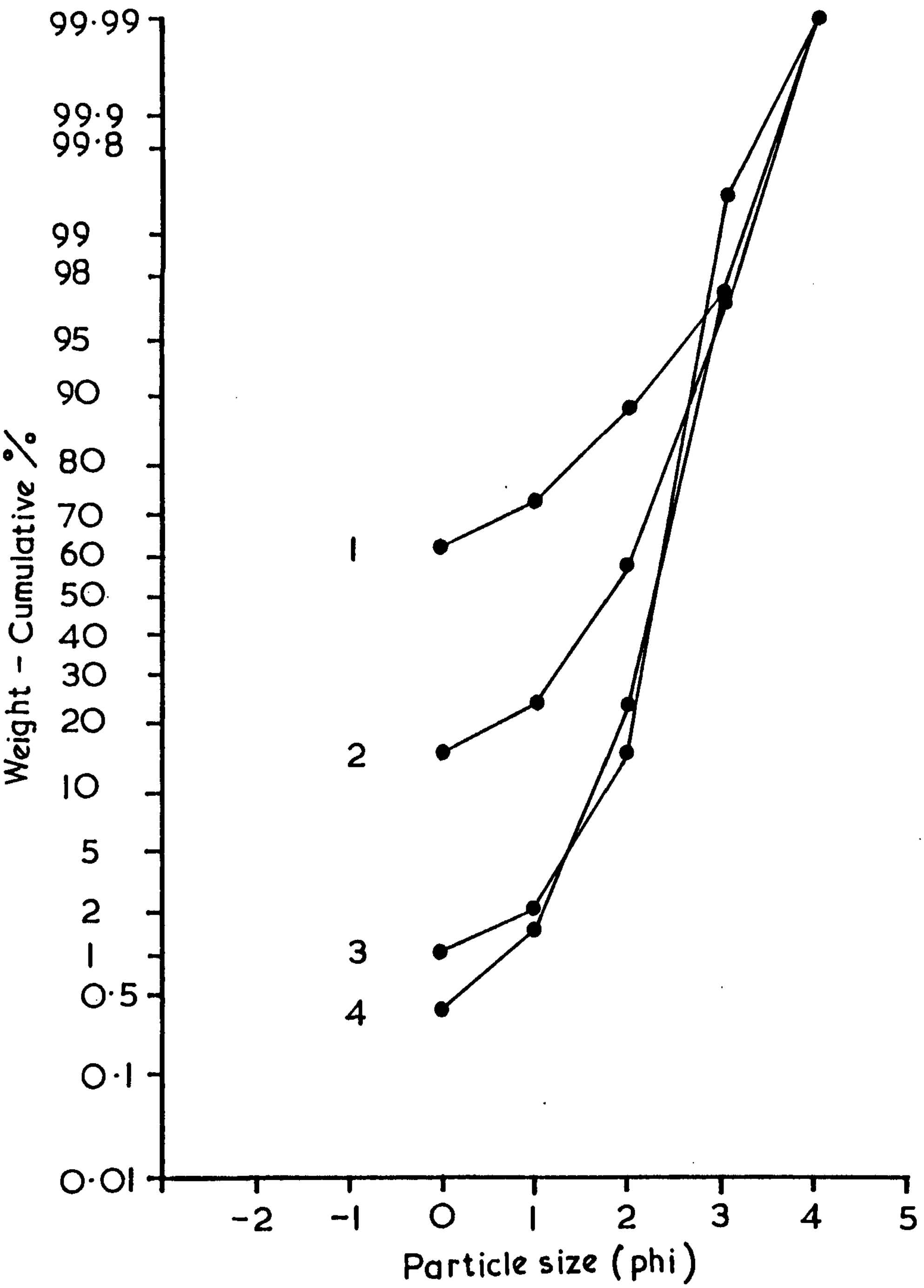
Fig. 2.5. Selected grain size data for King Saud Palace. 1 and 4 are the extremes, the remaining data are distributed between plots 2 and 4, eg. 3.

1 = top of shore, 9-12cm depth

2 = midshore, 28-33cm depth

3 = top of shore, surface

4 = lower shore, 10-30cm depth



99·99
99·9
99·8
99
98
95
90
80
70
60
50
40
30
20
10
5
2
1
0·5
0·1
0·01
Weight - Cumulative %
1
2
3
4
-2
-1
0
1
2
3
4
5
Particle size (phi)

O. ceratophthalmus) occurred ie. fine to medium usually well sorted sands. Also Jones (1974) for 3 Saudi Arabian beaches on which *O. saratan* occurred gave median grain sizes of 2.45Ø (sheltered depositional island shore), 1.94Ø and 0.94Ø (steep exposed shores). Fellows (1966) found that the Hawaiian beaches on which he studied *Ocypode* spp. (*O. pallidula*, *O. ceratophthalmus*) had median grain sizes between about 0.8Ø and 2.5Ø. Messana *et al.* (1977) gave data from Somalia which compare well with my observations. Their beach sands were medium-fine, well sorted and skewed towards the coarser particles. Chakrabarti (1980), however, demonstrated positive skewness in the distribution of sand grain frequency data in many of his Indian beach sediment samples and this he attributed to biogenic activity mixing different beach laminae. Within the limitations of sampling, all the present data were negatively skewed, ie. coarsely skewed. Nevertheless, the variation in median grain size, sorting and skewness almost certainly reflects the biogenic activity of *O. saratan* burrowing in addition to normal physical sorting by sea and wind.

Backbeach sedimentary processes consist of a number of complex interactions between aqueous and aeolian environments (Davis, 1978). Their sands are often finer and better sorted than seaward but there is great variation. Grain size will be controlled by the characteristics of the source sediment, the energy level of transporting medium and the beach slope (Folk, 1974; Komar, 1976). Sorting is strongly dependent on grain size (Folk, 1974). Negative skewness shows an overabundance of coarse grains or an underabundance of fine grains when compared to a normal Gaussian distribution and is a common feature of beach sands (Komar, 1976). Here it is the former and may represent the addition of coral and shell fragments. The modification of physical processes by biogenic activity is an additional complicating factor and according to Chakrabarti (1980) this 'needs critical attention' since it has been shown to be important in his study sites. In addition to burrowing activity, feeding behaviour (see Chapter 5) results in bivalve shells being transported up the beach and often into burrows.

For the present work, a proper explanation requires further detailed study but the data presented give some indication of the sedimentary environments in which the crabs burrow.

2.3.3. Tides

Morley (1975) indicates that tidal motion in the Red Sea is generated by the sea's own response to tide generating forces and also by the co-oscillating tide of the Gulf of Aden. This results in oscillatory semidiurnal tides (Morcos, 1970). High tide in the north of the Red Sea corresponds to low tide in the south and there is a 6h time difference between high tide in the north and high tide in the south (Morley, 1975). Morley (1975) indicates that the average spring range is 0.5m in the north and south, decreasing centrally, with no appreciable tide at the nodal point near 19°N. He also considered that daily changes in the coastal sea level were usually caused by the wind. Of the four causes for Red Sea water movement considered by Thompson (1939), ie. tides, winds, density changes and evaporative losses, wind was considered the most important. Irrespective of its effects on the water mass as a whole, it can certainly mask the presence of small tidal changes.

No accurate continuous tidal records exist for the study region although mean tide records exist for some years (see later). Limited data on tides were obtained during the present study and clearly show that at the study sites the tide has a small range and is semidiurnal. This is illustrated in Figs 2.6 and 2.7. The data illustrated in

Fig. 2.6. Tide trace taken 15km N of Jeddah using an automatic recording tide gauge from the 13th - 19th May 1984.

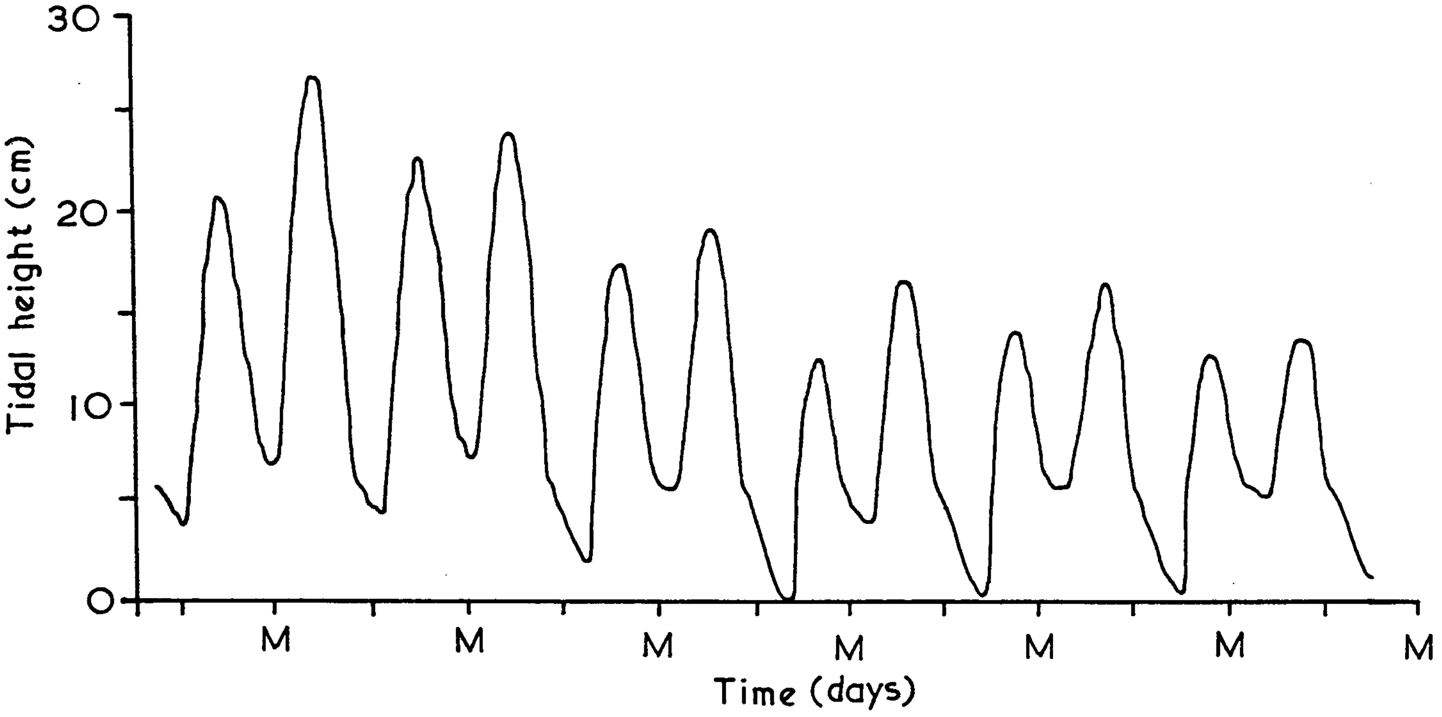

30
20
10
0
Tidal height (cm)
M
M
M
M
M
M
M
Time (days)

Fig. 2.7. a) Spring tides at Sharm Obhor, 14th - 15th May 1984

b) Neap tides at Sharm Obhor, 25th - 26th May 1984

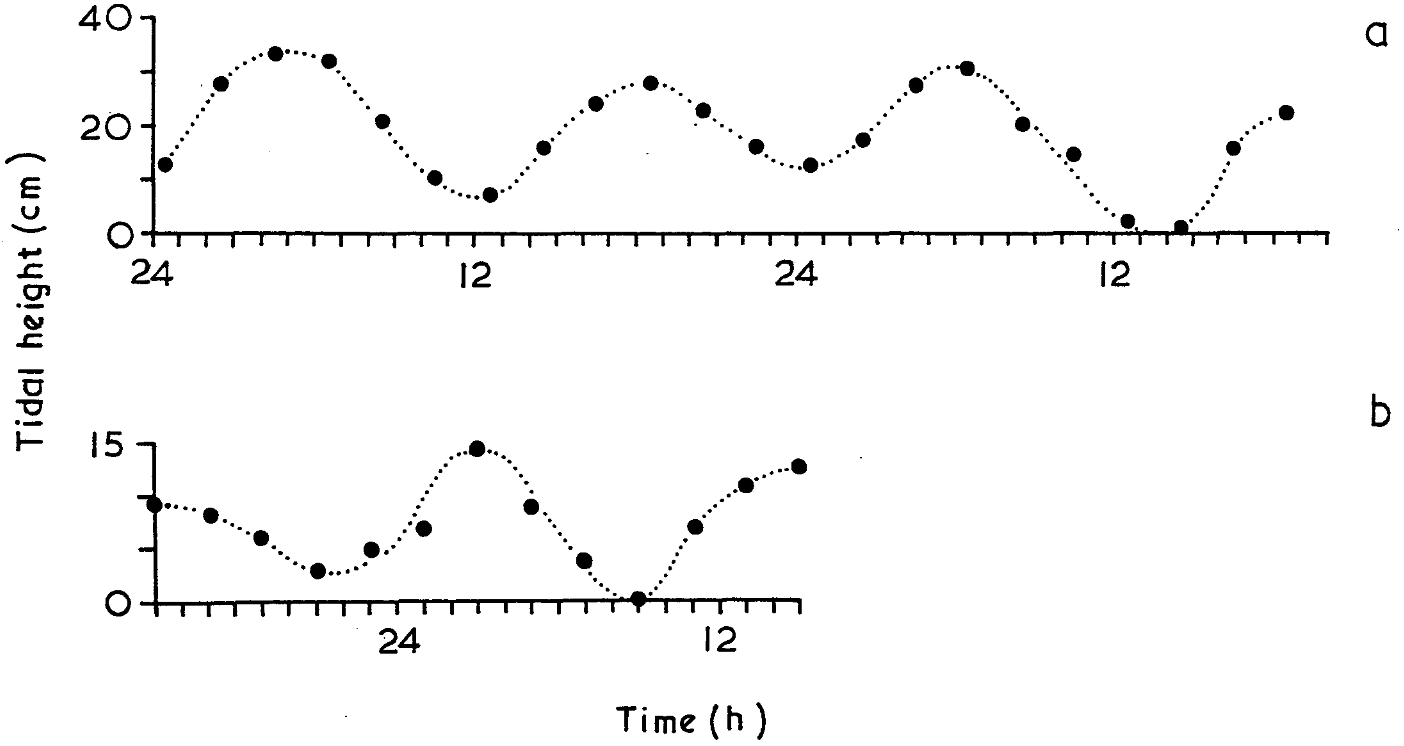

a
b
40
20
0
15
0
24
12
24
12
24
12
Tidal height (cm)
Time (h)

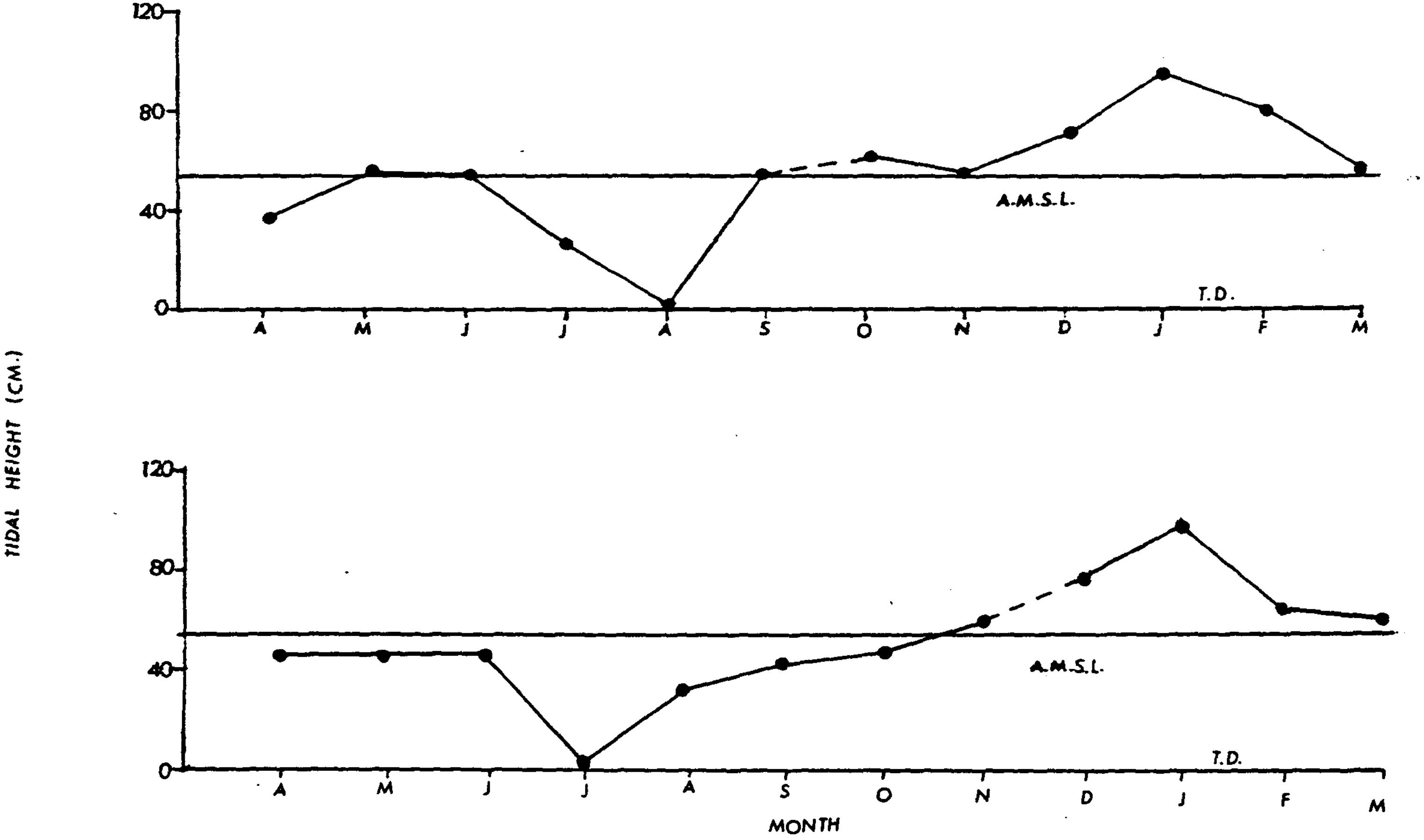
Fig. 2.6 were obtained from an unknown engineer who passed on the information to a colleague who knew of my interest. It relates to a site some 15km N of Jeddah and the record was obtained using an automatic recording tide gauge. The data illustrated in Fig. 2.7 were personally obtained at Sharm Obhor by manually measuring the tidal rise and fall in relation to a reference point. Both figures clearly show the semidiurnal nature of the tide - spring tide being illustrated in Figs 2.6 and 2.7a and neap tide in Fig. 2.7b. The tidal range varies from 10cm to around 30cm. The tides as illustrated are not related to any standardised datum. Although Morley (1975) states there is no appreciable tide in the Jeddah region, a small tide is to be expected from the appearance of the amphidromic system (see Koenig, 1982).

Despite their small magnitude, it will be seen that tides play an important part in the behaviour of O. saratan. Water level is, however, modulated by two other factors, wind effects which may mask tidal effects and seasonal changes in sea level.

2.3.4. Mean Sea Level

There is a marked seasonal variation in mean sea level in the Red Sea which is related to the monsoon winds in the Indian Ocean. Essentially, during the winter months the surface waters flow north, sink and return south as a warm subsurface current which flows out through the straits at Bab-el-Mandab. During the summer the pattern reverses and surface waters flow south causing upwelling in the north and a subsurface inflow through the Straits of Bab-el-Mandab (see Patzert, 1972, 1974). Patzert (1974) indicates that whereas, theoretically, astronomical effects, evaportion, precipitation, discharge, atmospheric pressure and steric effects may all influence sea level, in the

Fig. 2.8. Seasonal changes in Mean Sea Level. Upper = Sharm Obhor, lower = King Saud Palace. A.M.S.L. = Arbitrary Mean Sea Level. The data have been arranged with the months during which mean sea level was lowest presented first. The Sharm Obhor data were collected from Oct. 1983 until Sept. 1984. The King Saud Palace data were collected from Dec. 1982 until Nov. 1983.


TIDAL HEIGHT (CM.)
120
80
40
0
A.M.S.L.
T.D.
A
M
J
J
A
S
O
N
D
J
F
M
120
80
40
0
A.M.S.L.
T.D.
A
M
J
J
A
S
O
N
D
J
F
M
MONTH

Red Sea the monsoon wind reversal is the major factor controlling sea level. Morley (1975) summarises this by indicating that during the winter monsoon, predominantly SSE winds drive the surface waters of the Gulf of Aden northwards into the Red Sea. This inflow exceeds losses due to evaporation and subsurface outflow and results in increased sea level particularly between latitudes 19°N and 25°N where the currents oppose the NNW wind of the northern Red Sea. Mean sea level gradually falls from January to late July when monsoon reversal is complete and NNW winds blow throughout the Red Sea. There is a net loss of water, reducing mean sea level to an August minimum after which sea level gradually increases.

Morley's own data were recorded 10km N of Jeddah and he demonstrated dramatic short term coastal sea level fluctuations caused by transient changes in wind direction.

Koenig (1982), however, in a computer model, considers that surface circulation is mainly driven by the pressure gradient caused by the density field and not by the wind. He does state that his baroclinic model requires refinement and testing in nature.

Whatever the factors controlling circulation are, the resulting sea level changes are clearly seen. For the present study Fig. 2.8 clearly illustrates the seasonal change in sea level. My measurements agree with those of Patzert (1974) and Morley (1975). The levels recorded are not true means and are not standardised to the tidal cycle. They simply represent the height of the tide related to a standard reference point at each period of observation. Tidal fluctuations, however, are small and often masked by the wind, and the overall trend is clear.

An attempt to obtain mean sea level records from Jeddah Islamic

Harbour proved unsuccessful. Some data were obtained but records were not consistently available so have been discounted.

2.3.5. Temperature and Relative Humidity

Situated between the African and Arabian deserts, the Red Sea experiences high temperature and low precipitation. The relative humidity along the sea shore is usually high, reaching as much as 100% during the night but occasionally dropping to 10% or below when a NE wind is blowing from the desert. Table 2.2 is a summary of climatological data obtained with the assistance of the Faculty of Meteorology, King Abdul-Aziz University, Jeddah, from the Kindgom of Saudi Arabia Ministry of Defence and Aviation, General Directorate of Meteorology. The data for 1983 may be taken as representative and indicate the extremes of temperature and relative humidity that the ghost crab O. saratan potentially faces. As shall be seen later, many field measurements of air, soil and water temperature and relative humidity were taken in the present study but these do not present so comprehensive an analysis as the above table. Measurements in the present study were mainly directed into examining microclimatic conditions.

Sea surface temperatures range from around 25°C to 31°C in the Jeddah region (Bemert and Ormond, 1981) and according to Morley (1975) coastal waters south of latitude 20°N are approximately 2°C warmer than offshore waters. As might be expected, the water temperatures at the tide edge and experienced by O. saratan are several degrees warmer again.

Beach sand surface temperatures approaching 50°C were measured in this study (see later).

For comparison with the data of Table 2.2, Table 2.3 presents air temperature data collected during this study at Sharm Obhor during beachwork. All measurements were taken at 1400h and 2400h using an electronic digital thermometer.

Table 2.2. Monthly Climatological Data for Jeddah in 1983

MONTH	Temperature (^{o}C)			Relative Humidity (%)			Rainfall (mm)
	maximum	minimum	mean	maximum	minimum	mean	
Jan.	30.4	12.0	20.5	98	10	58	3.0
Feb.	32.0	12.0	21.3	96	10	56	0.0
Mar.	34.0	11.0	22.6	99	10	57	0.0
Apr.	37.4	14.0	25.9	95	13	57	0.7
May	42.0	19.5	30.2	100	12	52	0.0
June	44.0	22.5	31.5	100	15	58	0.0
July	42.0	23.0	31.7	100	15	56	0.0
Aug.	42.0	22.5	31.6	96	11	57	0.0
Sept.	40.4	23.0	31.3	100	18	63	0.0
Oct.	40.3	20.0	28.6	96	3	65	0.0
Nov.	37.0	19.0	27.0	96	16	67	0.0
Dec.	34.0	14.6	20.3	95	19	59	2.0

Data were continuously recorded, 24h a day, by the General Directorate of Meteorology, Ministry of Defence and Aviation, Kingdom of Saudi Arabia.

Table 2.3. Air Temperature records at Sharm Obhor

Month	Days recorded	1400 (°C)	2400 (°C)	mean (°C)
Jan.	5	30.2	16.5	24.3
Feb.	6	32.6	18.2	22.5
Mar.	8	32.0	24.0	26.4
Apr.	14	37.3	22.0	28.9
May	20	43.0	33.0	29.3
June	4	36.0	32.9	33.2
July	3	43.0	34.5	36.2
Aug.	2	38.0	32.9	34.4
Sept.	14	35.7	33.0	34.4
Oct.	10	37.0	30.0	32.3
Nov.	5	33.0	28.5	30.5
Dec.	3	31.0	29.0	29.7

CHAPTER 3. THE BURROWS AND BURROWERS

3.1. Introduction

Burrow structure and the burrowing behaviour of crabs of the genus *Ocypode* has been reviewed by Vannini (1980a) to which may be added several other recent studies (eg. Frey and Mayou, 1971; Hill and Hunter, 1973; Shuchman and Warburg, 1978; Brooke, 1981; Chakrabarti, 1981; Hill, 1982). Vannini (1980a) compared information on the structure of the burrows of 13 species of *Ocypode*. For some of these (*O. ceratophthalmus*, *O. cordimana*, *O. pallidula*, *O. quadrata*, *O. ryderi*, *O. stimpsoni*, *O. macrocera*) information is available on the structure of the burrows of juvenile and adult crabs but for the remainder only adult burrows have been described. In the case of *O. saratan* the only burrows described are those of sexually mature males (Parenzan, 1931; Al-Kholy, 1959; Magnus, 1960; Linsenmair, 1965, 1967). Only Linsenmair (1965, 1967) realised the significance of the burrow type; Parenzan (1931) misidentified the crabs as *O. ceratophthalmus* and only Al-Kholy (1959) prepared casts of the burrows. Linsenmair (1967) who appeared unaware of Al-Kholy's work, dug up 1000 burrows of sexually mature males and described their structure as 'spiral'. Al-Kholy (1959) demonstrated burrows of more complex structure than that indicated by Linsenmair (1967) and this thesis reports burrows more complex still. Here, however, the burrows of juvenile crabs and mature female crabs are described in addition to those of mature males. Linsenmair (1965, 1967) referred in passing that burrow types other than spiral ones existed, but presented no information other than referring enigmatically to 'sleeping holes, eating holes, living holes and moulting holes'.

In this Chapter, therefore, I examine various aspects of the shore distribution of *O. saratan* and present some data on its population structure. The burrows are examined in some detail and the in-burrow environment is considered. Results are then discussed against the background of *Ocypode* literature and that relating to other relevant species. The work of Fellows (1966, 1973) on *O. ceratophthalmus*, *O. pallidula* and *O. cordimana* is particularly relevant and so are the observations of Barrass (1963), Hughes (1966, 1973) and Jones (1972) on *O. ceratophthalmus* and the observations of Jones (1972) and Vannini (1976a) on *O. ryderi*. Vannini (1976a, 1980a) has provided excellent reviews of various aspects of the behavioural ecology of *Ocypode* species but as shall be seen there are many gaps in knowledge and many inconsistencies when comparing the work of various authors. Both Vannini (1976a, 1980a) and Fellows (1966, 1973) draw attention to this. Whereas for *Ocypode* spp. there is a reasonably extensive, though sometimes contradictory, literature on burrow structure, there is much less information on population biology and most of the information that does exist is derived secondarily from burrow distributions. A comprehensive study of the population biology of *O. saratan* has not been attempted here but some information has been obtained while concentrating primarily on the burrows.

The importance of the burrows in giving protection from environmental extremes is best known in *Uca* spp. (Edney, 1961; Smith and Miller, 1973; Powers and Cole, 1976) and in *Gecarcinus lateralis* (Bliss, 1968). Its importance in *O. saratan* is indicated here. The burrows also protect crabs from natural predation and from crushing from 4-wheel drive vehicles (see Wolcott and Wolcott, 1984, for *O. quadrata*). Human impact effects on *O. saratan* are briefly examined, the most serious of which is the distruction of habitat.

3.2. Material and Methods

Zonation data on O. saratan were obtained from the King Saud Palace site from December 1982 until November 1983 and from the Sharm Obhor site from October 1983 until September 1984. Each site was visited monthly. A rope grid divided into metre squares was used to map the distribution of crab burrows (Plate 3.1a). At King Saud Palace the grid used was 10m x 10m which covered the narrow supralittoral zone occupied by the crabs. At Sharm Obhor, the flatter beach required a grid of 10m x 20m to cover the wider area in which the crabs occurred (see Chapter 2). On each visit the beach was surveyed using a theodolite (see Chapter 2) so that the position of crab burrows could be related to the tidal datum established for the study (lowest water level encountered, see Chapter 2). On most occasions the grid was established so that its lower edge was at the low tide mark of the day and its upper edge extended to the dune at King Saud Palace and the limestone raised reef at Sharm Obhor. In summer when the reef flat was exposed the lower edge of the grid corresponded to the lower boundary of the supralittoral sand beyond which no crab burrows occurred.

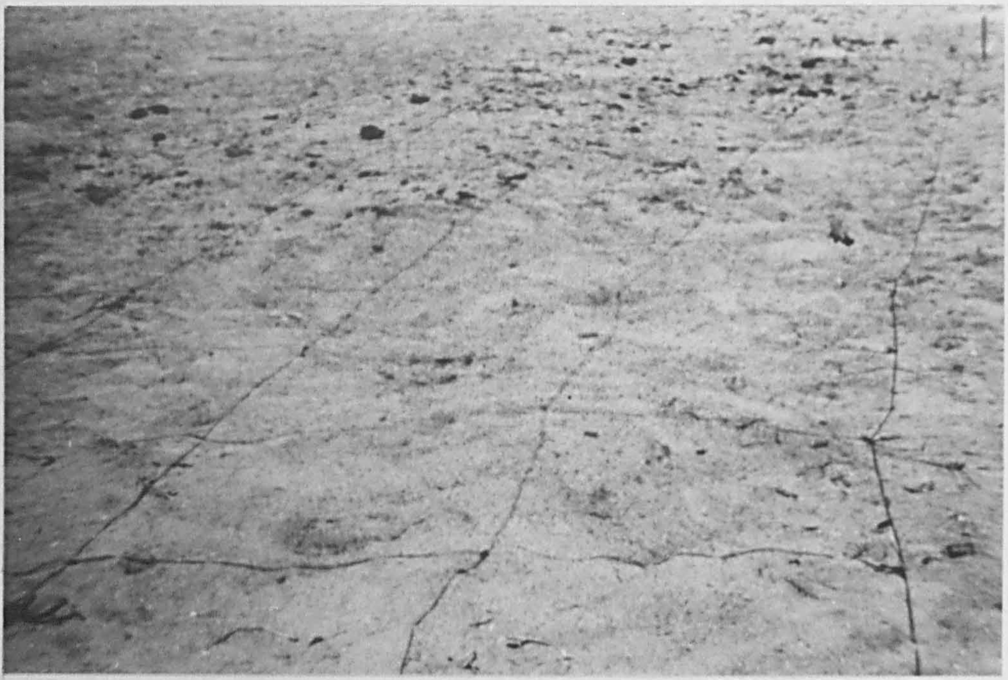
All O. saratan burrows encountered were mapped on graph paper corresponding to the grid dimensions so that distribution and density could be determined. Burrow width was recorded and also burrow slope, orientation and where relevant sand pyramid dimensions, and distance between sand pyramids and corresponding burrow entrances. On many occasions the burrow was then excavated to capture the inhabitant whose size and sex was then determined.

The King Saud Palace site became increasingly subject to human disturbance during the study. The isolated Sharm Obhor site, however, remained undisturbed and from here crabs were collected by trapping.

Plate 3.1. a) Rope grid on beach at Sharm Obhor.

b) Pouring polyester resin down an O. saratan burrow at Sharm Obhor.

a



b

Buckets buried in the sand near the tide edge, in the centre of the beach and near the top of the beach served as pitfall traps. They were usually baited with small dead fish or with bivalves (*Mesodesma* sp.). Sand near the tide edge was sieved through a 1mm mesh sieve in an attempt to collect very small crabs. Out of their burrows on land, crabs were far too rapid to catch. Some crabs encountered on the beach were chased into the water where they became comparatively inactive within minutes, often burying in the sand and were relatively easily caught by hand. Crabs trapped or otherwise caught each month, together with those collected by digging out burrows were measured to the nearest 0.1mm using vernier callipers and sex, colour and handedness (ie. side of largest cheliped) were recorded. Several crabs were retained for anatomical studies and the remainder were released so as not to deplete the study population.

Details of burrow structure were obtained by three methods: 1, hand excavation and observation; 2, casting burrow using gypsum (Plaster-of-Paris) and 3, casting burrow using polyester resin (Plate 3.1b). A very liquid gypsum slurry was prepared using transported freshwater and poured into juvenile and adult burrows. Accurate but brittle casts were obtained and these were carefully excavated, washed down, measured and photographed. The plaster casts of male crab burrows were incomplete - the material had not fully penetrated the deep, extensive systems before setting as evidenced by careful excavation. Polyester resin did give complete penetration but had the disadvantage of penetrating the sand surrounding the burrow giving casts of exaggerated width (see Farrow, 1971, 1975). Sectioning, however, showed the true burrow dimensions. The resin technique is detailed by Farrow (1975) and Atkinson and Chapman (1984). At the high environmental temperatures encounted, resin cured rapidly following the addition of between 1% and 2% catalyst. Saturation of the sand with seawater did not significantly either moderate the speed of curing or reduce penetration of the sand by the resin.

Some 200 burrows were cast in all, mostly by using Plaster-of-Paris. Not all of these casts were complete, however, but sufficient detailed information was obtained to enable the burrow forms to be described.

The least accurate technique for assessing burrow structure was digging when sand collapse made it extremely difficult to map a complex burrow. Crabs were usually trapped within casts. Those that did escape from burrows were captured whenever possible.

Burrow elevation, width, slope, orientation and in the case of male burrows, pyramid height and distance from the burrow were recorded prior to casting. The sex and size of the inhabitant of each burrow cast was recorded. General burrow terminology follows Simpson (1975) and detailed male burrow terminology follows Linsenmair (1967).

Climatic and microclimatic recordings were taken using digital combined psychrometer and temperature probes (Theis Clima, Model 462; Kane-May Model 8001) which enabled records to be routinely taken up to 20cm into crab burrows and with care, deeper still (Plate 3.2a). Digital thermocouple probes were used to measure soil and water temperature.

Photographic records were obtained using either a Nikon F3 35mm camera or a Nikonos IV 35mm camera which had the advantage of being waterproof and sandproof.

Plate 3.2. a) Measurement of temperature and relative humidity within an O. saratan burrow. The burrow is orientated to open towards the sea.

b) O. saratan burrow in the dune at King Saud Palace. This burrow opens away from the sea.

a

b

3.3. Results

3.3.1. Distributions, densities and bionomics

3.3.1.1. Zonation

At both King Saud Palace and Sharm Obhor O. saratan exhibits a clearcut zonation pattern. The position of crabs on the shore varies seasonally.

In the 'summer' (April-November) the crab burrows develop throughout the supralittoral sand. Beyond this the reef flat exposed in July and August and partially covered tidally is utilized for feeding. The crabs cannot utilize this exposed area for dwelling burrows because it is superficially muddy at Sharm Obhor and is rocky at King Saud Palace. It also becomes very warm during the day. The smallest juveniles occur at the junction between the beach sand and the tidal flat, while larger juveniles occur further inshore, followed by mature females and then mature males, with some overlap between zones.

In the 'winter' (December-March) when mean sea level is at its highest then the crabs move up the beach, particularly the juveniles and adult females, to avoid being covered by the water. Zones are more compressed at this time.

These points are illustrated in Figs 3.1 and 3.4 and can also be seen in Tables 3.4 and 3.5.

Zonation is examined in more detail in the section on population bionomics.

3.3.1.2. Burrow orientation

Fig. 3.2 presents orientation data for O. saratan burrows at

Fig. 3.1. Overall zonation pattern of O. saratan. The beach profile presented is that of November 1983. There is some monthly variation, eg. the beach sand does not always form a small 'hump' in the middle of the beach. The rise in sea level pushes the crabs up the beach in winter. A.M.S.L. = Arbitrary Mean Sea Level (see Chapter 2).

A = the vertical zone of the beach dominated by adult male crabs.

B = the vertical zone of the beach dominated by adult female crabs.

C = the vertical zone of the beach dominated by the larger juveniles (1.7-2.9cm carapace width).

D = the vertical zone of the beach dominated by the smaller juveniles ($<$ 1.7cm carapace width).

There is some overlap between zones.

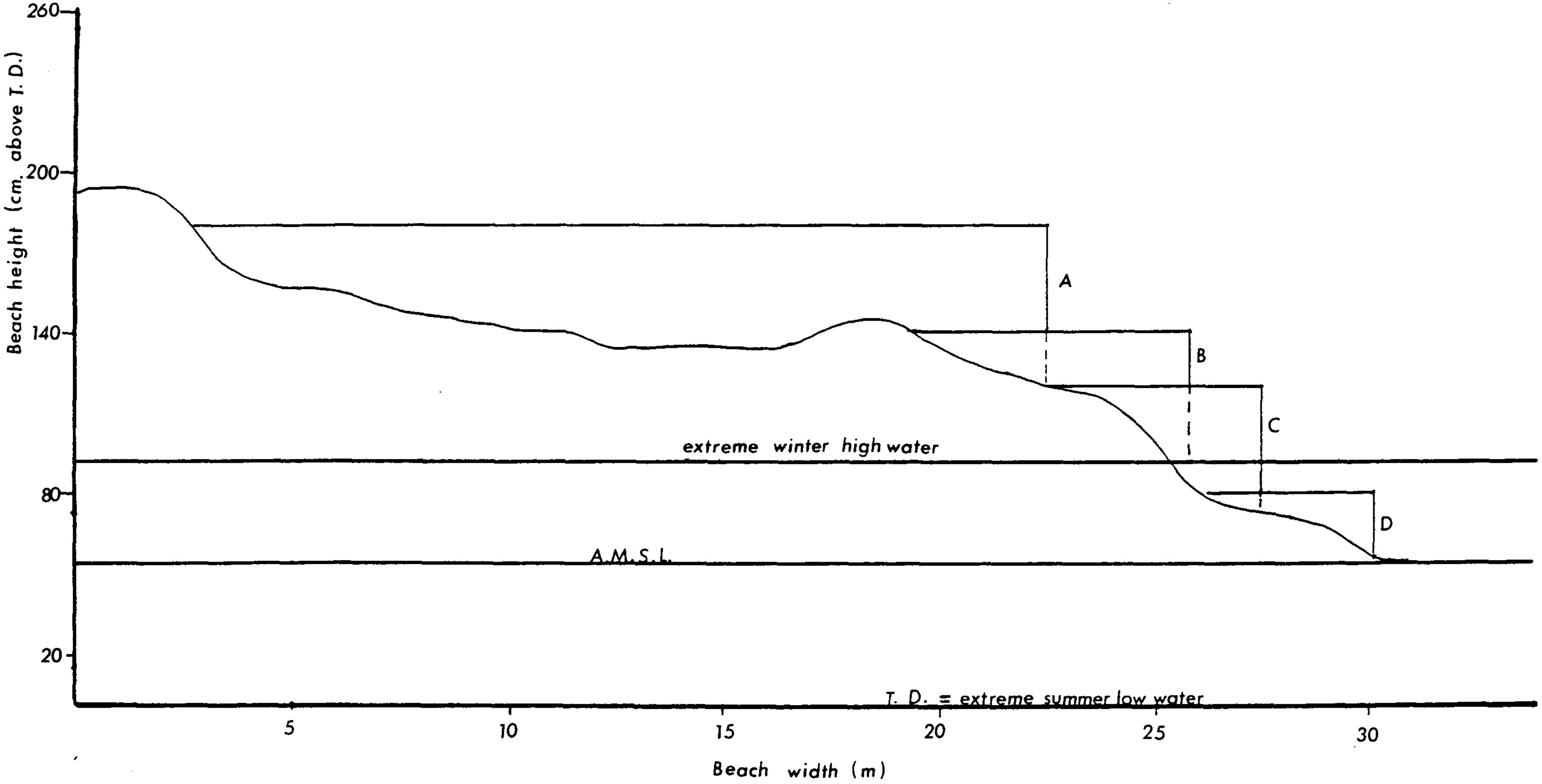
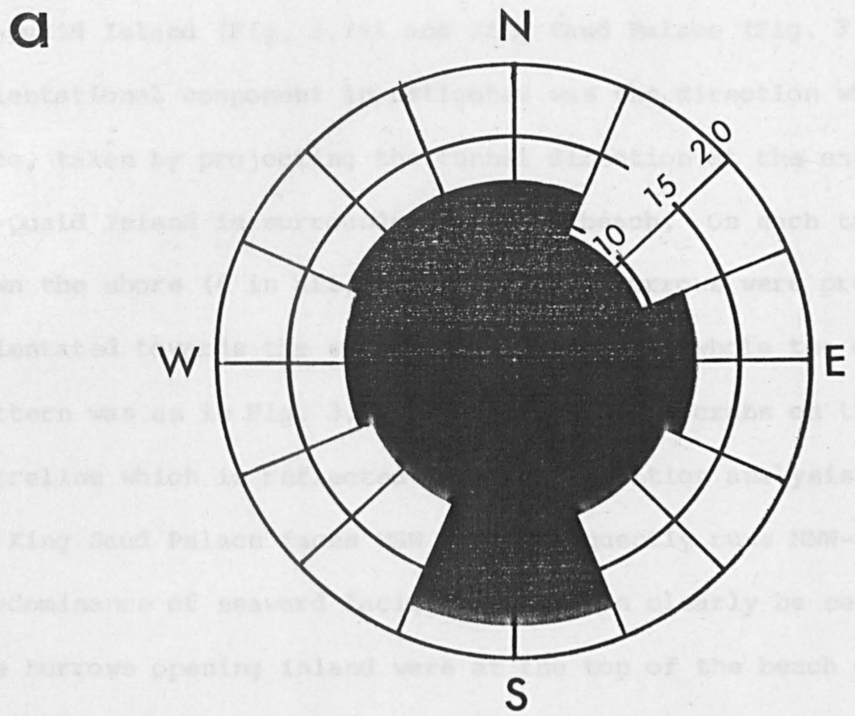

Beach height (cm. above T. D.)
260
200
140
80
20
A
B
C
D
extreme winter high water
A.M.S.L.
T. D. = extreme summer low water
5
10
15
20
25
30
Beach width (m)

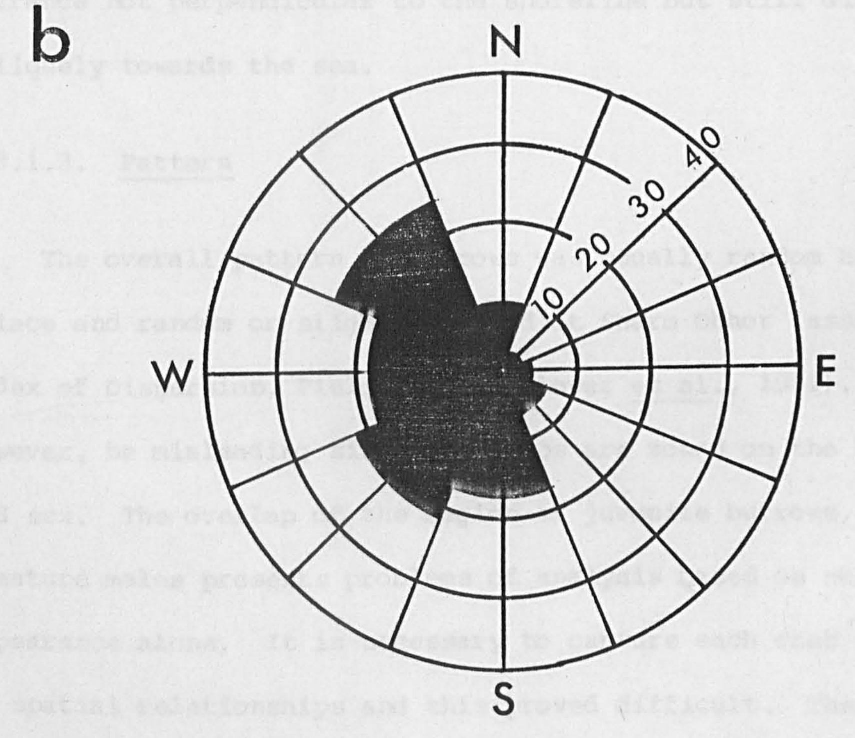
Fig. 3.2. Orientation of the burrows of O. saratan.

a) At Al-Quaid Island

b) At King Saud Palace

The numerals indicate numbers of burrows.


a
N
W
E
S
10
15
20


b
N
W
E
S
10
20
30
40

Al-Quaid Island (Fig. 3.2a) and King Saud Palace (Fig. 3.2b). The orientational component investigated was the direction which burrows face, taken by projecting the tunnel direction at the entrance. Al-Quaid Island is surrounded by sandy beach. On each transect taken down the shore (4 in all, N, S, E and W) burrows were predominantly orientated towards the sea so that taken as a whole the orientation pattern was as in Fig. 3.2a. There were more crabs on the S facing shoreline which is reflected in the orientation analysis. The beach at King Saud Palace faces WSW and consequently runs NNW-SSE. The predominance of seaward facing burrows can clearly be seen. Most of the burrows opening inland were at the top of the beach or amongst the dunes (Plate 3.2b). That numerous burrows are orientated in NW and S directions reflects the spiral nature of male crab burrows, the dextral or sinistral spiral of the burrow often resulting in an entrance not perpendicular to the shoreline but still directed obliquely towards the sea.

3.3.1.3. Pattern

The overall pattern of burrows was usually random at King Saud Palace and random or slightly spaced at Sharm Obhor (assessed using Index of Dispersion, Pielou, 1969; Blower et al., 1981). This can, however, be misleading since the crabs are zoned on the bases of age and sex. The overlap of the region of juvenile burrows, females and immature males presents problems of analysis based on surface burrow appearance alone. It is necessary to capture each crab to be certain of spatial relationships and this proved difficult. Therefore, it was decided at this stage to restrict further pattern analysis to mature male crab burrows with pyramids since these were unambiguously recognisable without needing to capture the occupant.

Fig. 3.3. Spatial distribution of O. saratan burrows at Sharm Obhor in July 1984.

Triangles = sand pyramids (NB one burrow with 2 pyramids).

Large closed circles with triangles = burrows of mature male crabs of estimated carapace width > 4.2cm.

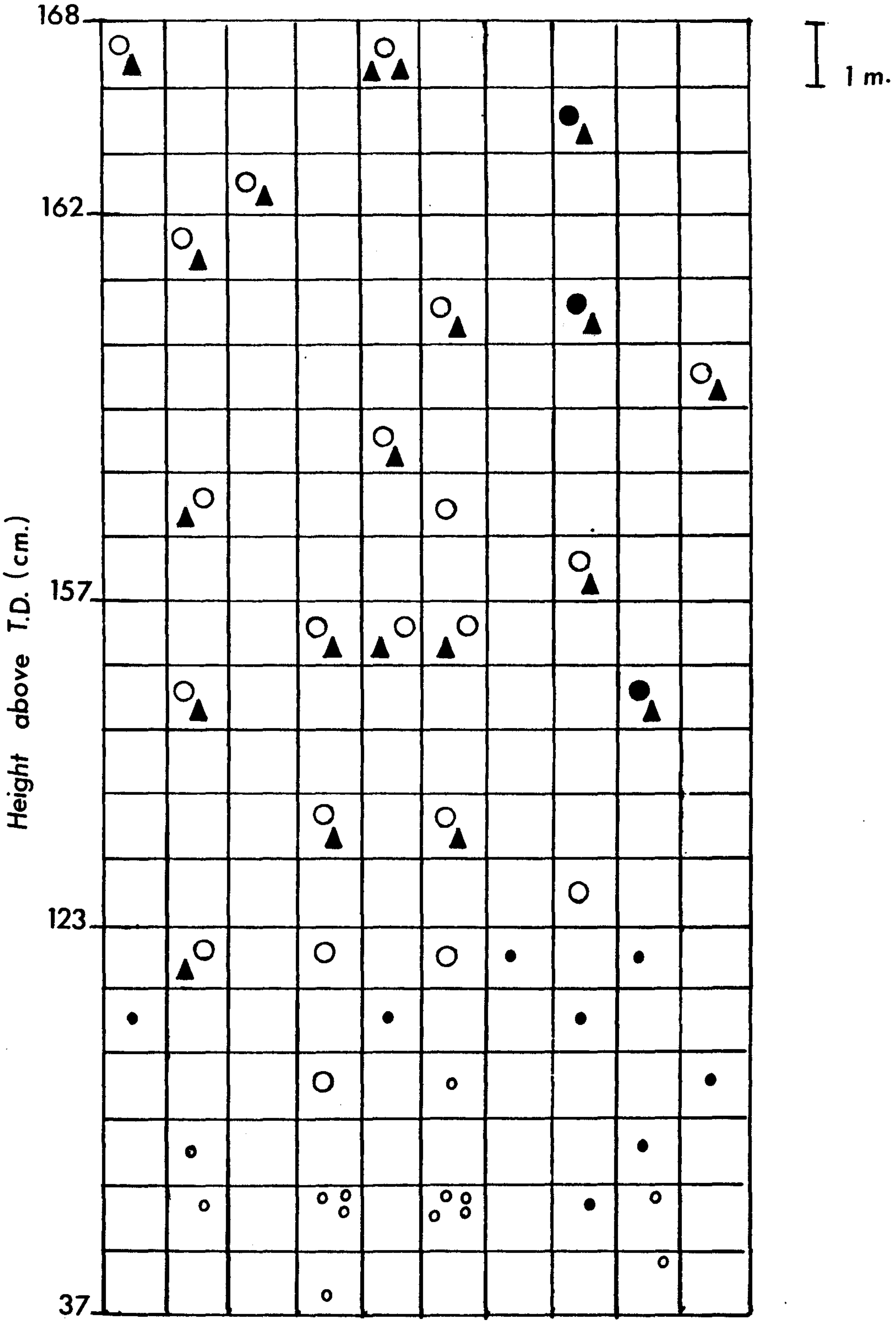
Large open circles with triangles = burrows of mature male crabs ($<$4.2cm carapace width).

Large open cirlces without triangles = burrows of adult female crabs ($>$3.0cm carapace width).

Small closed circles = juveniles of estimated carapace width 1.7-2.9cm.

Small open circles = juveniles of estimated carapace width $<$ 1.7cm.

T.D. = Tidal Datum.


168
162
157
123
37
Height above T.D. (cm.)
1 m.

The results were that male burrows were usually randomly distributed but at Sharm Obhor in March, April and May male burrows were spaced. This period coincided with the establishment of pyramids. At King Saud Palace densities were low (Table 3.1) and the area was subject to so much human interference (Section 3.3.1.6.) that I do not place much confidence in the pattern data. Overall burrow distribution at King Saud Palace was random except during May when aggregation was demonstrated ($P < 0.01$) and both male burrows and female burrows contributed to this.

At Sharm Obhor overall burrow distribution indicated slight spacing ($0.05 > P > 0.005$) in January, February, March, April and August, presumably indicating territoriality. Other distribution was random ($0.05 < P > 0.95$). Fig. 3.3 illustrates the distribution of burrows at Sharm Obhor in July.

3.3.1.4. Density

The King Saud Palace site is geomorphologically typical of much of the Red Sea shoreline. Its narrow (10-15m), steep (gradient c. 1:7) sandy beach does not give much space for O. saratan, especially during winter when sea level is elevated. Burrow density is not high at King Saud Palace with overall monthly densities varying from $0.03.m^{-2}$ to $0.2.m^{-2}$ (Table 3.1). The density at the very similar Twwal site was $0.12.m^{-2}$ in October 1983 and this was the same as at King Saud Palace at this time. In each case densities were derived from a $100m^2$ grid of 10m x 10m divided into metre squares.

At Sharm Obhor, the more extensive beach (20-25m from top to tide) with its shallow gradient (1:15) gave more supralittoral area in which the crabs could burrow. Densities were derived from a $200m^2$ grid of 20m x 10m divided into metre squares. Monthly densities

Table 3.1. Burrow densities $.m^{-2}$

Month	King Saud Palace	Sharm Obhor
Jan.	0.03	0.20
Feb.	0.07	0.30
Mar.	0.12	0.23
Apr.	-	0.30
May	0.20	0.30
June	0.17	0.24
July	0.13	0.23
Aug.	0.12	0.21
Sept.	0.10	0.15
Oct.	0.12	0.41*
Nov.	0.17	0.23
Dec.	0.07	0.23

	Twwal	Al-Quaid
Jan.		0.34
Oct.	0.12	

NB		
	King Saud Palace	Dec. 1982 - Nov. 1983
	Sharm Obhor	Oct. 1983 - Sept. 1984
	Twwal, Al-Quaid	1983

* Only lower half of shore sampled here.

varied from $0.15.m^{-2}$ to $0.3.m^{-2}$ (the October data are not strictly comparable since only the lower half of the shore was surveyed - $100m^2$). This type of shore is typical of many sharms and islands in the Red Sea and burrow density is often high. At Al-Quaid in January 1983 the density of burrows was $0.34.m^{-2}$, comparing well with Sharm Obhor.

Two points should be noticed. Firstly, these are burrow densities not necessarily crab densities. Secondly, they are overall densities taking all size ranges of burrows into account throughout the area in which the burrows occur.

Collapsed burrows were ignored during mapping. The burrows mapped were those with fresh signs of occupancy. Closed burrows were normally revealed by surface features (tracks, pyramids) and would not often have been missed under undisturbed conditions. Person and vehicle disturbance of the sand, however, disrupted surface features and low density estimates may sometimes reflect this at King Saud Palace. Very small O. saratan, not all of which burrowed, were almost certainly underestimated.

3.3.1.5. Population bionomics

An analysis of the population biology of O. saratan was not a primary objective of this study but in examining burrows and observing the size and sex of the occupants some information has been obtained and was supplemented by crab collections.

Size composition

From measurements of crab size and the corresponding burrow width, a regression analysis enabled crab size to be estimated from burrow width. Because of the difficulties in accurately measuring

Fig. 3.4. The seasonal variation in the vertical distribution of O. saratan at Sharm Obhor. The data are arranged so that the months coincide with the sea level data presented in Fig. 2.8. For each month there are four half-kite diagrams. From left to right these represent the distribution of juvenile crabs of estimated carapace width < 1.7cm; juvenile crabs of estimated carapace width 1.7 - 2.9cm; adult crabs of estimated carapace width 3.0 - 4.2cm - mostly adult females seawards; and adult crabs of estimated carapace width > 4.2cm - mostly adult males shorewards, respectively. The total length of the scale bar represents 10 crabs.

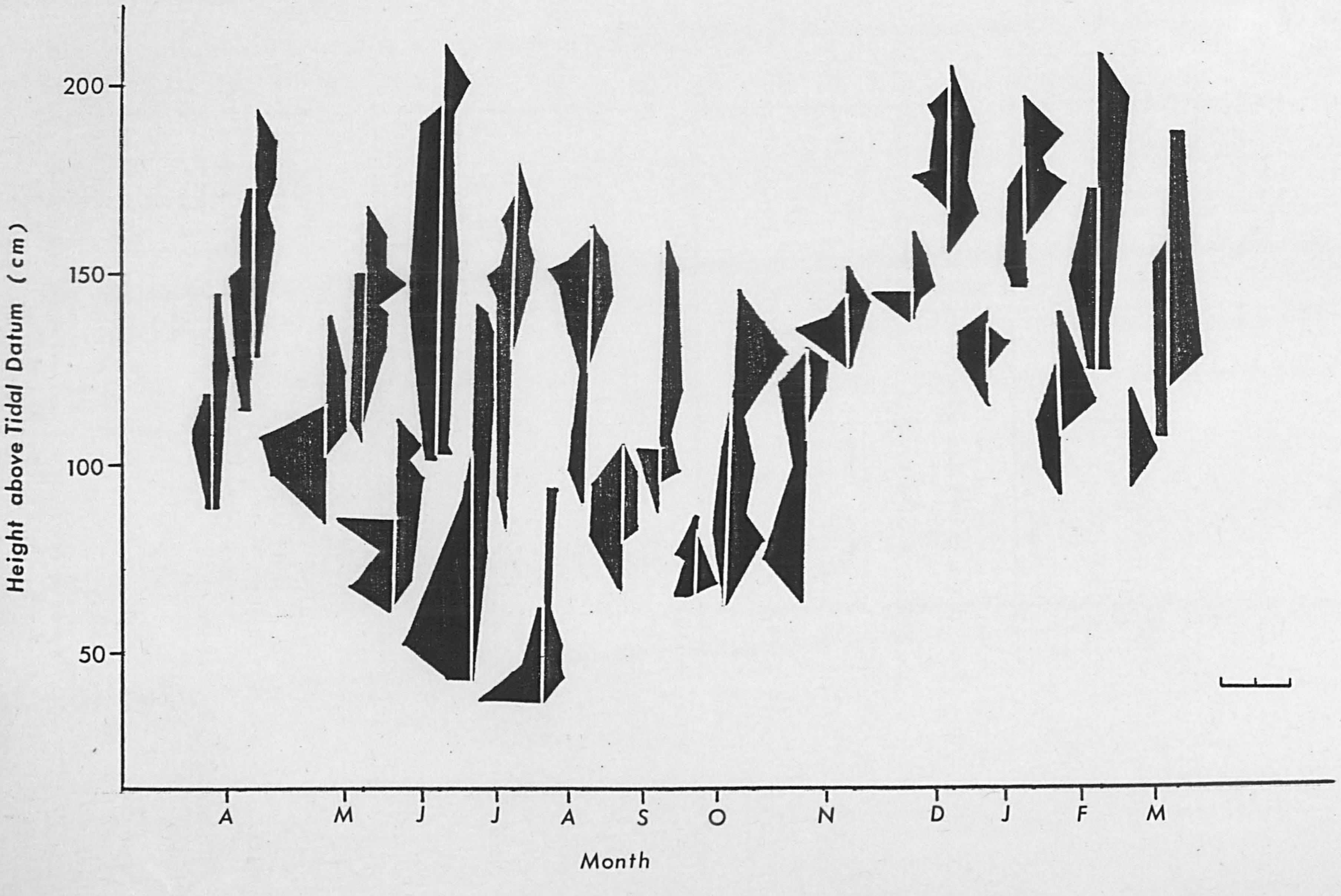
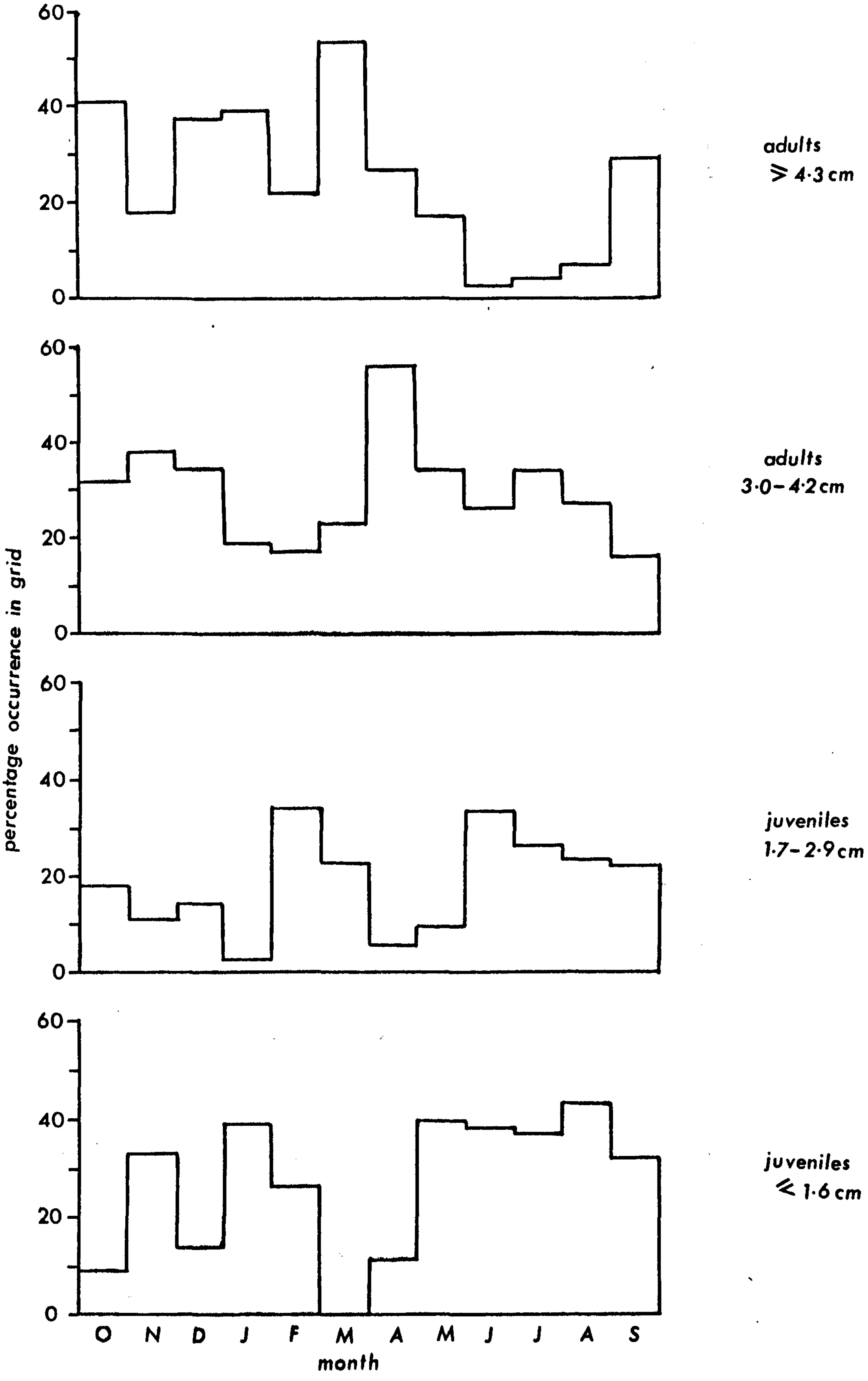

Height above Tidal Datum (cm)
200
150
100
50
A
M
J
J
A
S
O
N
D
J
F
M
Month

Fig. 3.5. Percentage occurrence of different size groups of <u>O. saratan</u> in the monthly sampling grids at Sharm Obhor.



60
40
20
0
adults
⩾ 4·3 cm
adults
3·0–4·2 cm
juveniles
1·7–2·9 cm
juveniles
⩽ 1·6 cm
percentage occurrence in grid
O
N
D
J
F
M
A
M
J
J
A
S
month

burrow widths in the field, the data collected have been grouped. The size grouping, though arbitrary, is roughly based on size groupings suggested by the different types of cast. The seasonal pattern of size distribution is illustrated in Fig. 3.4. The figure also indicates the seasonal change in position on the shore which is related to mean sea level changes (Chapter 2). The data are differently presented in Fig. 5 which shows variations in the size composition in each month (see Discussion).

The relationship between carapace width and burrow width is expressed by the equation

$$\log y \text{ (burrow width)} = 0.042 + 1.03 \log x \text{ (carapace width)}$$

$$r = 0.99, \; n = 63$$

The relationship between carapace width and carapace length is expressed by the equation

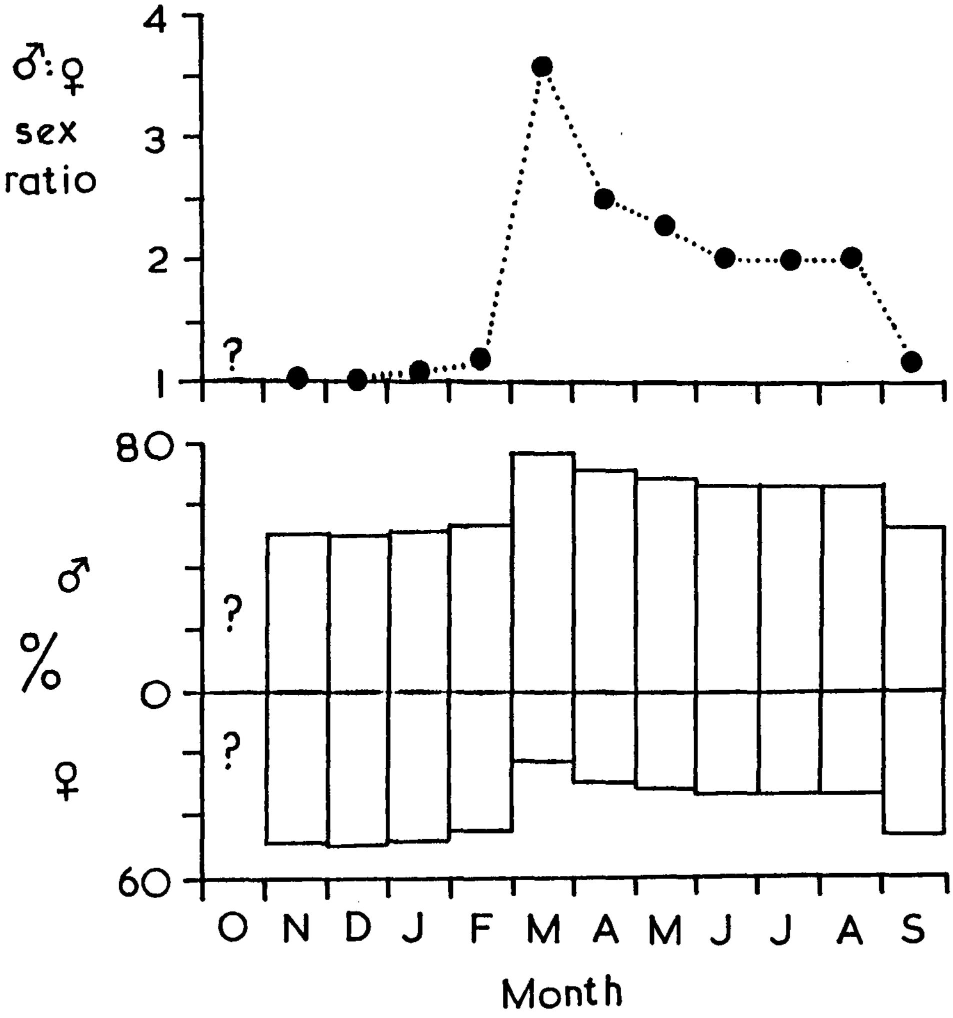
$$\log y \text{ (carapace length)} = 0.102 + 1.09 \log x \text{ (carapace width)}$$

$$r = 0.97, \; n = 39$$

Sex ratio

The sex ratio is probably 1:1 and the differences in Fig. 3.6 (Sharm Obhor) probably reflect sampling inadequacy rather than true deviations from equal numbers of each sex. The deviation from a 1:1 sex ratio in March coincides with the start of the breeding season as evidenced by the establishment of the signal pyramids of the males. During this period many females remain underground in the male copulation burrows and are therefore not caught at the surface. At the end of the breeding season the sex ratio is again 1:1. Of the 278 crabs collected in this analysis, 166 were males and 112 were females, giving an overall male to female ratio of 1.48.

Fig. 3.6. Sex ratio of *O. saratan* from Sharm Obhor.


♂:♀
sex
ratio
4
3
2
1
?
80
♂
?
%
0
?
♀
60
O
N
D
J
F
M
A
M
J
J
A
S
Month

At King Saud Palace some crabs were caught at the water's edge each month and although numbers were generally small the same summer trend was apparent, ie. more males than females were caught during summer. Here, however, the situation was reversed in winter so that, overall, of 170 crabs collected throughout the year 86 were females and 84 were males giving a male to female ratio of 0.98. The explanation for this difference with Sharm Obhor is probably related to behavioural differences reflected in the different capture methods.

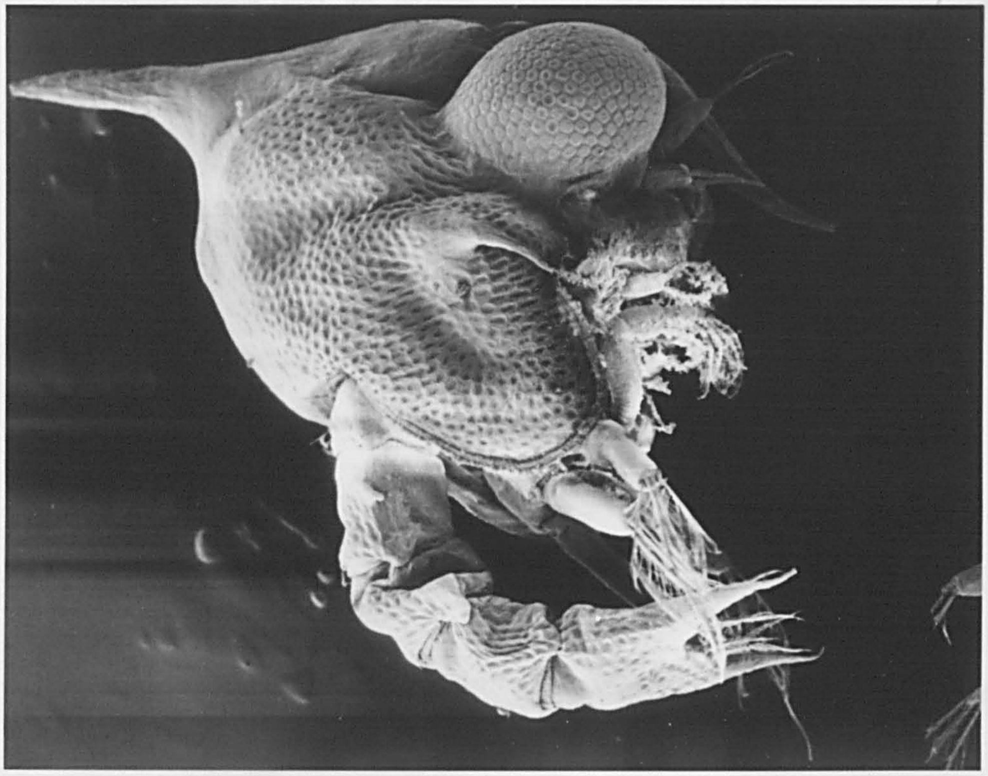
Larvae

Two ovigerous female crabs were caught in the field (May and July, 1983) and placed in a laboratory aquarium. The aquarium had an inclined floor and contained aerated seawater at one end only. Following transference to the laboratory the eggs were carried for about 10 days.

The egg mass then became loose and was shed into the water. Larvae began to hatch almost immediately. I removed the females since they attempted to eat the eggs. Al-Kholy (1959) indicated that females may produce 140,000 eggs per batch, each egg being 96-116µm in diameter.

Attempts to rear the larvae were unsuccessful beyond the first zoeal stage and mortalities were due to unsatisfactory water quality and the reluctance of the larvae to feed on the *Artemia* provided. Al-Kholy (1959) has described the eggs and first zoea of *O. saratan*. I present a photograph of my zoea (Plate 3.3) taken using a Philips SEM 500 scanning electron microscope at Glasgow University. For SEM methods see Chapter 5.

Plate 3.3. First zoea of <u>O. saratan</u>.



Handedness

The major cheliped can be either on the right or the left hand side. At Sharm Obhor, the crabs collected from burrows during mapping were examined for 'handedness' and the results are shown in Table 3.2.

Table 3.2. Side of Major Cheliped

Year	Month	No. of Crabs	L:R major cheliped ratio
1983	O	-	-
	N	48	1.09
	D	32	1.00
1984	J	31	1.07
	F	22	1.20
	M	23	0.92
	A	25	0.92
	M	23	0.92
	J	12	0.71
	J	18	0.80
	A	18	0.80
	S	26	1.00
	Total	278	138L:140R = 0.99

Therefore, there were equal numbers of right and left handed crabs (odd numbers in samples are bound to cause the ratio to deviate from 1). No examples of crabs were found in which the cheliped arrangement was abnormal, ie. both of the same type and size.

At King Saud Palace, of 156 crabs in which the side of the major cheliped was assessed, 73 were left handed and 83 were right handed, giving a L:R ratio of 0.88.

Colouration

Ocypode species are known to be able to change colour to some extent and in this study it was noticed that crabs placed in reduced light for several hours became darker, often appearing slightly greenish-blue, but became lighter when returned to normal daylight.

For crabs collected in the field, five main colour modes have been recognised in my observations.

Small crabs up to around 0.9cm carapace width have a carapace dorsal surface which is yellow with scattered small brown spots. The tips of the chelae are white and the remainder of the chelipeds are yellow but covered with scattered small red/brown spots.

Table 3.3. Adult Crab colouration %

Year	Month	Bluish	Yellow	Sandy yellow	Sandy
1983	O	-	-	-	-
	N	16	5	20	59
	D	30	3	21	46
1984	J	36	7	14	43
	F	-	-	-	-
	M	13	4	35	48
	A	24	8	24	44
	M	21	9	26	44
	J	16	16	2	66
	J	22	11	30	37
	A	27	2	16	55
	S	21	8	14	57

data from Sharm Obhor: n values as in Table 3.2.

Larger juveniles and adult crabs are more uniformly coloured and can be yellow, sandy yellow, sandy or bluish. The sandy colour, ie. good colour match to the natural sand, was commonest and Table 3.3 presents data on crabs collected from Sharm Obhor.

Of 100 crabs examined from King Saud Palace, 46 were sandy coloured, 31 were sandy yellow, 12 were bluish and 11 were yellow.

3.3.1.6. Agencies of disturbance

In the last decade there has been a tremendous increase in the population of Jeddah. The expansion of the city has attracted many foreign companies and there has been a great influx of workers both from within Saudi Arabia and elsewhere (Pakistan, Philippines, Egypt, etc.). As a consequence the beaches are under increasing pressure as recreation areas and the O. saratan populations have been disturbed.

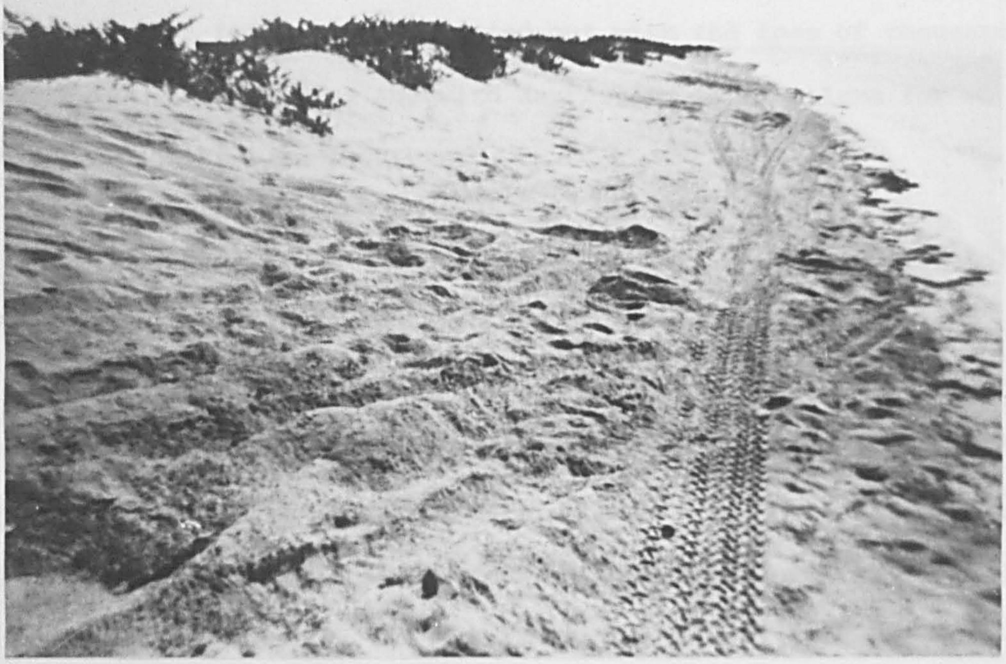
In camping areas along the shores the tracks of four wheel drive vehicles cover the sand causing the obliteration of burrow openings and sand pyramids (Plate 3.4.a). Children dig out crabs from their burrows and some oriental communities use them for food. On one occasion at Al-Quaid Island I met Philippinos who had dug out more than 200 O. saratan for food.

The most devastating development in the Jeddah region has been the construction of a coastal highway, Al-Corniche (Plate 3.4.b). This has been disastrous not only for O. saratan but for the whole coastal ecosystem. Most of the road has been built in the lagoon of the fringing reef, often near the reef crest. Infilled rubble has provided the bed of the road and suspended material has blanketed the reef with lethal effects. The original beach has been cut off from the sea and its crab populations have died. Al-Corniche extends from

Plate 3.4. a) 4-wheel drive vehicle disruption of the beach at King Saud Palace.

b) Al-Corniche coastal highway built in the lagoon near the reef crest. The old shoreline can be seen in the foreground and some hypersaline water remains in the lagoon.

a



b

near Shoiba south of Jeddah to beyond Obhor to the north of Jeddah, a distance of some 150km and may be extended further.

Such lagoon as remains landwards is hypersaline and virtually abiotic. Most of the lagoon has dried out with the loss of thousands of animal and plant species and with depressing implications for fisheries and coastal productivity.

Assuming a density for O. saratan of $0.3.m^{-2}$ (see density data) and a coastal strip of sand between 10m and 20m in width (cf. King Saud Palace and Sharm Obhor) then, at a given point in time, the crab populations along the route of Al-Corniche would number from 450,000 to 900,000. This would almost certainly be an underestimation due to the difficulties of accurately assessing the numbers of small crabs and it, of course, takes no account of productivity. These crabs and more seriously their habitat have been destroyed.

An examination of the seaward edge of the road banking south of Jeddah showed that in places where sand occurred amongst the rock rubble very limited recolonisation by O. saratan had occurred.

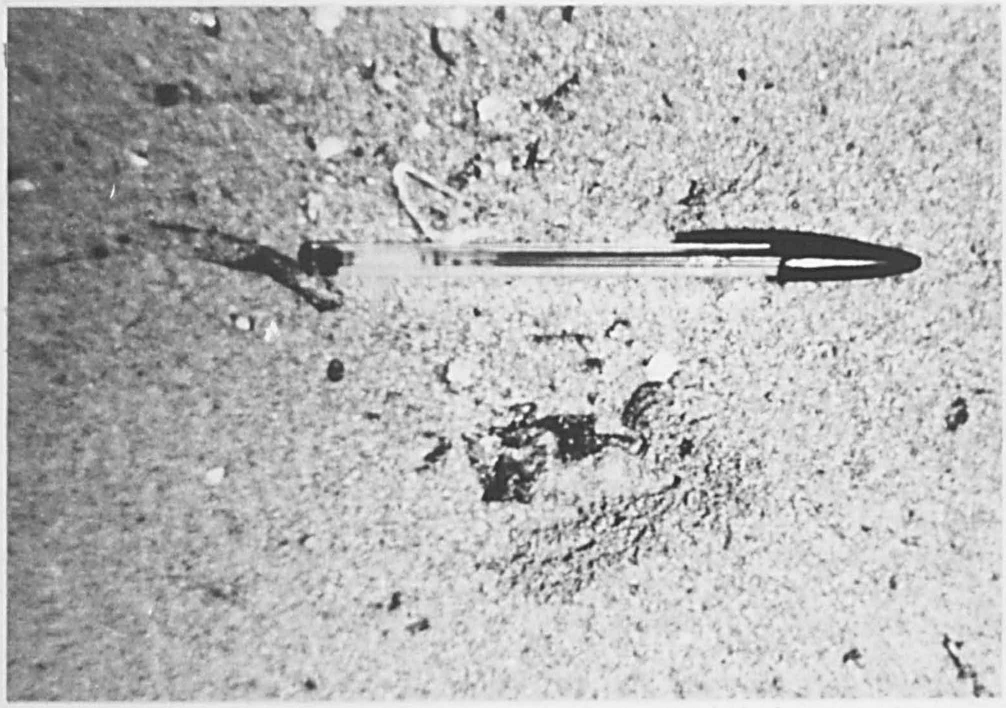
The Sharm Obhor private beach site almost suffered the same fate. Rubble was bulldozed on to the coral fringe as the roadbed construction commenced. Then, at the last moment the road was diverted and both the beach and the Marine Station's seaward developments were saved. The month this study concluded, the owner of the private beach bulldozed the beach, obliterating the crab burrows in preparation for beach hut development.

The effect of human disturbance at the King Saud Palace site can be judged from the low burrow densities (see Table 3.1). The beach was increasingly used throughout the study and it was eventually judged impossible to continue working there.

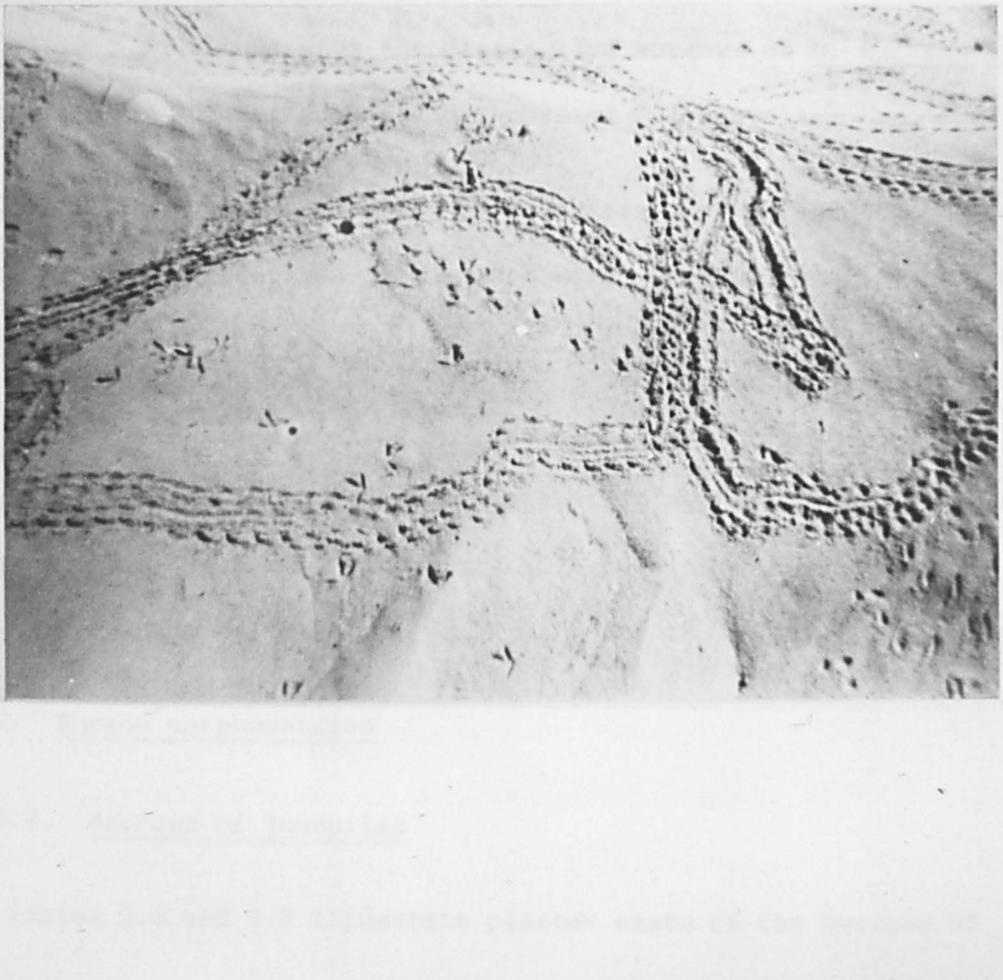
Plate 3.5. a) Dotilla sulcata burrow surrounded by minute sand pellets (lower right). The pen is 15cm in length.

b) Tracks of Coenobita scaevola (the regular tracks that are commonest in the photograph). Bird tracks (lower left) and O. saratan tracks (centre) can also be seen.

a



b



3.3.1.7. Associated species

O. saratan is the most conspicuous inhabitant of the supralittoral sand. There are several other crustaceans, however, that are abundant on the beaches. The small ocypodid crab Dotilla sulcata is abundant along the tide edge, its burrows occurring in the narrow littoral zone and therefore occurring just below the zone occupied by the smallest juvenile O. saratan (see Fishelson, 1971, 1983; Lewinsohn, 1977).

The land hermit crab Coenobita scaevola is widespread occurring from the tide edge to sometimes 100m from the shore. Their characteristic tracks criss-cross the sand and they either burrow into the sand for protection or hide in crevices in the limestone, usually at the base of the low 'cliff' at the back of many beaches, eg. Sharm Obhor (see Magnus, 1960; Fishelson, 1971).

Plate 3.5a illustrates the distinctive burrows of D. sulcata and Plate 3.5b the characteristic tracks of C. scaevola.

The other abundant crustaceans are talitrid amphipods that burrow in the sand and are found under wood, weed and stones throughout the beach.

Other upper beach species include the isopod, Tylos exiguus, reported by Jones (1974) who also lists other shore species including a high shore oligochaete. These may have been present at my sites but I did not record them.

3.3.2. Burrow morphometrics

3.3.2.1. Burrows of juveniles

Plates 3.6 and 3.7 illustrate plaster casts of the burrows of juvenile crabs and further information is given in Tables 3.4 and 3.5. Juvenile O. saratan burrows are either I, J, Y, U or L-shaped and are similar to those of other Ocypode species (see Vannini, 1980a). The commonest burrow form was the Y-shape (c. 75%) (Plate 3.6b-f, Plate 3.7a, b). Only one dichotomy of the Y is normally open, though there are exceptions (Plate 3.6c). J-shaped burrows (Plate 3.7d, e) were the next commonest (c. 20%) with the ascending shorewards branch often reaching almost to the surface. Occasionally such a burrow was open at each end giving a U-shape. Normally the ascending shaft of burrows terminated several centimetres from the surface. I-shaped and L-shaped (Plate 3.6a) burrows were presumably incomplete burrows under construction.

The orientation of burrows was always the same; the entrance was towards the sea with the burrow extending at right angles to the shoreline.

The zonation studies previously reported indicated that juvenile burrows could be divided on a positional basis into two groups. The smallest burrows occurred just above the tide edge and predominantly larger juvenile burrows occurred a little further up the beach. The smallest burrows were I or Y-shaped, similar to those of larger juveniles but rarely penetrated more than 15cm into the sand. Plate 3.6b is an example. Note the steep shafts ($80^{\circ} - 90^{\circ}$) in contrast to the more open Y of the larger juveniles (Plate 3.6c, d). Many of the small burrows were simple, almost vertical, unbranched shafts (I-shaped) (see Table 3.5).

For the larger juveniles whose burrows descend to around 30cm the casts indicate that the descending branch may be fully constructed before any ascending shaft (cf. Plate 3.7c and b). Most casts,

Plate 3.6. a–f) Plaster casts of the burrows of juvenile O. saratan.

Scale bar = 30cm.

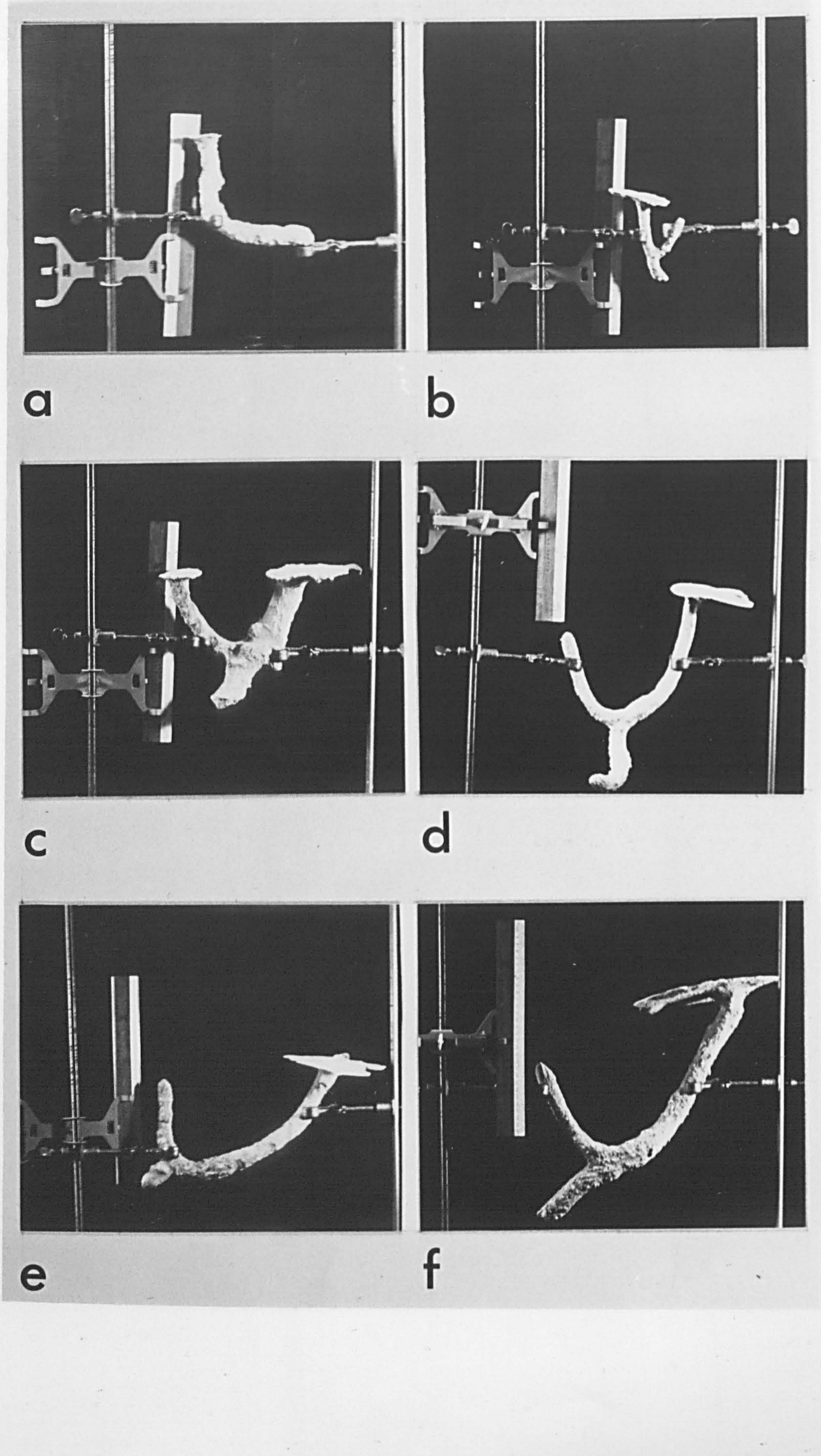

a
b
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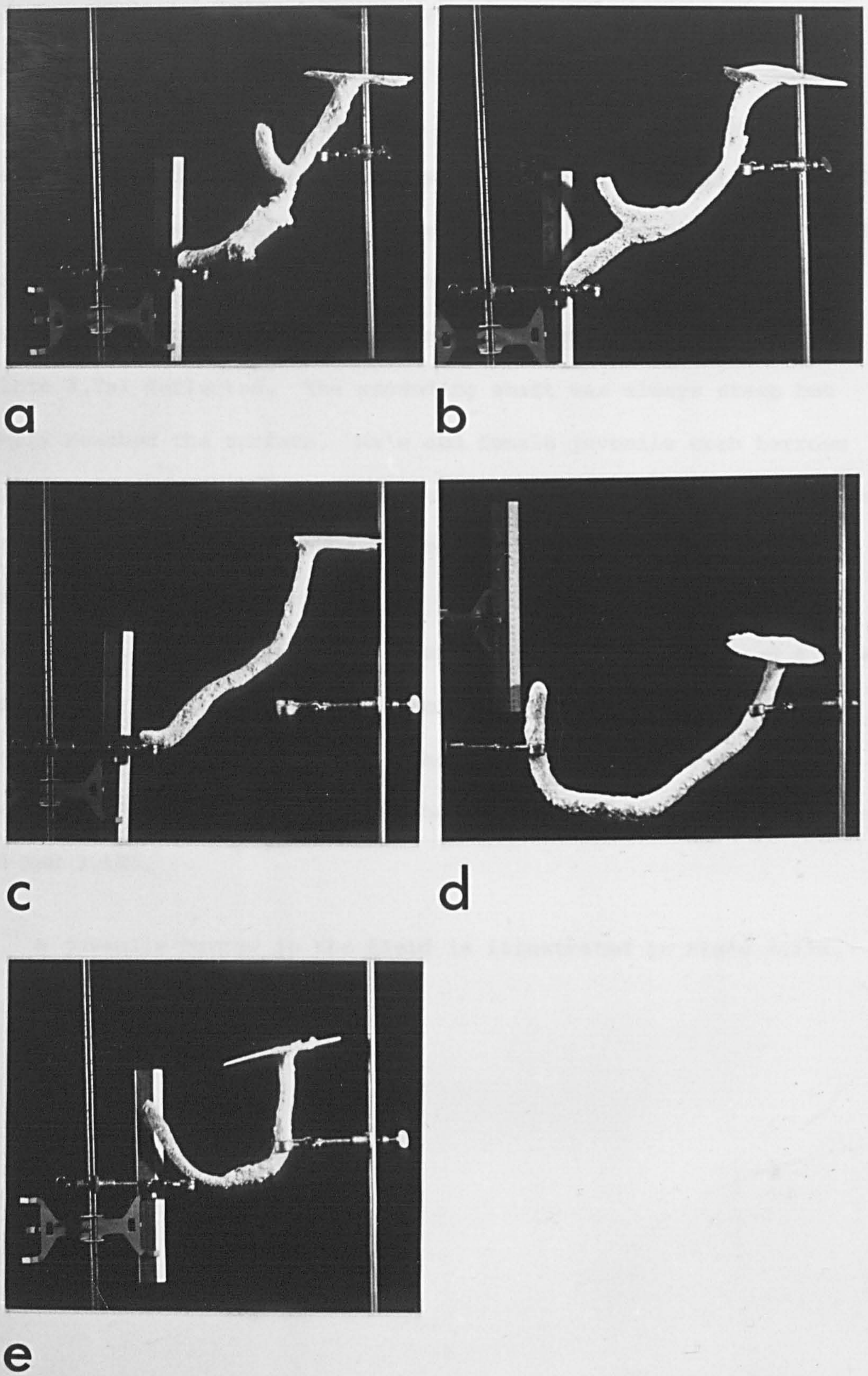
Plate 3.7. a-e) Plaster casts of the burrows of juvenile <u>O. saratan</u>.

Scale bar = 30cm.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e

however, indicate that the J or U is constructed before excavating the descending lower chamber (cf. Plate 3.7d and Plate 3.6e, f). Juvenile burrows usually descended steeply (70° - 90°) into the sand and at a depth of around 15cm the angle often shallowed to around 50°. This change in angle was often fairly abrupt (Plate 3.7b, c, d). On other occasions the transition to the curve of the J or U was more gradual (Plate 3.6e) or the angle of the descending shaft remained steep until it was horizontally (Plate 3.7e) or vertically (Plate 3.7a) deflected. The ascending shaft was always steep but rarely reached the surface. Male and female juvenile crab burrows appeared similar. Plate 3.6c illustrates a burrow of larger diameter than the other juvenile crabs and contained a female nearing mature size. Its burrow has similarities with those of mature females (Plate 3.8). Plate 3.6f illustrates a burrow which contained a male crab of near adult size and this and several similar burrows which were cast occurred at the top of the juvenile zone (see Table 3.5). They have some similarities with the burrows of mature males (Plates 3.9 and 3.10).

A juvenile burrow in the field is illustrated in Plate 3.11a.

Table 3.4. Burrow details from selected casts

Burrow width	Carapace width of occupant (cm)	Crab Sex	Distance from sea (cm)	Height above sea level when cast (cm)	Burrow Shape	Depth in sand (cm)	Angle of descent from main opening
1.5	1.4	?	150	nm	Y	18	88°
2.1	1.4	?	170	nm	Y	25	88°
1.8	1.6	F	200	nm	Y	25	87°
2.1	1.9	F	240	nm	Y	23	87°
2.1	2.0	F	180	18	Y	18	63°
2.2	2.0	F	270	nm	Y	24	88°
2.5	2.3	F	230	nm	J	22	84°
2.5	2.4	F	200	22	Y	23	75°
2.8	2.5	F	180	nm	J	23	66°
2.8	2.7	F	300	35	Y	23	63°
3.0	2.8	F	160	21	/	18	77°
3.7	3.5	F	180	22	U	22	65°
4.5	4.1	F	640	66	U	42	66°
4.5	4.3	F	320	38	U	29	72°
4.9	4.7	F	650	61	/	55	74°
5.4	4.9	F	250	34	U	20	65°
5.5	5.1	F	600	66	/	65	73°
5.5	5.1	F	830	74	/	82	73°
5.5	5.2	F	700	74	/	66	78°
5.9	5.6	F	710	67	Y	61	83°
1.8	1.7	M	190	22	Y	16	83°
2.2	2.1	M	150	25	Y	23	75°
2.6	2.3	M	300	nm	J	30	85°
2.7	2.4	M	220	nm	Y	29	85°
2.8	2.5	M	150	nm	Y	25	88°
2.9	2.6	M	270	nm	U	23	86°
3.2	3.1	M	300	35	U	25	66°
3.5	3.4	M	200	22	U	22	70°
4.2	4.0	M	270	38	U	27	71°
4.5	4.1	M	1250	109	'S'	98	83°
4.8	4.6	M	1330	112	'S'	68	79°
5.0	4.7	M	1480	118	'S'	67	88°
5.1	4.8	M	730	65	/	55	77°
5.1	4.9	M	350	44	'S'	37	85°
5.4	5.1	M	500	57	'S'	50	58°
5.4	5.2	M	350	40	U	30	60°
6.0	5.3	M	1050	77	'S'	71	86°
6.0	5.7	M	800	74	/	62	78°
6.0	5.7	M	1430	120	'S'	71	85°
6.1	5.7	M	1000	77	'S'	65	73°
6.0	5.8	M	1640	120	'S'	81	80°

nm = not measured

'S' = spiral

/ = descending shaft of incomplete burrow

NB. The U shaped burrows occupied by some males were almost certainly female burrows that had been taken over.

Table 3.5. Burrow details from selected casts

	Burrow width (cm)	Carapace width of occupant (cm)	Crab Sex	Height above Tidal Datum (cm)	Burrow shape	Depth in sand (cm)	Angle of descent from main opening	Horizontal interbranch distance (cm)*
small juveniles	1.6	1.4	?	65	I	12.0	90°	-
	1.9	1.6	?	65	Y	12.4	90°	3.8
	2.1	1.8	?	65	Y	13.6	90°	4.2
	2.2	1.8	?	65	Y	15.3	90°	4.4
juveniles	2.5	2.3	M	115	Y	26.0	80°	15.3
	2.6	2.4	M	105	Y	23.5	70°	13.0
	2.9	2.6	F	110	Y	25.3	70°	15.4
	3.2	2.7	F	110	Y	25.0	70°	14.5
'adolescent' males	3.3	2.9	M	125	Y	34.0	80°	18.5
	3.4	3.0	M	120	Y	25.0	80°	23.5
	4.3	3.6	M	130	Y	34.0	80°	22.2
adult female †	3.9	3.3	F	139	U	26.0	50°	35.2
	4.2	3.8	F	132	U	25.0	50°	34.4
	4.7	4.3	F	135	U	24.0	50°	37.3
	4.8	4.3	F	135	U	26.0	50°	33.2
	5.3	4.5	F	140	U	28.0	50°	34.3
mature male	3.9	3.6	M	180	'S'	112.0	60°	-
	4.3	3.9	M	140	'S'	98.0	60°	-
	4.8	4.3	M	185	'S'	110.0	65°	-
	5.4	4.6	M	190	'S'	112.0	65°	-
	5.2	4.8	M	190	'S'	115.0	60°	-

* This is the horizontal distance between the upper branches of the Y at the level of the top of the ascending branch.

† These burrows alone had two openings to the surface.

'S' denotes spiral

3.3.2.2. Burrows of adult females

Mature female crabs may excavate a linear shaft which descends from the sand surface at a variable but often shallow angle to a depth of 40cm to 50cm (Plate 3.8a-c). Plates 3.8a-c also illustrate evidence of a shallow blind shaft descending near vertically below the entrance: the main angled shaft descends past this feature. This characteristic is also evident in Plate 3.8d. This burrow branches to form a shallow U-shaped upper portion. In fact, most female burrows examined were of a shallow U-shape (Plates 3.8e, f) and in some of these there is some indication that the ascending section was excavated from above the base of a descending shaft rather than as a continuously excavated U (see Plate 3.8f). In other cases the U is without evidence of branching. The base of the U is almost always shallower than 30cm beneath the sand surface (cf. Plate 3.8c with 3.8f). The descending tunnel angle may be relatively shallow (often around 50^{o}) while the ascending branch is steep and sometimes vertical (Plate 3.8e). The horizontal distance between the front opening and rear of a typical burrow is around 35-50cm. In most cases, however, the rear ascending portion of the burrow did not open to the surface but stopped just short of it. In many cases, though, there was evidence that this had been periodically opened to the surface and then replugged. The rear opening was seen to be used when the burrow was flooded by the sea and presumably it also serves as an escape route from predators.

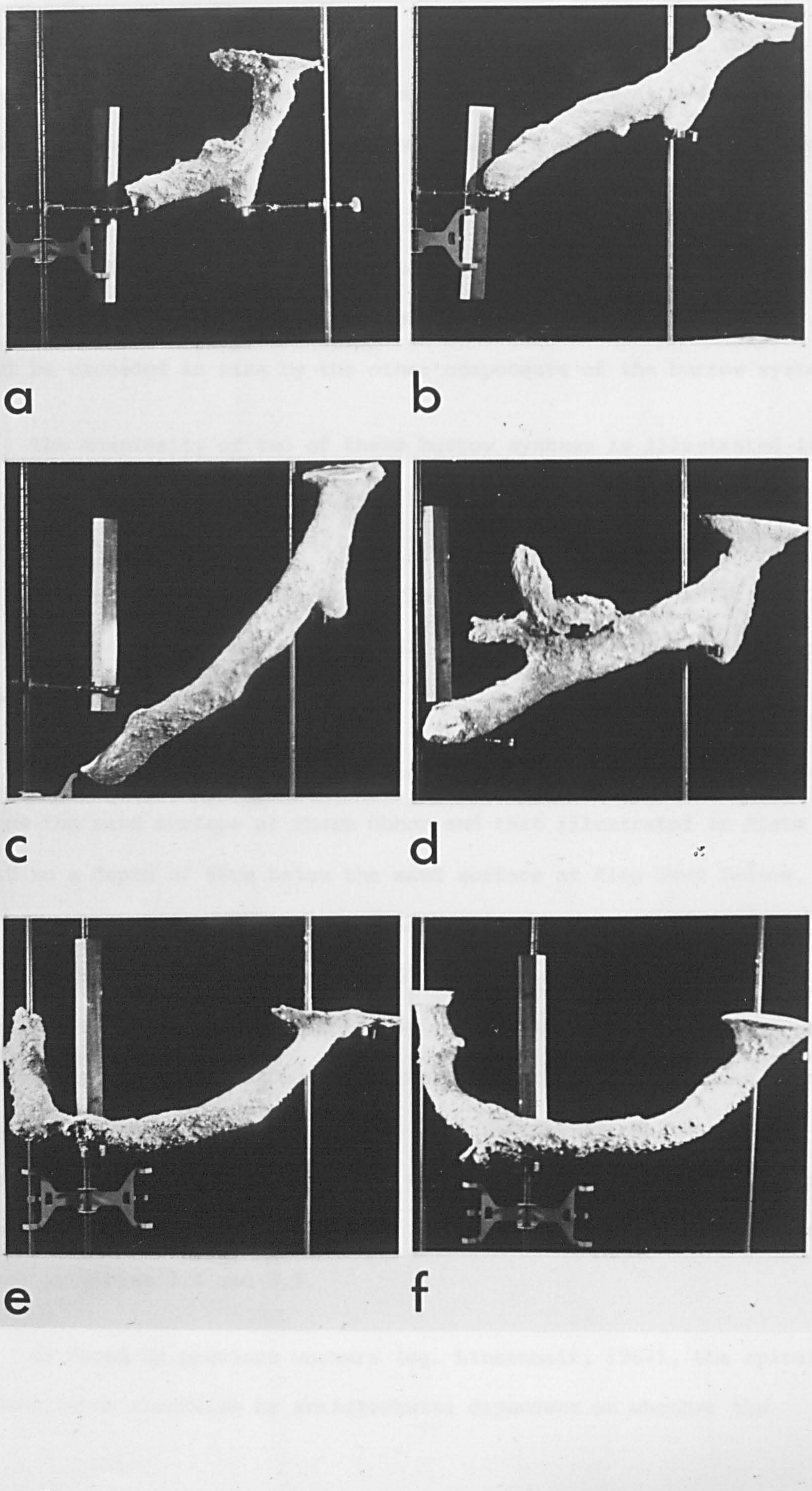
A field example of a mature female crab's burrow is illustrated in Plate 3.11b.

3.3.2.3. Burrows of adult males

Hand excavation and incomplete plaster casts indicated that the

Plate 3.8. a-f) Plaster casts of the burrows of adult female <u>O. saratan</u>.

Scale bar = 30cm.


a
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e
f

burrows produced by mature male crabs in the breeding season were more complex than had been reported by previous workers (Parenzan, 1931; Al-Kholy, 1959; Magnus, 1960; Linsenmair, 1965, 1967; see Discussion). These workers had described the burrow as a descending spiral, sometimes with short side branches. A sand pyramid occurred near each burrow entrance.

Polyester resin casts indicated that the spiral section of the burrow could be but one part of a much more complex system and in fact be exceeded in size by the other components of the burrow system.

The complexity of two of these burrow systems is illustrated in Plates 3.9 and 3.10. In each case the burrows were filled with polyester resin and the casts were laboriously and carefully excavated. In the case of the larger system (Plate 3.9) the resin quantity was insufficient and part of the 'spiral' section had to be completed with Plaster-of-Paris.

The burrow illustrated in Plate 3.9 extended to a depth of 110cm below the sand surface at Sharm Obhor and that illustrated in Plate 3.10 to a depth of 98cm below the sand surface at King Saud Palace. It has been shown that at Sharm Obhor, spiral burrows only occurred in that part of the beach where the water table was at least 55cm beneath the sand surface. At the region of the beach where the burrow illustrated in Plate 3.9 occurred, the water table was detected at a depth of 120cm. The burrow at King Saud Palace was nearer the tide edge but again some 10cm above the water table at its lowest point at the time of casting and measurement. Further positional details are given in Tables 3.4 and 3.5.

As found by previous workers (eg. Linsenmair, 1967), the spiral tunnel turns clockwise or anticlockwise dependent on whether the

Plate 3.9. a-c) Excavation of a complex polyester resin cast of the burrow of a male O. saratan at Sharm Obhor. Some breakages cannot be avoided. The burrow, correctly assembled is illustrated in the accompanying figure (Fig. 3.7.). Its true shape is obscured by the sand penetration of the resin.


a
b
c

Plate 3.10. a) Excavation of polyester resin cast of male _O. saratan_ burrow at King Saud Palace.

b) _In situ_ view of partly excavated cast. Note the burrow entrance where the true burrow width can be seen (inner dark circle of resin).

c) Sand being washed from excavated cast.

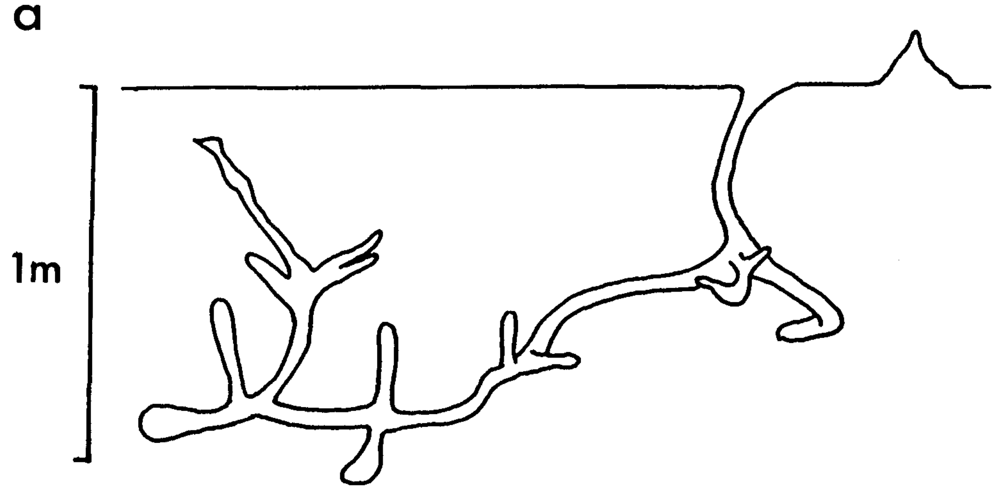

a
b
c

Fig. 3.7. Complex burrows of male O. saratan.

a) The burrow shown in Plate 3.9. but with the resin impregnated sand removed.

b) The burrow shown in Plate 3.10. on the same basis as (a).

a



b

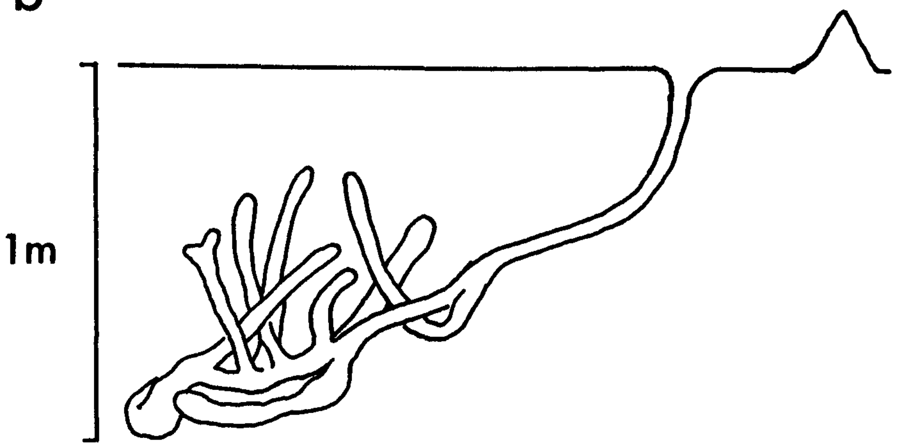
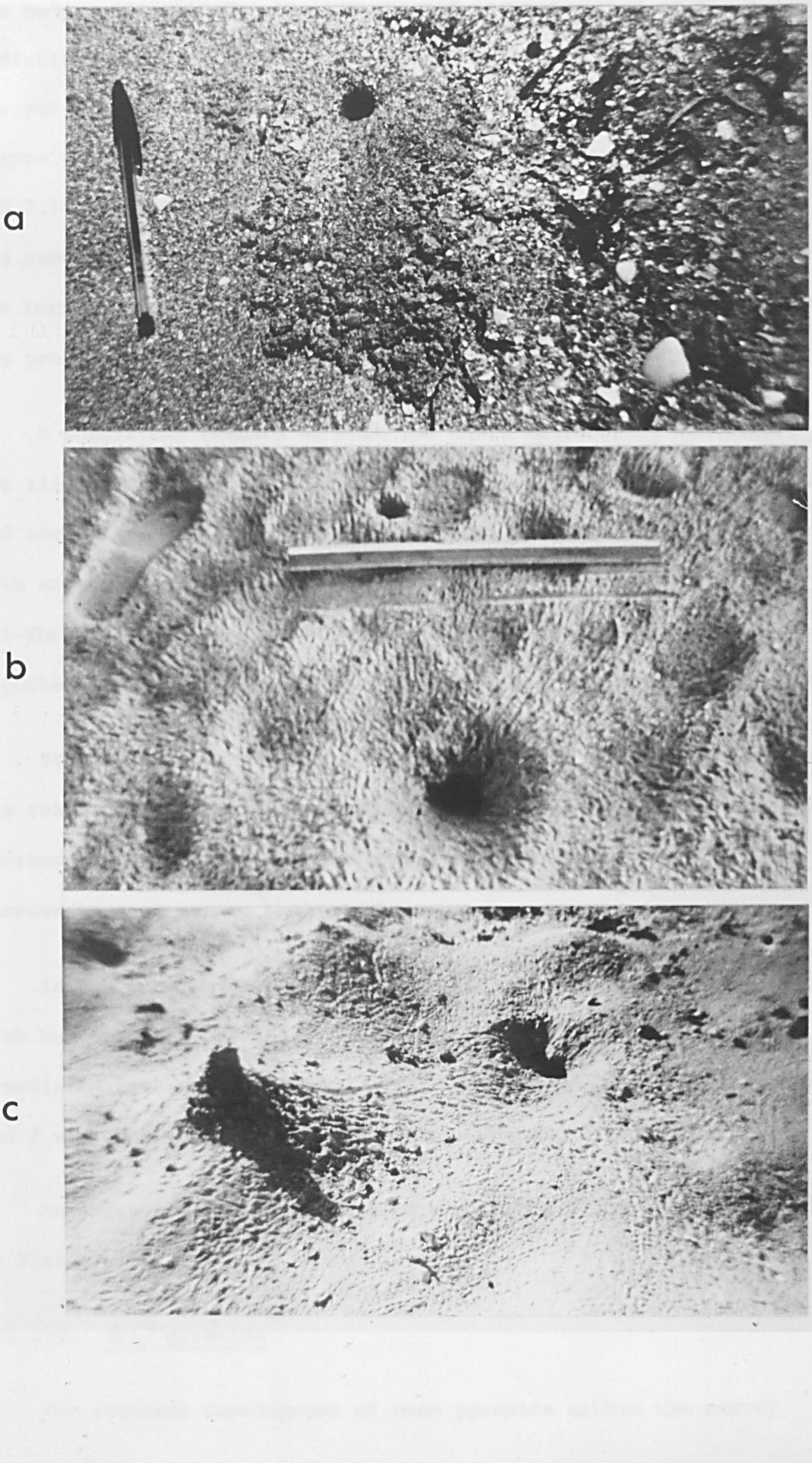


Plate 3.11. a) Burrow of juvenile O. saratan. Note the excavated damp sand. The pen is 15cm in length.

b) Burrow of adult female O. saratan. The larger of the two openings is towards the sea. The scale bar is 50cm in length.

c) Burrow of mature male crab. The burrow entrance faces the sea. Mesodesma shells can be seen around the burrow and many footprints. The distance from the burrow entrance to the pyramid is around 40cm.


a
b
c

excavating crab has its larger cheliped on the left or right side of the body, respectively. A sand pyramid is constructed at the end of a distinct path leading from the burrow opening. Normally, a single pyramid was seen but occasionally two or even three were seen at a burrow entrance (Plate 3.12). The burrows illustrated in Plates 3.9 and 3.10 had a characteristic sand pyramid at the entrance. There was another sand pyramid approximately above the end of each system. The burrow system only contained a single crab and the second pyramid was probably associated with the burrow of an adjacent crab.

A consistent feature of both the casts illustrated and others not illustrated, is the occurrence of numerous subsurface galleries and ascending branches which stop short of the sand surface. Burrows with side shafts have been reported previously for O. saratan (Al-Kholy, 1959; Magnus, 1960) but nothing of this complexity has been reported for O. saratan or any other Ocypode species.

It must be remembered that the width of the burrows produced by the resin casting method is exaggerated by resin penetration of the surrounding sand. Fig. 3.7 indicates the true proportion of the burrows in contrast to their casts.

In the dune region of King Saud Palace I excavated several male crab burrows that descended for almost 2m. Such burrows were not associated with sand pyramids. These burrows had many side branches and I was unable to excavate the whole systems.

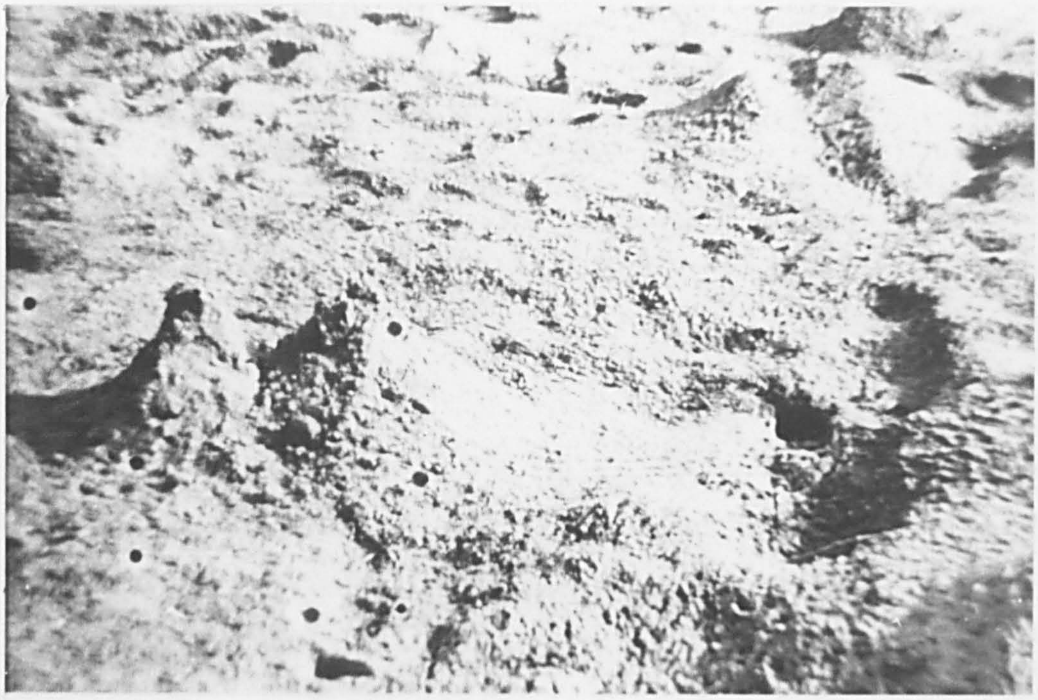
An example of a mature male burrow in the field is illustrated in Plate 3.11c.

3.3.2.4. Sand pyramids

The seasonal development of sand pyramids within the survey

Plate 3.12. a) two sand pyramids at the entrance to the burrow of a mature male O. saratan.

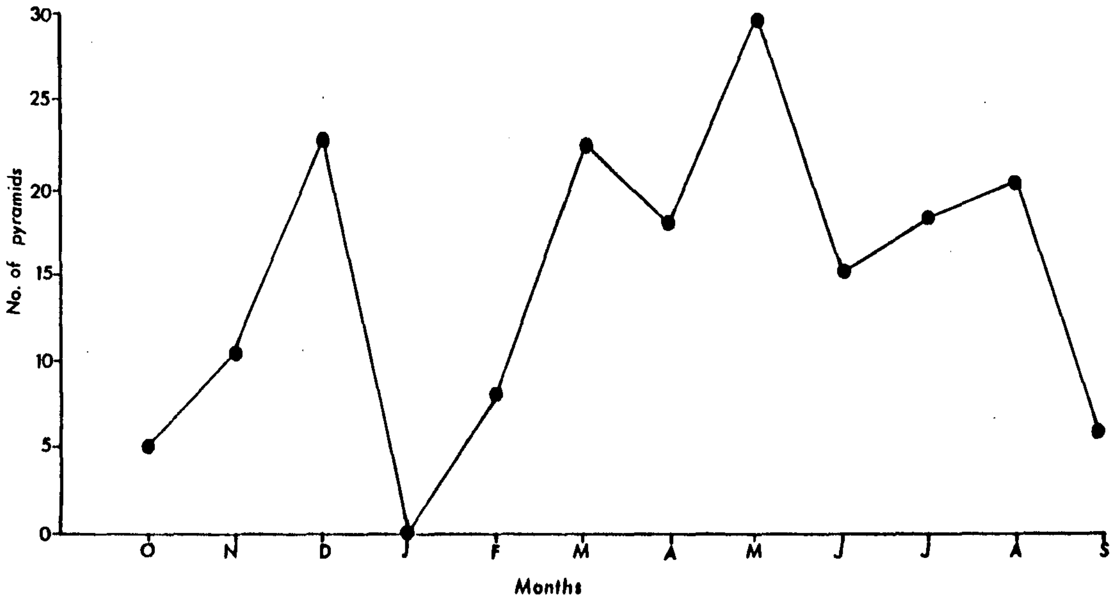
b) as above but with three sand pyramids.



a

b

Fig. 3.8. Monthly variation in sand pyramid numbers within the sampling grid at the Sharm Obhor site.


30
25
20
15
10
5
0
No. of pyramids
O
N
D
J
F
M
A
M
J
J
A
S
Months

grids at Sharm Obhor is given in Fig. 3.8. At King Saud Palace few pyramids developed within the survey area in contrast to Sharm Obhor. At King Saud Palace pyramid formation commenced in March and extended until September. At Sharm Obhor pyramids first occurred in late February and extended until December. Only in January were no pyramids seen.

The mean diameter and standard deviation of 47 burrows associated with pyramids was 5.41 ± 0.64cm. The associated pyramid height was 15.70 ± 2.33cm and the distance from the burrow to the centre of the pyramid was 45.39 ± 7.82cm. Of 24 of these burrows examined for the side occupied by the pyramid, 13 had pyramids to the right of the burrow, 10 had pyramids to the left (from crab's viewpoint) and one crab had two pyramids, the newer one being to the right, the older to the left. This signifies that a crab of different handedness had taken over the burrow (Linsenmair, 1967).

3.3.3. The burrow environment

3.3.3.1. Temperature and relative humidity

The data presented in Tables 3.6-3.9 and 3.13-3.15 indicate clearly that conditions within the burrow are cooler and more humid than the conditions outside. In January when the outside air temperature was 31°C, air temperatures ranged from 22°C to 24°C at the base of burrows (Table 3.6). In August when the outside air temperature was 39°C, at the base of the burrow the air temperature was 10°C cooler, ie. 29°C (Table 3.7). In April, conditions were intermediate; outside air temperature was 33°C and burrow air temperature was 25°C below 30cm (Tables 3.8 and 3.9).

Further evidence of the cooler conditions that might be expected within burrows are provided by sand temperature measurements. Beach sand surface temperatures are warmest away from the sea (Tables 3.10, 3.11) and the sand is much cooler at the depths reached by burrows than at the surface. For example, Table 3.12 indicates, for May, a temperature difference at the top of the beach of 20°C between sand surface and a depth of 104cm - a depth obtained by many male crab burrows. It can be seen that the greatest temperature drop is in the first few centimetres. The deeper sand remains relatively cool and provides an environment for maintaining cool and stable air temperatures.

The data obtained in Table 3.13 were obtained by excavating holes at intervals from the water's edge and then forming an 'artificial burrow' in the wall of the hole using a core tube to remove a horizontal cylinder of sand. Each hole was dug to the water table and it was noticed that in the case of the hole at the top of the shore, the water level was 5cm higher than the sea level. Assuming surveying accuracy, this would indicate capillarity. The sand was noticeably damp to some 30cm above the water table.

Measurements of temperature and relative humidity were taken in the holes and artificial burrows and even though conditions differed from true burrows, air temperature was still lower in the excavations than outside during the afternoon and relative humidity was consistently higher in the excavations than outside (Table 3.13).

In burrows proper, the relative humidity relationships are clearly seen. Tables 3.14 and 3.15 present data on temperatures and relative humidities in and out of burrows, and also sand surface and water edge temperatures. Table 3.14 indicates monthly readings, Table 3.15 daily fluctuations. In each case the measurements were taken 20cm within the burrow. Although, as seen in the previous tables, it was possible to take temperature readings deeply in burrows, it was not possible to do this for relative humidity because of the shape and size of the probes. Excavation of the burrow to achieve deeper probe penetration destroyed microclimatic conditions but always gave high relative humidities ($>70\%$). Nevertheless, the readings at 20cm depth clearly show that temperature within burrows is generally lower than outside and relative humidity is correspondingly higher.

Some of the data presented in Table 3.15 are illustrated in Fig. 3.9 (see also Chapter 4 where further data are added). At 20cm within the burrow the air temperatures closely resembled the outside temperature but relative humidities were consistently higher than outside. An unexpected but consistent feature was that the air temperature outside the burrow was often just a little lower than at 20cm within the burrow. Several possible explanations of this are examined in the Discussion. Both the temperature/humidity probes in use showed the same effect. Sand surface temperature was much higher than air temperatures during the day but followed them at night. Sea surface temperature at the water's edge varied slightly with higher temperatures by day as might be expected (see Table 3.15).

Table 3.16 presents data on burrow plugging and there appears to be a correlation between low outside relative humidity and the incidence of burrow plugging. Additional data on this are presented in Chapter 4. Unfortunately it did not prove possible to measure relative humidity within closed burrows but some temperature measurements were taken. At an outside air temperature of 31°C the temperature just behind the plug was 22°C in one case and 23°C in another. Plate 3.13 illustrates a closed burrow.

Fig. 3.9. Upper graph = sea temperature at the tide edge.

Middle graph = soil and air temperature: closed circles = sand temperature, open circles = air temperature, crosses = air temperature 20cm within burrow.

Lower graph = relative humidity: open circles = air 20cm within burrow, closed triangles = air outside burrow.

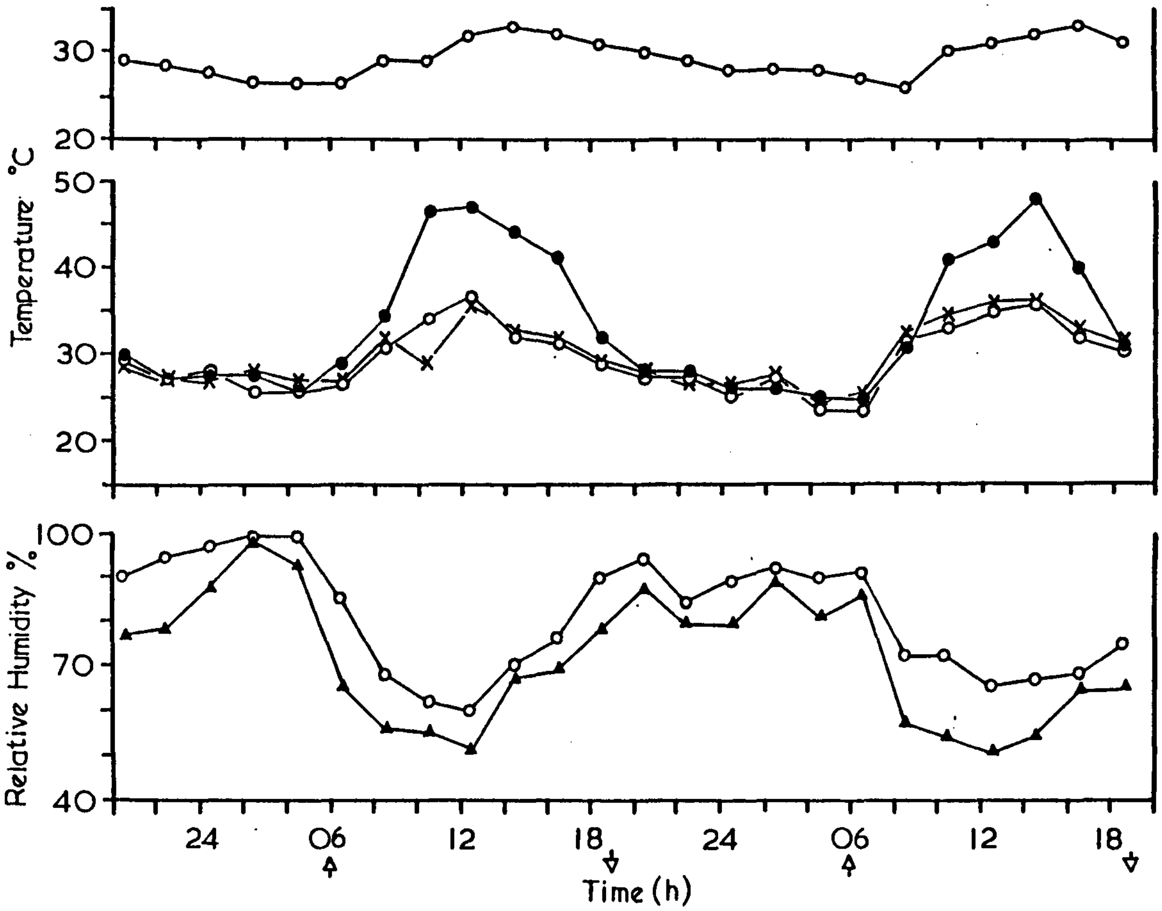

30
20
50
40
30
20
Temperature °C
100
70
40
Relative Humidity %
24
06
12
18
24
06
12
18
Time (h)

Table 3.6. Burrow size, position, air temperature, 25 Jan. 1984, 1150h

Burrow size (cm) entrance diameter	 burrow depth	Distance from sea (m)	In-burrow air temperature °C
0.8	12	2	22
1.2	12	3	24
1.3	12	2.5	23
3.8	35	6	24
5.3	70	10	24
closed	35	7	22

Out-of-burrow air temperature, 31°C

In-burrow temperatures taken at bottom of burrows.

Site, Sharm Obhor

Table 3.7. Burrow Air Temperatures, 25 Aug. 1984, 1130h

Depth into burrow (cm)	Temperature (°C)	
0	39	39
10	38	38
20	37	34
30	36	32
40	35	32
50	32	30
60	30	30
70	29	29

Site, Sharm Obhor. Spiral burrows.

Table 3.8. Burrow Air Temperatures, 29 April 1984, 1350h

Depth into burrow (cm)	Air Temperatures (^{o}C)
0	33
5	30
10	30
17	26
20	26
30	25
42	25
53	25

Site, Sharm Obhor.

Table 3.9. Burrow Air Temperatures and Relative Humidities, 29 April 1984, 1350h

Depth into burrow (cm)	Air Temperature (^{o}C)	Relative Humidity
0	33	66
5	30	66
10	30	70
17	28	72
0	33	66
5	30	66
10	28	67
17	26	78

Site, Sharm Obhor.

Table 3.10. Sand Temperatures, 25 Jan. 1984, 1150h

Horizontal distance from sea at Sharm Obhor (m)	Sand surface temperature (^{o}C)
1	36
2	38
4	39
10	41
12	41

Air temperatures = 31^{o}C. Site, Sharm Obhor.

Table 3.11. Sand Temperatures, 25 Jan. 1984, 1515h

Depth into substratum (cm)	Temperature (°C) 1m from sea	Temperature (°C) 12m from sea
0	30	36
2	30	35
4	28	32
6	28	30
8	26	27
10	22	22
12	21	22

Air temperature, 31°C. Site, Sharm Obhor.

Table 3.12. Sand Temperature Profiles in beach excavations, 15 May 1984

Horizontal distance from sea

15.5m		9.5m		4.5m		2.0m		
depth (cm)	temp. (°C)	depth (cm)	temp. (°C)	depth (cm)	temp. (°C)	depth (cm)	temp. (°C)	
0	46							
4	35	0	44					
14	32	9	32					
24	31	19	30	0	33			
34	30	29	29	7	32			
44	30	39	28	17	30			
54	29	49	28	27	29	0	33	
64	29	59	28	37	29	9	31	
74	28	69	28	47	28	19	28	
84	28	79	27	57	28	29	28	water table
104	26	99	26	77	28	49	28	
Time (h)	1430	1500		1515		1530		

Table 3.13. Air temperature and Relative Humidity in beach excavations *, 15th May 1984

Time (h)	1430	1845	1500	1845	1515	1845	1500	1845
Air temp. in main excavation (°C)	33	31	33	31	32	31	32	
Air temp. in artificial burrow (°C)	33	31	33	31	32	31	32	filled by incoming tide
RH% in main excavation	79	74	76	78	80	75	83	
RH% in artificial burrow	83	80	77	73	80	80	83	
Outside air temp. (°C)	36	31	36	31	36	31	36	
Outside RH%	55	65	55	65	55	65	55	

* A hole was dug to the water table and a 30cm artificial 'burrow' was cored horizontally 20-30cm above the base of the hole. The thermocouple probe measured sand temperature 20cm below the water table as well as above it.

Table 3.14. Temperatures and Relative Humidities 20cm within and outside of burrows

Month 1983/84	In-burrow air temp. (°C)	Outside air temp. (°C)	In-burrow RH%	Outside RH%	Sand surface temp. (°C)	Sea temp. (°C)
Oct.	24	31	69	55	37	29
Nov.	28	32	77	76	35	29
Dec.	25	30	65	50	33	28
Jan.	25	31	-	-	35	27
Feb.	25	27	69	57	38	27
Mar.	25	28	66	46	33	26
Apr.	28	32	72	66	34	29
May	31	34	72	66	42	30
June	31	35	72	66	39	29
July	32	38	73	67	42	30
Aug.	34	39	82	83	44	34
Sept.	-	32	-	-	42	32

Site, Sharm Obhor

Table 3.15. Daily variations in temperature and relative humidity in air outside and 20cm inside burrows, soil temperature variations and water temperature variations at the tide edge. 13th - 15th May 1984.

Time	Burrow Air Temp. °C	Burrow RH %	Air Temp. °C	Air RH %	Soil Temp. °C	Water Temp. °C
2030	28.6	90.1	29.0	77.1	30.0	29.0
2230	27.5	94.6	27.0	78.4	27.2	28.4
0030	27.2	96.7	27.6	88.0	27.5	27.5
0230	28.1	100.0	25.6	99.0	27.0	26.5
0430	27.0	100.0	25.6	93.0	26.1	26.3
SR 0630	26.8	85.0	26.7	65.0	29.0	26.5
0830	32.0	67.9	31.1	56.0	34.4	29.0
1030	29.0	62.4	34.1	54.7	46.3	29.0
1230	35.4	59.9	36.7	51.0	47.0	32.0
1430	32.7	69.7	32.1	67.0	44.0	33.2
1630	32.1	76.2	31.3	69.0	41.0	32.0
SS 1830	29.3	89.0	29.1	78.1	32.0	31.0
2030	27.9	93.7	27.8	86.6	28.0	30.0
2230	27.0	84.0	27.2	79.3	28.0	29.0
0030	26.6	89.0	25.5	79.4	26.0	28.0
0230	27.3	92.0	27.0	89.0	26.0	28.0
0430	24.4	90.1	23.6	81.0	25.0	28.0
SR 0630	25.7	90.9	23.5	85.5	25.0	27.0
0830	32.8	71.7	31.6	57.0	31.0	26.0
1030	34.8	72.0	33.0	54.4	41.0	30.0
1230	36.6	65.0	35.0	50.0	43.0	31.0
1430	36.5	67.0	36.0	54.5	48.0	32.0
SS 1630	33.0	68.0	32.0	64.0	40.0	33.0
1830	31.0	75.0	30.5	65.0	31.0	31.0

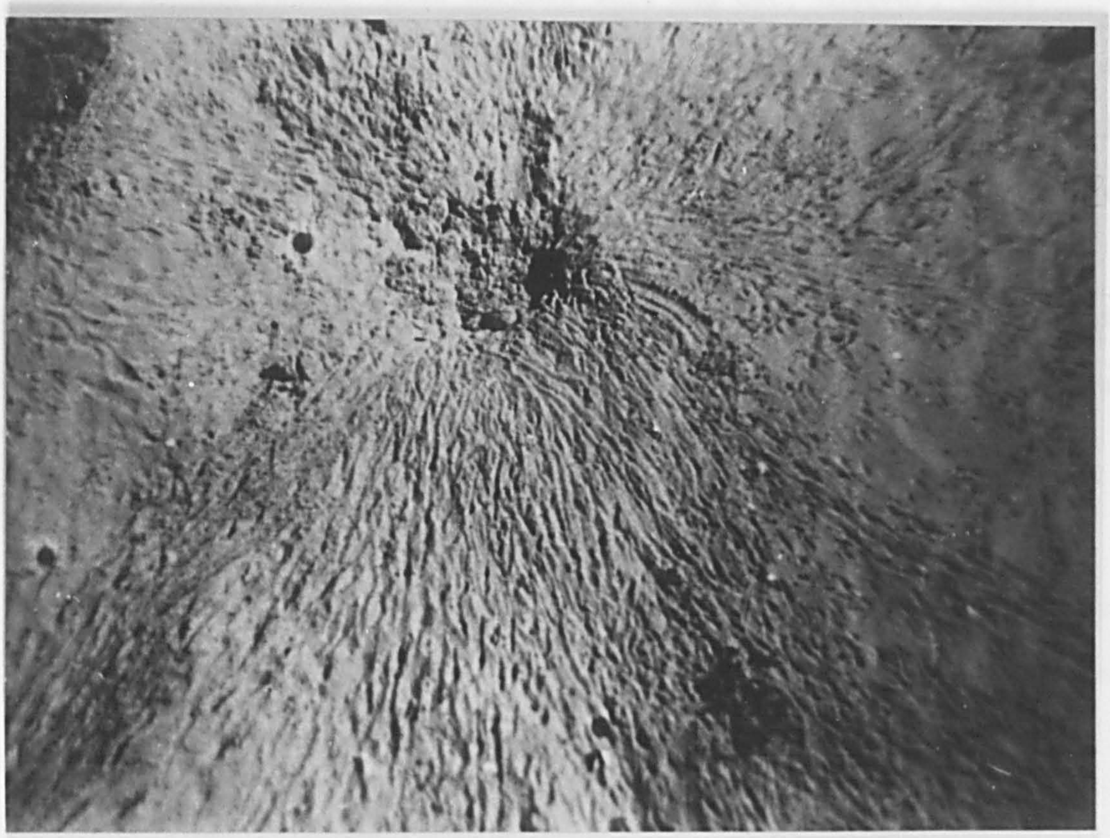
Table 3.16. Burrow Plugging observations at Sharm Obhor

Month (1983/84)	Time	Air Temperature °C	Relative Humidity %	Burrow counts Open	Closed
Oct.	1130	33	-	17	0
Nov.	1300	32	77	14	0
Dec.	1400	30	50	22	10
Jan.	1400	31	77	16	1
Feb.	1300	27	56	19	7
Mar.	1400	28	65	18	0
Apr.	1350	32	66	20	0
May.	1400	34	86	14	0
June	1530	35	66	16	0
July	1430	36	67	19	0
Aug.	1130	39	83	17	0
Sept.	1350	32	82	11	0

The important feature is not season but relative humidity.

These data were taken from walks along the beach each month. The grid data showed the same thing. The numbers of open burrows:closed burrows were - Dec. 35:12, Jan. 35:1, Feb. 47:12, ie. the proportion of closed burrows was 25%, 3% and 20% respectively.

Plate 3.13. Closed burrow of <u>O. saratan</u>. Note the sand plug and the numerous footprints.



3.3.3.2. Water table relationships

The previous section indicated that the water table profile at the Sharm Obhor site closely follows sea level with some suggestion of slight capillary elevation in the beach. If the beach profile is examined (Fig. 3.1) and compared with burrow depths (Tables 3.4, 3.5) there would appear to be some correspondence between burrow depth and the position of the water table. Certainly the deepest burrows occur highest on the beach. When burrows were dug out, however, their lowest points were not in direct contact with the water table but the sand was distinctly damp to the touch. Male burrows examined normally terminated 5-10cm above the water table at the time of excavation but juvenile burrows near the sea showed evidence that the lowest component of the Y proceeded to or near to the water table at least in winter. Plate 3.6d illustrates a burrow in which a lateral deflection at the base of the Y may have been caused by water in the bottom of the burrow.

The smallest juvenile crabs excavate burrows of up to around 15cm in depth. Larger juveniles excavate to around 30cm, or deeper in the case of young males. Adult females may excavate to over 40cm but their U-shaped burrows are usually less than 30cm in depth. Mature males may excavate to deeper than a metre. The distribution of these groups of crabs is given in Figs 3.1 and 3.4. AMSL (arbitrary mean sea level, see Chapter 2) is roughly the lowest level at which crabs burrow at any time of the year. Extreme winter high water and summer low water (T.D.) also closely define the extreme levels of water in the beach. In winter, therefore, the lowest parts of the burrows of all groups of crabs must be near the water table but in summer with the exception of mature male crabs, burrows would have to be much deeper than observed in order to reach it.

Could it be that the complex galleries at different levels in the burrows of mature males are related to changing water levels within the burrow? This point is examined in Discussion.

3.3.3.3. Water content of sand

Table 3.17 indicates that the water content of the sand increases with depth. Except near the waterline, the sand at and near the surface is very dry but the pore spaces become increasingly saturated towards the water table. Porosity proper was not determined. The low water content value for 36cm depth in Table 3.17 is curious and is not supported by observational and tactile impressions of sand dampness at that depth: it probably represents measurement error.

Table 3.17. Water Content of Sand

a) Near water edge (1.8m horizontally from waterline)

Depth (cm)	Wet Weight of Sand (g)	Dry weight of Sand (g)	Water Weight (g)	% weight
0	16.4	14.2	2.2	13
18	17.6	15.8	1.8	10

b) In pyramid zone (10.8cm horizontally from waterline)

Depth (cm)	Wet Weight of Sand (g)	Dry Weight of Sand (g)	Water Weight (g)	% weight
0	20.3	20.1	0.2	1
17	23.1	22.0	1.1	5
36	27.0	26.7	0.3	1
50	21.5	19.1	2.4	11
70	40.6	32.9	7.7	19
80	48.7	37.8	10.9	22

3.4. Discussion

Where several species of *Ocypode* occur together in the same area they are zoned. Usually this involves one species occurring supra-littorally or extra-littorally and the other occurring near to the sea. For example, *O. cordimana* always occurs further away from the sea than *O. ceratophthalmus* where the two species co-exist (Fellows, 1973; Vannini, 1976a) and *O. africana* similarly occurs landwards of *O. cursor* (Gauld and Buchanan, 1956). Also, within the distribution of a single species there may also be zonation though the records in the literature are limited to a few species and are often contradictory. Fellows (1973) concluded that there was a very noticeable lack of agreement among the various authors working on the behaviour and ecology of *O. ceratophthalmus* and the lack of quantified data made such differences irreconcilable. In relation to differences in burrow structure, he suggested that the explanation of intraspecific behavioural differences throughout the Indo-Pacific might be genetic rather than environmental.

To give some zonation examples, in Hawaii Fellows (1966) analysed burrow distribution in the extralittoral *O. pallidula* and the littoral *O. ceratophthalmus*. In *O. pallidula* the males occurred nearer to the sea than the juveniles and females. In *O. ceratophthalmus* large males with spiral burrows and juveniles of both sexes inhabited a shifting 'daily intertidal zone' whereas mature females and adolescent males were restricted to the dry beach zone above the daily intertidal.

Fellows (1966) initially suggested that there was a reproductive behaviour explanation for the zonation patterns of juvenile and adolescent *O. pallidula* and *O. ceratophthalmus*. In the former, the juveniles were morphologically similar to the mature males and so might be forced higher up the beach by them. In O. ceratophthalmus the juveniles were morphologically distinct (not stylophorous) and would be ignored while smaller adolescents (partly stylophorous) would be driven further up the beach away from the mature males. Fellows (1966), however, found that desiccation tolerance was completely uncorrelated with zonation pattern and he concluded that minimal sand moisture content was not limiting. In O. saratan, desiccation data correlated well with the size distribution of crabs on the beach (see Chapter 9). Smaller O. saratan were less resistent to desiccation than larger ones.

Fellows (1966) observed 'the females must pass through the male zone to reach the intertidal feeding area. If courtship and copulation take place in the male burrow then male-female contact at the entrance to the male burrow would be facilitated by such a zonation pattern.' This is the opposite to the situation in O. saratan (see below).

Returning to O. ceratophthalmus, Fellows (1973) found that at Fanning Atoll Line Islands, the zonation situation was different from that at Hawaii. Mature male O. ceratophthalmus still occurred intertidally but many adolescent males and mature females occurred low on the shore and juveniles occurred above the level of the preceding nocturnal tide. Fellows (1973) noticed that in Hawaii O. ceratophthalmus male adolescents and females preyed upon O. pallidula in the same zone but at Fanning Atoll they fed on juvenile conspecifics whose zone they overlapped, so he postulated a possible feeding explanation. O. cordimana at Fanning Atoll was zoned such that juvenile and mature females occurred inland and mature males occurred on the beaches. Horch (1975) found female O. cordimana behind the beach in the Marshall Islands and suggested that this protected the females from intraspecific predation. Vannini (1976a, 1980a) reported that male and juvenile O. ryderi in Somalia dug burrows at a lower shore level than females.

Contrasting with this, Chakrabarti (1981) indicated that on Indian beaches on east and west coasts, O. ceratophthalmus was zoned such that adult crabs occupied the backshore region while the young individuals restricted their activity to the foreshore slope. Chakrabarti (1981), however, did not examine and sex the crabs and did not observe any spiral burrows of males. He studied the burrows in winter and his observations may therefore have a seasonal explanation.

Barrass (1963) found zonation unrelated to size in O. ceratophthalmus in Mozambique with crabs of all sizes found anywhere within the overall crab zone. Also for this species, Takahasi (1932) found adults higher on the beach than juveniles in Taiwan but found no sexual zonation. Hayasaka (1935) also showed juveniles nearer the sea in Taiwan. Barrass (1963), Hughes (1966) and Jones (1972) all demonstrate a tidal influence on general zonation with the zone moving in response to the semi-lunar spring-neap cycle. Hughes (1966) found adult O. ceratophthalmus lower on the shore than juveniles in Mozambique (cf. Takahasi, 1932; Barrass, 1963) and both he and Jones (1972) considered beach profile important in governing distribution. O. pallidula on the Marshall Islands appeared to be distributed randomly (Fellows, 1975).

This is quite different from O. saratan in which the burrows of mature males occur highest on the shore and those of juveniles occur nearest to the sea, with female crabs burrowing in the intermediate zone. In O. saratan, therefore, the females move away from the sea in order to encounter male crabs. They are attracted by the males' sand pyramids which act as static sexual signals (Linsenmair, 1965, 1967). Male O. saratan do not engage in any visual sexual display other than this. O. saratan is not unique in building sand piles but its pyramids appear to be more developed and longer lasting than those of other species (see Vannini, 1980a). Without their attraction, females would not come into contact with male burrows. Since copulation occurs in the burrows (Kopulationschölen; Linsenmair, 1967) of O. saratan such contact is of fundamental importance. So, if Fellows (1966) is correct in his partial explanation of zonation of other species, then the powerful attraction to females of the sand pyramids of males enables the males to occur away from the sea behind the female zone. Also, it has been shown here that the spiral burrows of mature males are not developed if there is insufficient depth of unwaterlogged sand. Male O. ceratophthalmus, in contrast, excavate their spiral burrows intertidally and such behaviour is correlated with full moon in the Seychelles (Brooke, 1981).

The zonation of O. quadrata appears to have common features with O. saratan in that the juveniles are reported to burrow near the sea and the larger crabs (sex not determined) further back (Milne and Milne, 1946; Frey and Mayou, 1971; Hill and Hunter, 1973). This is also true of O. cursor in the East Mediterranean where the peak occurrence of small crab burrows was 10.5m from the sea (Mediterranean: no tide) and the peak of large crab burrows was 18.5m from the sea, though sex again was not determined (Shuchman and Warburg, 1978). Sand moisture content was important in determining the dispersal of this species (Gilad-Shuchman and Warburg, 1977; Warburg and Shuchman, 1979).

The position occupied on the shore by the O. saratan populations varies seasonally with the variation in mean sea level. Magnus (1960) mentioned that O. saratan burrows were flooded in late autumn causing them to move further inland and I have detailed this zone change.

The seaward orientation of the burrow openings of O. saratan (ie. the burrows descended in a landward direction) that was observed in the study is also mentioned by earlier workers (Parenzan, 1931; Magnus, 1960; Linsenmair, 1967). This is shared by O. ceratophthalmus (though not in all cases), O. convexa, O. pallidula, O. stimpsoni and O. quadrata (Vannini, 1980a) and is probably common to the littoral and supralittoral species but this may not be so marked in extra-littoral species. I observed outlying O. saratan burrows amongst the dunes that were not orientated towards the sea and this was also occasionally true in the main male burrow zone. Vannini (1980a) cites a personal communication from Fellows that in O. pallidula seaward orientation decreased landwards. In O. quadrata, Hill and Hunter (1973) showed that burrows were near vertical on the foreshore, were randomly orientated in the foredune ridge but descended obliquely landwards on the backshore. This orientation which was oblique to the shoreline trend was subject to further study and Hill (1981) indicated that the orientation conformed to the mean downwind direction of onshore winds. Further back, amongst the dunes, Frey and Mayou (1971) described burrows to be aligned normal to the individual dune faces but opened toward the sea on the lower backshore and at the foreshore-backshore transition. Foreshore burrows were mostly vertical.

Chakrabarti (1981) reported for O. ceratophthalmus in India that burrows were always orientated shorewards irrespective of the prevailing wind direction. Hughes (1966) reported that the burrows of this species in Mozambique did not have any preferred orientation.

At all my study sites the burrows were clearly orientated to open towards the sea and the data from Al-Quaid and King Saud Palace would argue against any obvious imposed orientation to the direction of the prevailing northwesterly winds.

The densities of various *Ocypode* species are usually referred to in relative terms, eg. 'scarce', 'common', 'abundant' in much of the literature but some authors present quantitative data. For example, densities of *O. quadrata* are presented by Frey and Mayou (1971), Hill and Hunter (1973), Fisher and Tevesz (1979), Wolcott (1978), Wolcott and Wolcott (1984). Some of the authors considered variation in density in different beach zones (Frey and Mayou, 1971; Hill and Hunter, 1973) and some investigated human disturbance effects (Fisher and Tevesz, 1979; Wolcott, 1984). The work shows wide density variations, some of which are difficult to cross compare. For example, Wolcott (1978) expressed density per linear metre of beach by size class throughout the year whereas Frey and Mayou (1971) express the densities of discrete beach divisions as numbers per square metre. Fisher and Tevesz (1979) give only beach length and the numbers of adult and juvenile crabs so that density has to be deduced from their data and Hill and Hunter (1973) express density per $9m^{-2}$. Although some of these authors differentiated juveniles from adults, none differentiated sex. According to Frey and Mayou (1971), at Sapelo Island, Georgia, the most abundant *O. quadrata* burrows were those of adults in the upper backshore (0.3 to $0.4.m^{-2}$), declining to $0.1.m^{-2}$ or less within and below the foreshore-backshore transition. Their juvenile burrows were mainly at this transition and only extended below on broad beaches with a gentle slope. In contrast, on the wider beaches of Padre Island, Texas, Hill and Hunter (1973) found the greatest density of burrows in the upper foreshore. These were small burrows and their density reached as high as $8.m^{-2}$ but elsewhere on the beach densities were lower ($< 1.m^{-2}$ but graphs not precise enough to determine low values accurately). Fisher and Tevesz (1979) overall burrow densities on Virginia and North Carolina beach transects appear to vary from 0.2 to $0.7.m^{-2}$. Wolcott (1978) and Wolcott and Wolcott (1984) give gross densities, and densities $.m^{-2}$ cannot be determined from their data or from the data of Steiner and Leatherman (1981) who counted not burrows but nocturnally active crabs.

For other species of *Ocypode*, Jones (1972) gives densities of *O. ceratophthalmus* and *O. ryderi* in Kenya based on counts of occupied burrows along transects. The maximum *O. ceratophthalmus* density varied from $0.6.m^{-2}$ to $7.1.m^{-2}$ depending on the transect and similarly, the maximum *O. ryderi* density varied from 1.2 to $5.4.m^{-2}$. The densities of Hawaiian ghost crabs studied by Lighter (1976) varied from 0.48 to $1.01.m^{-2}$. In Somalia Vannini (1976a) gave burrow densities for *O. ryderi* of up to $3.m^{-2}$ with the shore position occupied by most crabs varying with the spring-neap tidal cycle. In certain areas of the beach there were 4-5 burrows $.m^{-2}$ (Vannini, 1980b). Chakrabarti (1981) gave densities from 1 to $3.m^{-2}$ for *O. ceratophthalmus* burrows in India, the highest densities occurring nearest to the sea. Densities of *O. cursor* reported by Shuchman and Warburg (1978) were all less than $1.m^{-2}$ on an east Mediterranean beach but showed dramatic positional density changes throughout the year. Peak densities occurred in a narrow beach zone in autumn (up to $0.98.m^{-2}$) but elsewhere densities were usually less than $0.2.m^{-2}$.

Against this background, densities of *O. saratan* can be assessed. Jones (1974) gave beach densities varying from 0.1 to $1.8.m^{-2}$ at one Saudi Arabian site but two other sites had maximum densities of 0.7 and $0.8.m^{-2}$. The maximum densities occurred on the upper beach and lower down densities varied from 0.1 to $0.4.m^{-2}$. The data presented here for O. saratan are similar to those of Jones (1974). Bemert and Ormond (1981) show a photograph of a shore burrowed by O. saratan where the density is probably higher than anything found in my study or by Jones (1974). Fishelson (1971), without giving values, says that the highest density of O. saratan is in the southern Red Sea.

Considering pattern analysis, there are few studies. Fisher and Tevesz (1979) studied within habitat spatial patterns of O. quadrata and showed that adult burrows were evenly dispersed rather than random at 8 sites while juveniles were aggregated at 11 sites. In 4 sites the distribution of juveniles and adults was random. They speculated that both patterns reflected territorial behaviour with adults defending a larger area than juveniles.

In O. ceratophthalmus in Hawaii, Lighter (1976) examined 13 natural crab populations. In 10 of these the spatial pattern of burrows was random but of the remaining 3, 2 showed aggregation and the other spacing. Reproductively active males at densities below $0.6.m^{-2}$ were uniformly spaced but at higher densities their distribution was random. Males prevented other males from burrowing within a 71cm radius centered on their burrow and Linsenmair (1967) showed a similar thing for O. saratan. He stated that the mean distance of 620 pyramid to pyramid measurements was 188cm. The mean distance between pyramids remained relatively constant if immigration and emigration were in equilibrium. He stated that when animals constructed a new pyramid in low density regions the mean distance from already existing pyramids was 134±44cm (n = 100). When the population was more dense, this value was only insignificantly reduced (125±44cm). Greater distances occurred by passive increase in areas where there was much emigration and little immigration.

Evans *et al.* (1976) showed that in *O. ryderi* in Kenya, agonistic interactions appeared to affect the dispersion of crabs on the shore. Without discriminating between size and sex, they found that burrows tended to be more evenly distributed than expected by chance.

My data for *O. saratan* indicate mostly randomness at the low densities of King Saud Palace and spacing in some months in the higher densities of Sharm Obhor populations. Considering male burrows alone, at Sharm Obhor there was evidence of spacing in the early part of the breeding season.

There is very little detailed work on the population biology of *Ocypode* spp. Fellows (1966, 1973) has provided valuable information on *O. pallidula*, *O. cordimana* and *O. ceratophthalmus*. He has given indices of maturation and examined the size and sex composition of populations in several habitats. Indices of maturity are also provided for *O. platytarsis* and *O. cordimana* by Paulraj *et al.* (1982) and Haley (1969, 1972, 1973) has done the same for *O. quadrata*. They did not, however, relate this to the abundance and distribution of crabs in the field. Crane (1941), however, examined the growth and general ecology of *O. gaudichaudii*, and less so *O. occidentalis*, giving some information on population biology. Many of the detailed studies of burrows have been approached from a geologist's viewpoint (eg. Hayasaka, 1935; Farrow, 1971; Frey and Mayou, 1971; Braithwaite and Talbot, 1972; Hill and Hunter, 1973; Chakrabarti, 1981) so it is not surprising that such studies have not been accompanied by a study of the biology of the crabs. Information on the size and particularly sex distribution of *Ocypode* species would go some way to resolving the zonation problems outlined previously, particularly if combined with a clear differentiation between immature and sexually mature crabs.

Maturity indices were not established in my work for O. saratan but I have looked at the size and sex distribution of crabs on the beach. Sandon (1937) looked at growth in O. saratan where his data suggested that there were significant changes in growth rate apparently occurring somewhere between 20 and 30mm carapace length. This is suggestive of the change to sexual maturity but unfortunately Sandon did not examine testes (he only used male crabs) and he had no specimens in the probably critical size range of 24.8 to 31.0mm carapace length (see Haley, 1973). Present data suggest 20mm carapace length = 23mm carapace width and 30mm carapace length = 34mm carapace width.

My data for O. saratan show that small juvenile crabs (< 1.7mm carapace width) were most abundant from May to September but there was also a smaller bimodal winter peak with greatest numbers in November and January. Similar peaks appear in the data for the larger juveniles but at about 1 month later than in the smaller ones which may indicate the rate of growth. Crabs larger than 3.0cm carapace width were most abundant (as judged by their burrows) in the spring and this may reflect a progression of the peak seen in the juveniles. The March peak in the largest crabs (> 4.2cm carapace width) coincides with the establishment of pyramids. Considered together, crabs above 2.9cm carapace width are fairly evenly distributed throughout the year as judged by burrow dimensions with greatest numbers in early winter and mid spring. Growth rate studies have not been conducted in Ocypode spp. although relative growth and maturity indices have been looked at in some species (Sandon, 1937; Haley, 1969, 1972, 1973; Paulraj et al., 1982). From burrow morphometrics, sexual maturity in O. saratan is attained close to 3.0cm carapace width. Certainly, all the males with pyramids had mature gonads (Linsenmair, 1967 and my observations) but my collection of gonad material at smaller sizes was lost in a refrigeration accident so I cannot establish the onset of sexual maturity with precision.

The sex ratio of O. saratan trapped or caught by hand appears to indicate equal numbers of males and females in the population and the decline in the numbers of females recorded in the warmer months probably reflects the courtship behaviour of the crabs with many mature females remaining underground in the male burrow (Linsenmair, 1967).

Equal numbers of right and left handed crabs were found in respect of the side of the major claw and this agrees with the findings of Linsenmair (1967) but is not true of all Ocypode species. For example, Vannini (1980a) found that most O. ryderi in Somalia had the major claw on the right but Barrass (1963) showed that in Mozambique the handedness ratio was 1:1 for male O. ceratophthalmus and Brooke (1981) found the same in the Seychelles. Linsenmair (1967) found that 28 female crabs he dug out of male crab burrows all had the same handedness as the occupant males showing that only crabs with the same claw arrangement mate in O. saratan. Brooke (1981), however, found that in O. ceratophthalmus, the mating crabs were as likely to be of different handedness as of the same handedness, eg. there was no evidence of selection of males by females on the basis of handedness. The handedness of male O. saratan is reflected in the direction of the spiral of the burrows. When the major claw is on the left the burrow spirals downwards in a clockwise direction and when the major claw in on the right the burrow spirals downwards in an anticlockwise direction (Linsenmair, 1967; this study).

Differences in colouration probably reflect crab age, the stage in the moult cycle and differences in illumination and temperature. As early as 1908, Cowles investigated colour change in O. quadrata and found that the hypodermal colour pattern beneath the carapace changed in intensity under different conditions of temperature and light. It was light coloured between 22°C and 45°C in the dark, dark in diffuse light and in light at temperatures below 35°C and light coloured above 35°C independent of light intensity. Cowles (1908) observed that on the beach crabs seen during the middle of the day were light while those just emerged from their open burrows were dark. During late afternoon and on cloudy days the crabs were dark. Occasional light crabs at this time had probably emerged from closed burrows. He presented no nocturnal field observations. Rao (1966, 1968b) has investigated relationships between colour change and moulting in O. macrocera. Several types of chromatophore contributed to changes in body shade. He showed that at high temperatures blanching occurred (leucophores dispersed pigment and other chromatophores concentrated it) and this was probably thermoregulatory as in Uca (Smith and Miller, 1973). O. macrocera showed marked adaptation to background colour with melanophore pigments dispersing on a dark background and vice versa. The neurosecretory processes underlying colour change are very complex and sexual, visual, moult control, chromatophore dispersal and other physiological processes are interrelated (Rao, 1985). Present observations can do little more than report colours observed. The juvenile O. saratan were cryptically coloured against the often damp low shore sand and its drift and the sandy coloured adult crabs matched the background colour of the supralittoral dry sand. Possibly the yellowish ones had just moulted, or were blanched, the sandy yellow ones may have been partially blanched and the bluish ones presumably had fully dispersed pigments in their dark chromatophores. It would be interesting to examine this further.

There is, of course, an immense amount of literature on human impact on coastal regions but two papers are of particular relevance to my study. Steiner and Leatherman (1981) have examined recreational impacts on the distribution of O. quadrata at Assateague Island on the Maryland-Virginia border, USA. They showed that off-road vehicles (ORVs) had harmful effects on crab populations by direct means (crushing and burying) and indirect means (disrupted reproductive cycle and altered environment). In contrast, pedestrians appeared to have no harmful effects on O. quadrata and the density of crabs at the swimming beaches was significantly greater than that of the natural beach, presumably due to picnic waste providing an additional food source for the crabs.

Wolcott and Wolcott (1984) have further analysed the impact of ORVs on beach macroinvertebrates, including O. quadrata, at Cape Lookout National Seashore, North Carolina. They found that burrows as shallow as 5cm gave complete protection against crushing and therefore the crabs were protected during the day but could be killed in large numbers by ORVs at night when the crabs were out of their burrows and feeding. From observations, they predicted population mortalities of 14 to 98% per vehicle-km for a 100 vehicle passes. The Wolcott's considered direct crushing to be the only disruptive effect of ORVs in contrast to Steiner and Leatherman's conclusions. The mole crab, Emerita talpoida and the bivalve Donax variabilis (prey items for O. quadrata) were not susceptible to ORV damage.

The situation in O. saratan may not be the same as in O. quadrata because of the disruption to pyramid building in the former species. The continuous flattening of pyramids by 4-wheel drive vehicles of various types at Jeddah might be expected to disrupt reproductive activity significantly since male O. saratan rely on their pyramids to attract receptive females and the pyramids are important in colony development and spatial maintenance. However, the timidity and agility of the crab may prevent crushing during daylight when crabs are easily frightened into their burrows if on the surface. To be balanced against this, O. saratan undoubtedly gain much food from that discarded following picnics but it is my impression that 4-wheel drive vehicles have had the greatest effect at the King Saud Palace site where there are now relatively few crabs.

At King Saud Palace the habitat, although under pressure, is still intact. Unfortunately, over tens of kilometres the coastal road development of Al-Corniche has destroyed the habitat completely.

I have little information on natural predators. Feral domestic cats predated crabs at Sharm Obhor and so did gulls. I once saw an octopus in a position near the sea edge that suggested that it was a predator on paddling crabs and I have seen large Portunus pelagicus partially buried just below the tide edge, possibly for a similar reason. At King Saud Palace fox tracks in the sand suggested that these were amongst the predators of O. saratan. Vannini (1976a) summarised information on natural predation of Ocypode spp. to which may be added observations by Vader (1982) and McLachlan (1980). Most predators listed are birds or mammals and Parenzan (1931) suggests birds ('plovers, herons, ibises, etc.') for O. saratan though I have seen none of these take them.

Not a great deal is known about the other invertebrates that occur with O. saratan. Coenobita scaevola (= C. jouseaumei) is the most conspicuous and it has been studied by Magnus (1960) who showed that it too could burrow into the sediment. *C. scaevola* tracks can be seen several hundred metres behind the shoreline where they forage at night. Small ones can be seen by day but large ones only at night. Vannini (1975a, b, 1976a, b) presents information on the behaviour and ecology of *Coenobita* species and he shows how the nutritional requirements of *C. rugosus* interrelate with those of *O. ryderi* which was never seen to feed on it. *C. scaevola* apparently feeds mainly on washed up *Sargassum* and other plant material but will eat faeces and can be cannibalistic (Magnus, 1960). In my observations they do well from human picnic refuse. Occasionally they were seen in *O. saratan* burrows but never when the crab is in residence. Magnus (1960) also reported this.

Previous information on the burrows of *O. saratan* is limited to male burrows. I have described the structure of juvenile and female burrows and found male burrows that are both more complex than anything previously reported for *O. saratan* and also far more complex than anything reported for any *Ocypode* species (see Vannini, 1980a).

The burrows of juveniles and females, however, have much in common with those of other species. Juvenile *Ocypode* burrows in addition to being small, tend to be more vertical and shorter than those of adults (Vannini, 1980a). Vannini (1980a) compared the structure of the juvenile burrows of seven species and concluded that, except for the spiral, they were essentially the same shape as adult burrows. Juvenile *O. saratan* burrows have common features with the burrows of females but those of mature males are quite different. The smallest *O. saratan* burrows were I or Y shaped and larger juvenile burrows were in addition L, J or U shaped. An L is probably a variant on a J and as Fellows (1966) pointed out an I could be a finished burrow or a developing burrow stage. It can be seen from the casts how different burrow structures can grade into one another: J-shapes can become U's and Y-shapes can develop into or from these shapes as well as being separately developed. To properly determine such relationships for O. saratan would involve observing subsurface excavations against the walls of laboratory aquaria as attempted by Fellows (1966) for Hawaiian O. ceratophthalmus. He was unable to make many quantitative observations and some laboratory burrow structures differed slightly from those in the field.

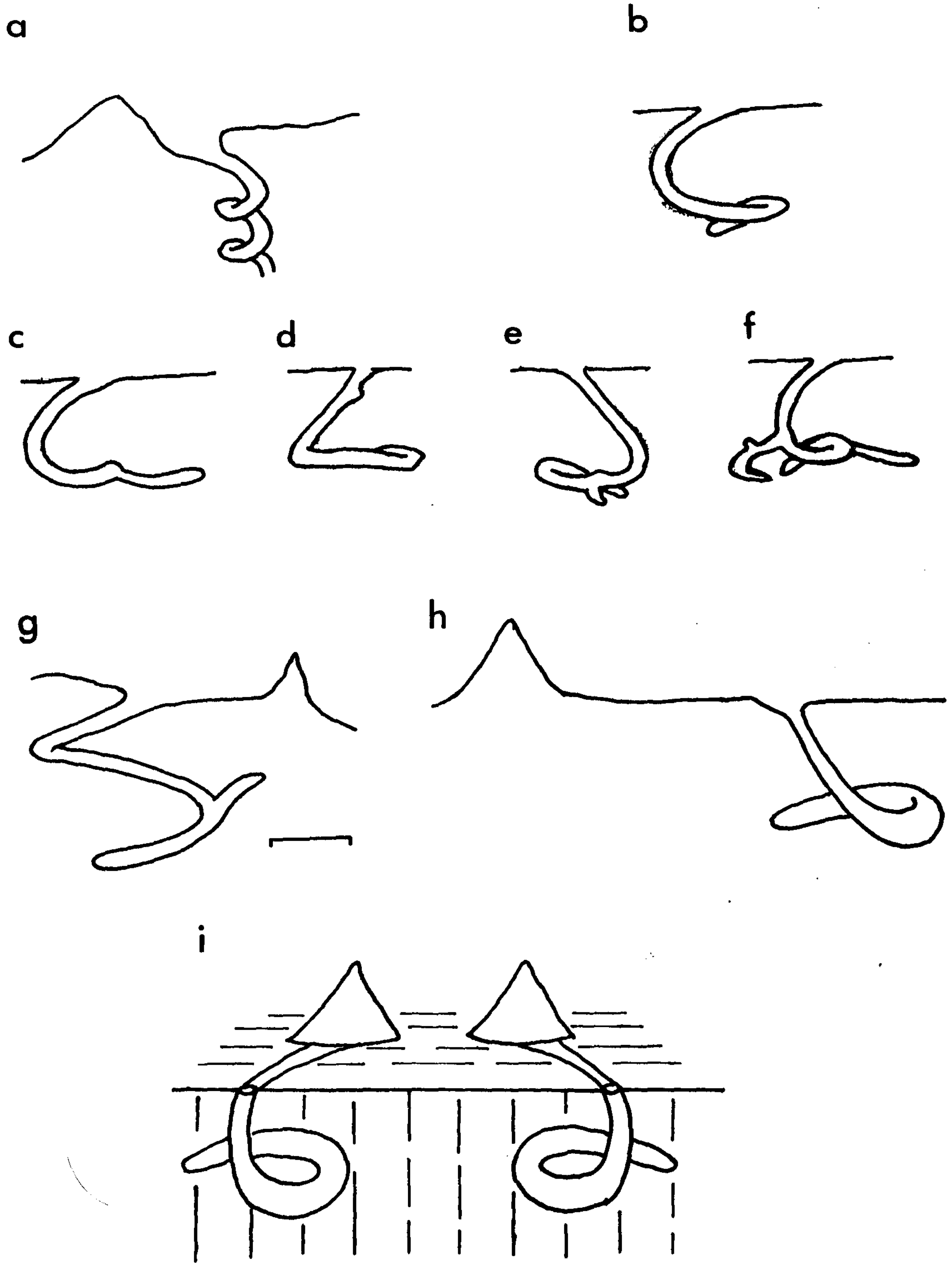
The burrows of female crabs were simple. They were either oblique descending straight shafts or were somewhat Y-shaped or more usually shallow U-shaped. There is probably a developmental sequence through each of these stages. Many of the U-shaped burrows are perhaps better termed J-shaped in that the up-shore section of the burrow stopped just short of the surface with evidence in many cases that it had been opened and plugged. This almost certainly acts as an escape route from sea water flooding and predators. The same explanation holds for the upshore section of juvenile Y-shaped and J-shaped burrows.

Mature male crabs in the breeding season transform the appearance of Red Sea beaches by the production of sand pyramids. These pyramids mark the extrances of their burrows which have been described as spiral (Parenzan, 1931; Al-Kholy, 1959; Magnus, 1960; Linsenmair, 1965, 1967), sometimes with sidebranches (Al-Kholy, 1959; Magnus, 1960) and Linsenmair (1965, 1967) termed these "Kopulationschölen" and the pyramid the "Signalpyramide" though he thought of the burrow as a simple spiral. The spiral burrows of O. ceratophthalmus are generally simple (Vannini, 1980a) and so probably are those of O. gaudichaudii (Crane, 1941) but those of O. saratan may be complex. An indication of this complexity can be seen from Magnus (1960) and particularly Al-Kholy (1959). My observations show burrows of even

Fig. 3.10. Summary of previous information on the spiral burrows of *O. saratan*.

a)	Parenzan (1931)
b-f)	Al-Kholy (1959)
g)	Magnus (1960)
h)	Linsenmair (1965, 1967)
i)	Linsenmair (1967). The burrow on the right was constructed by a left handed crab and *vice versa*.

Only Magnus gave a scale bar (=25cm) but the other diagrams are approximately to the same scale.


a
b
c
d
e
f
g
h
i

greater complexity but their relationship to casts produced by Al-Kholy is fairly clear. Al-Kholy's simplest casts are not unlike the burrows described by Linsenmair (1965, 1967) whereas his most complex cast has common features with my casts. I wonder whether the burrows described by Linsenmair were really all simple spirals or whether they had further complexities which were missed because he didn't use the casting technique. I suspect the latter given my own experiences of hand excavating burrows. The upwardly directed side-branch illustrated by Magnus (1960) was certainly a feature of some of the burrows I examined and on a few occasions I was able to manoeuvre a humidity probe into this branch following some excavation of the spiral. Magnus (1960) said 'the burrows frequently have one or two blind side alleys but the meaning of these is unknown.' Previous information on the male burrows is summarised in Fig. 3.10.

It is quite clear from an examination of the literature on burrow structure in O. ceratophthalmus that there is considerable variation (Fellow's comment on this has already been mentioned) and this may also be the case for O. saratan. My experience, however, is that hand excavation can result in tunnels being missed and gypsum-based casting does not give complete casts of complex burrows. Resin, polyester or epoxy), although expensive and having the disadvantage of penetrating sand adjacent to burrow walls, does given a complete picture of burrow structure.

Linsenmair (1967) has given a thorough description of the structure and function of the spiral burrow, and the sand pyramid. He showed that male O. saratan construct a spiral burrow, vestibule, pathway and sand pyramid with the directions of the spiral and the pathway to the pyramid dependent upon the handedness of the crab. Initial burrowing was stimulated by dry sand with the burrow aperture directed towards the sea. Damp sand in the upper straight section of the spiral hole released construction of the pathway and damp sand in the curve of the burrow released 'base construction', ie. the construction of the base of the pyramid. After the exhaustion of the base construction drive, damp sand in the curve and terminal section of the burrow was used in 'peak construction', ie. careful deposition of sand loads to build the pyramid itself. Finally, the entrance to the burrow was consolidated. Linsenmair (1967) reported that a mean of 10 excavated sand loads were used to build the pathway and a mean of 19 loads to build the pyramid base. Some 30 loads were used to build the pyramid. 25 to 40cc of sand were transported in each load. Linsenmair (1967) showed that the pyramids were the most important sign-stimulus in colony foundation. The pyramids represented 'petrified display signals' that maintained spatial separation amongst males, motivated rival fighting with aggressive intruders, and attracted females to the male burrows.

But what of the burrow extensions seen by Al-Kholy (1959), Magnus (1960) and in my work? It is possible that the upward branch shown by Magnus and perhaps indicated in Al-Kholy's cast is an escape shaft and this may be true of the upwardly directed shafts illustrated in my casts. The volume of the non-spiral section of my two large casts, exceeded that of the spiral part and this invites the question of where was this sand placed? Was it used to rebuild pyramids once the sand resources of the lower spiral section had been exhausted? Linsenmair's description of a chain of building behaviour patterns released by sign stimuli may preclude this unless the sand used for the pyramid can be taken from side branches as well as the lower section of the spiral. Was the damp sand seen scattered around burrow entrances on hot non-humid days taken from this lower burrow region?

Also, there were galleries in the horizontal extension of the burrows I cast and these were at two levels in the two complex casts. Do the positions of such galleries (some 20cm vertical distance apart) reflect tidal or semi-lunar changes in water table level? It is impossible to answer these questions without further observation and experimentation.

Linsenmair (1967) indicated that in Egypt an individual male crab inhabited its burrow and territory for 4 to 8 days during which time it did not feed. After this time it left to feed and then re-entered the colony as an aggressive invader, settling anywhere. In Egypt the feeding area was some distance from the living area and Linsenmair found that in Ethopia where the living area was within the feeding area, crabs left their pyramids to feed and returned to them. I did not examine this aspect of feeding behaviour but the burrows were near the sea and male crabs were seen moving through the pyramid zone, were seen at the tide edge and were collected in pitfall traps on the beach (see Chapters 4 and 5). It may be that individual crabs maintained burrows for some time at my sites but even if they did not the burrow itself may have had a long 'life' with successive occupants. Marking individual crabs and examining the permanence of individual burrows would help resolve this.

Another point is that the extent of the underground complex may be much greater than is apparent at the surface. Could it be that the relatively large distance observed between male burrows in both my observations and those of Linsenmair, reflects the extent of underground tunnels, allowing room for them to develop without being intercepted by the burrows of other crabs? According to Linsenmair (1967) the crabs possess genuine distance perception. Both the complex casts I have illustrated terminated approximately beneath adjacent sand pyramids and did not extend beyond them.

Linsenmair (1967) dug 28 female crabs out of individual male burrows, presumably from the terminal section of the spiral but this is not clear. The male burrows I excavated were only occupied by males so I cannot determine which portion of my burrows would have been occupied by the females.

If burrows are permanent enough, their structure may have a seasonal explanation. Since Linsenmair has clearly shown that the behavioural sequence involved in the development of the pyramid requires sand to be excavated from specific burrow regions, could it be that the horizontal chambered burrow section represents a development of the winter burrow? I find it difficult to believe that burrows could be this permanent and in any case there is a seasonal change in the position of crabs on the shore. Maybe the spiral component is just for reproduction and the other portion has other functions. It is likely, whatever explanation of the whole structure, that ascending shafts that terminate just short of the surface serve as escape tunnels.

Linsenmair (1967), therefore, did not give a complete explanation for the structure of the burrows of O. saratan encountered in this study and also by Al-Kholy (1959).

Some of the burrows I looked at had more than one pyramid at the entrance (up to three). Linsenmair (1967) stated that an invading crab added to an existing pyramid if it was like-handed but a crab of different handedness would excavate an appropriate spiral below the straight section of the existing burrow and build a new pyramid opposite the old one. Multiple pyramids at the same side of a burrow may be because an individual crab has a critical path length. Entrance collapse can cause the path length to change and a new pyramid to be built (Linsenmair, 1967). Linsenmair's explanations therefore account for my observations of multiple pyramids. Magnus (1960) also noticed occasional double pyramids.

Although the burrows of O. saratan have a variety of other functions, eg. reproduction, predator evasion, food storage, etc., their ability to protect crabs from environmental extremes of temperature and, associated with this, relative humidity, is of great importance. The significance of the burrow in this respect has been recognised by various workers on burrowing crabs. Some of this information is discussed by Bliss (1968) who examined the transition to land in decapods and she presented clear evidence that the burrow gave protection from both high and low temperatures in a number of species. Uca species have received much attention in respect of their ways of coping with high temperatures and Edney (1961), Smith and Miller (1973) and Powers and Cole (1976) are amongst those who have shown the importance of the burrow protecting crabs from lethal high temperatures. These authors measured the actual body temperatures of the crabs and showed that the body temperature of Uca some 30cm within the burrows was at least 10°C cooler than the highest body temperatures at the surface. At the surface, crabs were 5-8°C cooler than outside temperature due to transpiration but within burrows high relative humidities prevented water loss and crabs were in thermal equilibrium with their burrows. Powers and Cole (1976) give a lot of information on the burrow environment of Uca spp., and indicate that the hoods that sexually active males of some Uca species build over their burrow entrances (see Crane, 1975) have the effect of keeping such burrows cooler at night and warmer in the day than non-hooded burrows but they had no measurement of relative humidity. They also indicated that an *O. quadrata* burrow in adjacent sand showed a temperature 20°C cooler than the white sand in direct sun around the opening. It is clear from the data on *Uca* spp. that environmental temperature not only regulates their activity on a daily basis, but also seasonally. In the winter, warm weather is required to stimulate *Uca* species to emerge from their burrows (Powers and Cole, 1976). It is not the only factor, however, and the effects of light and tide are well known (eg. Barnwell, 1963).

Bliss (1968) has shown that in an artificial burrow 40cm deep, simulating the environment of *Gecarcinus lateralis*, temperatures (compared with the outside) remained 'warm' (21°C - 24°C) in January when the outside temperatures varied from 13°C-29°C and 'cool' (28°C-32°C) in July and August when outside air and sand temperatures were 35°C and 50°C respectively. *G. lateralis* was not seen to emerge from its burrow at temperatures below 18°C and, experimentally, animals rapidly raised to 32°C did not survive more than a few days. Relative humidities at the base of burrows were estimated to be from 93-100% (surface means were 72-90%).

For *Ocypode* spp., the same principle seems to apply. Koepcke and Koepcke (1955) found *O. gaudichaudii* burrows gave good thermal protection and Vannini (1976a) showed that at 30cm depth within an *O. ryderi* burrow air temperature was relatively stable (c. 27-29°C) while the outside air temperature varied between c. 22°C and 45°C (values read from a graph). Rao (1968a) showed that in *O. cordimana* burrows 45-50cm deep the bottom temperature was 20-24°C and relative humidity 90-100%.

My results further confirm this trend. Within the burrow, temperatures are relatively constant and are consistently lower than outside day temperatures in summer and winter though at night in winter the burrows may be warmer than outside (see climatological data, Chapter 2). The sand surface temperature may become very warm ($50^{o}C$) during the day but the deep sand is relatively constant in temperature and maintains constant conditions within the burrow. Relative humidity within the burrow is always higher than outside the burrow and I think that burrow closing functions to maintain this during dry winds when the relative humidity of the outside air is low. I do not have much data on burrow microclimate within closed burrows. The few temperature records taken were lower than those outside (in contrast to the hooded burrows of Uca, Powers and Cole, 1976). Relative humidity will certainly be high. The danger of desiccation is greatest at high temperature and low relative humidity (see Chapter 9).

In the May 1984 temperature data, the slightly higher outside air temperatures when compared with burrow temperatures 20cm within burrows is also seen in some of the Uca data of Powers and Cole (1976), when their surface temperatures are compared with burrow temperatures. This probably represents evaporative cooling above the sand surface since it is predominantly a daytime effect. It may also reflect wind effects and the fact that it was not seen on other occasions may be due to differences in the position of the temperature probe relative to the sand surface and not just environmental differences.

It has already been indicated (Chapter 1) that there is disagreement between various authors as to whether Ocypode species excavate to the water table. It seems that in most places this is not the case. Statements of burrows reaching the water table may sometimes result from general impressions rather than critical measurements and this is probably true for the statment made by Magnus (1960) for O. saratan - 'the burrow develops in further left or right winding spirals into the depths until it reaches the water table'. Of O. saratan, Linsenmair (1965) said 'in damp areas the holes often reach down to the underground water table or at least into very damp sand.' Linsenmair (1967) said that 'at latest by 80cm deep the sand must be wet' when defining the sort of beach in which O. saratan burrowed. It seems clear to me that it is the moisture content of the sand which is important and not the water table itself. The two are, of course, connected and above the water table sand dampness will depend on its grain characteristics. Linsenmair (1967) has shown that damp sand is necessary for pyramid construction in O. saratan. For O. cursor, the water content of the sand has been shown to determine its distribution (Shuchman and Warburg, 1978; Warburg and Shuchman, 1979). Adult O. cursor were most abundant where soil moisture was 15% and were able to distinguish in experimental conditions between moisture alternatives differing by only 1% moisture. These authors did not investigate this in juveniles. Warburg and Shuchman (1979) concluded that although Ocypode (speaking generally) does not dig down to the water table, it can extract sufficient water for its survival. More is said of this for O. saratan in Chapter 7.

Fellows (1966) could not find any correlation between burrow depth and sand moisture content in Hawaiian O. pallidula, or any correlation between burrow depth and beach height or between burrow depth and location on the beach. He concluded the same for O. ceratophthalmus and noted that in this species the water table reached the burrow during tidal influx and not vice versa as suggested by Takahasi (1932).

All the data Fellows (1966) presented showed sands with a moisture content of above about 10% at the depths to which burrows of O. pallidula reached (20-25% moisture in the case of the intertidal sand). O. quadrata may occupy burrows in which the sand water content is as little as 4% by weight (Powers and Bliss, 1983) and can extract water from beach sand of water content as low as 3.5% but extraction is better above 5% (Wolcott, 1984). According to Rao (1968a), the water content of the sand at the bottom (45-50cm) of O. cordimana burrows was 8-12% 150-200 yards from the shore, while for the intertidal O. macrocera and O. platytarsis the sand was saturated in their 20-50cm deep burrows.

For comparison, Wolcott (1984) showed that Gecarcinus lateralis lived in burrows where the mean water content was from 6-15% but the species could not extract this by rapid bulk uptake means as could O. quadrata.

My data suggest that the moisture content at the bottom of O. saratan burrows will vary between 10 and 20% and in my experience the deepest portions of the burrow normally do not reach the water table itself but the bottom sand is often almost fully saturated with water (judging from Wolcott (1984) the water content of clean beach sands approaches 28% and dune sands 22%). All of these percentages are by weight.

DIVISION 2. BEHAVIOUR

CHAPTER 4. ACTIVITY PATTERNS

4.1. Introduction

Much of the information on activity rhythms in *Ocypode* species is discussed by Vannini (1976a) and it is clear that there is wide variation in the times at which various species are active out of their burrows and in the time spent engaged in various activities. In order to appreciate this, the textual information presented by Vannini (1976a) has here been tabulated, together with some more recent information (Table 4.1).

It appears that most *Ocypode* species are predominantly nocturnal but as can be seen from Table 4.1 some species are reportedly day active in one area and night active in another (eg. *O. ceratophthalmus*, *O. quadrata*, *O. saratan*). Vannini (1976a) states 'a comparison of the available data on *Ocypode* crabs is not easy because the reports are often contradictory and lacking in quantitative data'. The main problem is that most authors do not distinguish the different activities of the crabs. In much of the literature crabs observed out of their burrows by night are described as nocturnally active and those observed out of their burrows by day as diurnally active, irrespective of the type or degree of actively exhibited.

Also, it is generally accepted that juveniles of some *Ocypode* spp. are often diurnally active in contrast to the nocturnal adults of the same species (see Table 4.1).

The tidal cycle also may modulate activity as in *O. gaudichaudii* (Crane, 1941), *O. cursor* (Gauld and Buchanan, 1956), *O. ryderi*

Table 4.1. Activity Periods *

activity period	species	area	information source
predominently nocturnal	*O. convexa*	W. Australia	George and Knott (1965)
	O. fabrici	W. Australia	George and Knott (1965)
	O. cordimana	Sumatra	von Raben (1934)
		Taiwan	Takahasi (1935)
		W. Australia	George and Knott (1965)
		Line Islands	Fellows (1973)
		Somalia	Vannini (1976a)
	O. africana	Congo	Rathbun (1921)
		Ghana	Gauld and Buchanan (1956)
	O. cursor	Congo	Rathbun (1921)
		Israel	Shuchman and Warburg (1978)
	O. occidentalis	California	Rathbun (1918)
		W. Central America	Crane (1941)
	O. gaudichaudii	California	Rathbun (1918)
		Peru	Koepcke and Koepcke (1953)
	O. quadrata	New Jersey	Rathbun (1918); Milne and Milne (1946)
		Bermuda	Verrill (1908); Palmer (1971)
		Florida	Cowles (1908)
		Delaware	Flemister and Flemister (1951)
		Suriname	Holthuis (1959)
		Texas	Haley (1969)
		N. Carolina	Wolcott (1978); Wolcott and Wolcott (1984)
	O. saratan	Red Sea; Egypt	Al-Kholy (1959)
		Egypt and Ethiopia	Magnus (1960)
		Ethiopia	Linsenmair (1967)
	O. ceratophthalmus	Mozambique	Cott (1929)
		Taiwan	Takahasi (1935)
		Malaysia	Tweedie (1950)
		Hawaii	Daumer *et al*. (1963); Fellows (1966)
		Marshall Islands	Gross (1964)
		W. Australia	George and Knott (1965); Alexander and Ewer (1969)
		Kenya	Jones (1972)
		W. Inhaca Island (Mozambique)	Kalk (1954); MacNae and Kalk (1962); Barrass (1963); Hughes (1966)
		Aldabra	Farrow (1971)
		Line Islands	Fellows (1973)
		India (N.E. coast)	Chakrabarti (1980)
		Seychelles	Brooke (1981)
predominantly diurnal	*O. gaudichaudii*	Central America	Crane (1941, 1947, 1949)
	O. quadrata	Florida	Pearse (1929b)
		Georgia	Robertson and Pfeiffer (1982)
	" juveniles	Florida	Cowles (1908)
	O. saratan	Egypt	Linsenmair (1967)
		Aden	George and Knott (1965)
	O. ceratophthalmus	E. Inhaca Island (Mozambique)	Kalk (1954); MacNae and Kalk (1962); Barrass (1963); Hughes (1966)
	" juveniles	Mozambique	Cott (1929)
		Malaysia	Tweedie (1950)
		Hawaii	Daumer *et al*. (1963)
		Mozambique	Hughes (1966)
		Hawaii	Burrows and Hoyle (1963)
	O. occidentalis juv.	W. Central America	Crane (1941)
	O. ryderi	Inhaca Island (Mozambique)	Kalk (1954); MacNae and Kalk (1962)
	O. macrocera	India (E. coast)	Rajabai (1972)
predominantly crepuscular	*O. ryderi*	Somalia	Vannini (1976a)
day and night	*O. ryderi*	Kenya	Jones (1972)

* Based on textual information in Vannini (1976a) but extended.

(Vannini, 1976a) and O. ceratophthalmus (Barrass, 1963) with greatest activity reported around low tide. This is by day or night in O. ryderi, by day in O. gaudichaudii and by night in O. ceratophthalmus. Diel information is not given by Gauld and Buchanan (1956) for O. cursor.

Jones (1972) demonstrated an endogenous circadian rhythm of locomotor activity in O. ceratophthalmus with peak activity during 'expected' darkness. There was no circatidal rhythm evident. O. ryderi showed no endogenous rhythmicity. An endogenous circadian rhythm with nocturnal peaks of locomotor activity has also been demonstrated in O. quadrata (Palmer, 1971).

For O. saratan, Linsenmair (1967) has made by far the most detailed behavioural study. This was directed towards the sexual behaviour of male crabs with special reference to the construction and signal function of their sand pyramids which was analysed in great detail. No attempt is made to repeat this in the present investigation but rather to give a general description of the various activities of O. saratan in the field, together with laboratory observations and an investigation of endogenous locomotor activity.

4.2. Material and Methods

In addition to observations of crab activity during the regular monthly visits to the field study sites at King Saud Palace and Sharm Obhor, crab activity was continuously observed during a 54 hour beach experiment at Sharm Obhor from 13th to 15th May 1984.

Mains power was cabled 300m from the Marine Station (Faculty of Marine Science, King Abdul-Aziz University) at Obhor to the study beach where a tent was erected to serve as a closed circuit television control room. Another tent nearby served as sleeping quarters. The auto-iris television camera with zoom, focus and pan-and-tilt controlled from the tent was placed in the middle of the pyramid zone some 50 metres from the tent. Cable permitted the camera on occasions to be moved as far as 100m from the control point (Plate 4.1). The specification of the video equipment used is as follows: Sanyo low light, low voltage, Model VCN3524 TV camera with Vicon V12.5 - 75m motorized zoom, focus and auto-iris lens and Vicon V3000 PT pan-and-tilt; Sanyo monitors; Panasonic NV8050 time-lapse video recorder (VHS); Voltage and frequency stabilizer.

During the brightest part of the day the sensitive camera was protected with neutral density filters. By night red light bulbs were used to dimly illuminate sections of beach but the camera was also panned to beach areas in darkness when moonlight was often sufficient illumination to discriminate crab activity.

Additionally, photographic records were taken using Nikon F3 and Nikonos IV 35mm cameras and a Eumig Nautica Super 8 movie camera.

A tidal staff was established using a metre rule and read visually every 2 hours. Counts of crabs at the tide edge were taken at two-hourly intervals as were counts of open and closed burrows.

Air temperature and relative humidity was measured 20cm within the burrows and outside burrows at two-hourly intervals and sand surface temperature was also measured using the equipment detailed in Chapter 3. These records were continued for 48 hours, commencing 6 hours later than the behavioural observations.

The continuity of the observations and recordings was made possible by working a system of shifts during which the tent was used

Plate 4.1. a) Closed circuit television system set up on Sharm Obhor beach. The camera is in the foreground and the control systems are housed in the tent.

b) Detail of the control systems in the tent.

a

b

for rest periods. Dr Atkinson (Millport), and Dr Antonius, Dr Bodoy and Dr Oakley (Jeddah) assisted me in this.

In order to assess the possible influence of tides on behaviour, a further 24h period of observation took place during the following week (on 25/26th May 1984) when neap tides prevailed in contrast to the spring tides encountered in the 2-day study. The TV was not used but crab activity was observed at the tide edge using binoculars, a tidal staff was established using a rule and air temperature and relative humidity measurements were taken, together with sand surface temperature measurements.

Laboratory observations of behaviour were carried out on captive O. saratan maintained in a large outdoor 'aquarium' in which natural conditions were simulated. The aquarium was situated in a small courtyard totally enclosed by the Marine Station buildings but open to the sky. The aquarium consisted of a large glass fibre fishpond sunk into the ground. It was asymmetrical in shape with a maximum linear length of 3.4m, a maximum width of 2m and a depth of 1m. The bottom of three quarters of the tank was covered with a layer of gravel and this was covered with fine mesh plastic netting. Beach sand was added above the netting and banked up at one end to simulate the sloping beach. The tank was connected to the sea water circulation system such that water was introduced beneath the gravel layer and brought to just above the level of the mesh thus providing a water table beneath the sand and an area of free water at one end of the tank, simulating the sea. The system is illustrated in Plate 4.2. Two rooms in the marine station whose tinted windows overlooked the tank were used as observation areas. Crabs were unaware of observer presence. Observation was both direct and by using the closed circuit television in continuous or time-lapse mode. As in the field, the

Plate 4.2. Large glass fibre tank in which a simulated beach environment was set up for O. saratan in a laboratory courtyard at Sharm Obhor.

camera was protected by neutral density filters by day and by night dim red illumination was used if natural illumination (moonlight) was insufficient.

A room in the Marine Station at Obhor was prepared for actograph experiments and an actograph constructed such that when a crab emerged from its naturally constructed burrow it compressed water filled rubber tubes placed in the sand and the pressure pulse was detected using a Searle Bioscience PT400 Blood Pressure Transducer and recorded on an oscillograph (Washington: Searle Bioscience). It was not possible, however, to maintain constant conditions due to air conditioning and power failures and human disturbance (student classes using adjoining rooms) so this had to be abandoned. As an alternative, live crabs were flown to Glasgow and experimented on in constant conditions at the University Marine Biological Station, Millport, Scotland.

The <u>O. saratan</u> were collected at Obhor on the 26th January 1985, flown to Glasgow on the 28th and placed in a constant temperature room at 25°C, experiencing natural daylight backed up by artificial light alternating with darkness. On 1st February the crabs were transferred to the University Marine Biological Station Millport.

They were maintained at 25°C and 90% RH and subjected to various laboratory Light:Dark (L:D) regimes. The crabs were maintained in acrylic actographs with 10cm of sand in which they constructed shallow burrows. Out-of-burrow activity was recorded as 'spikes' on a Rustrak event recorder when crabs interrupted far-red beams of light focussed on photoresistors (method detailed in Atkinson <u>et al.</u> (1974)). The actograph was essentially a circular, square cross-section trough with a ventilated lid. The outside diameter was 40cm and the inside diameter 25cm, giving a width of 15cm for the circular 'run'. Both light emitters and photoresistors were placed outside of the actograph and the focussed beam was directed across the actograph to a mirror and reflected to the photocell, increasing the chances of beam interruption.

4.3. Results

4.3.1. Diel patterns of activity under natural conditions

4.3.1.1. 2 day field study

Figs 4.1 and 4.2 (and Table 3.15) present the results of a 2-day field experiment in which the behaviour of crabs was recorded together with environmental variables. The data on temperature and relative humidity have already been discussed in Chapter 3: here they are seen in relation to activity.

The number of crabs seen at the water's edge are shown in Fig. 4.1. These were determined by examining the same section of beach with binoculars at 2 hourly intervals. The television camera was used to search a section of beach within this area. It could not view all the beach at once so pan-and-tilt and autozoom were used to systematically search the selected area. Everything viewed by the camera was videotaped in time-lapse mode with behavioural acts of particular interest recorded in real time. The overall pattern of activity that emerged is illustrated in Fig. 4.2.

From about 2h before sunset to around 4h after sunrise crabs were active out of their burrows. Between 1000h and 1700h crabs were inactive and not seen out of their burrows in the region scanned by the camera. It was noticed, however, that adult crabs were often seen immobile in the section of the burrow near the entrance. Some adult

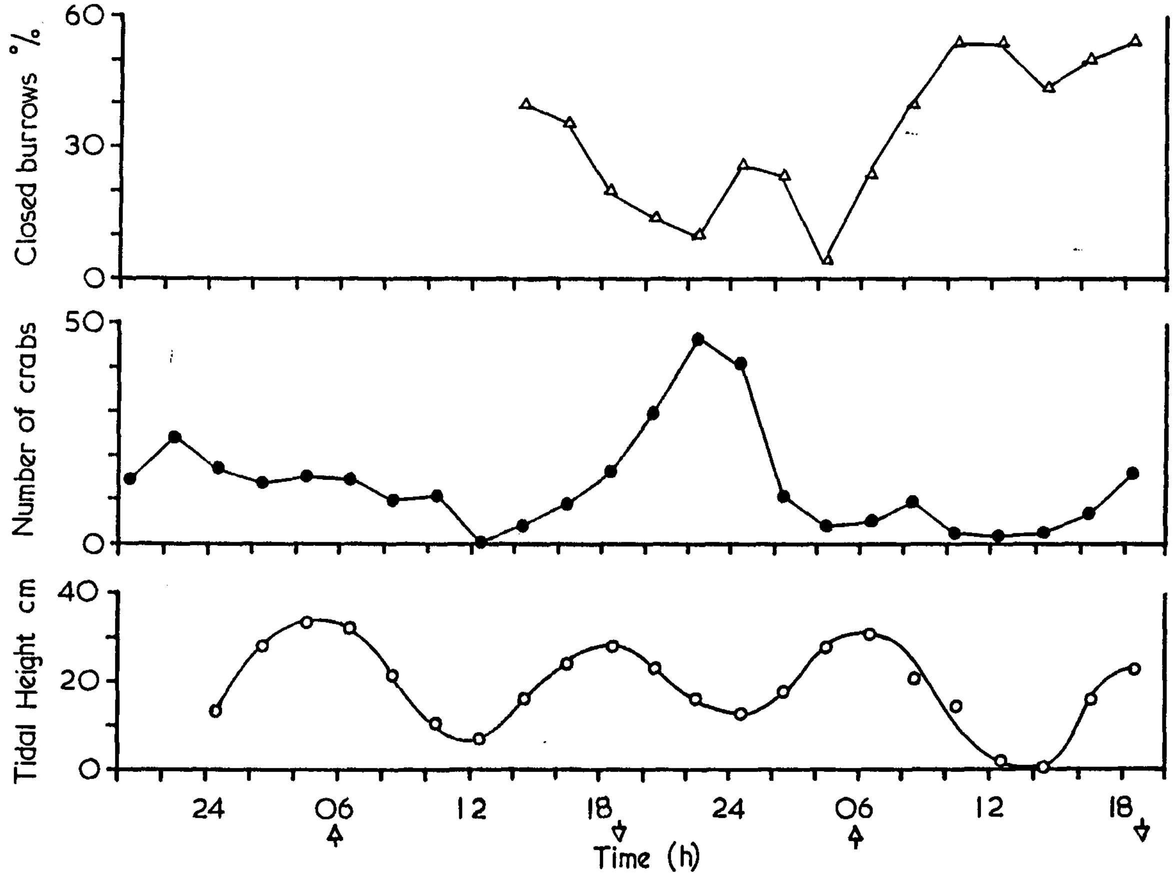
Fig. 4.1. 2 day field experiment at Sharm Obhor (13th-15th May 1984).

For relative humidity, open circles = air 20cm within burrow, closed triangles = air outside burrow.

For the lower temperature figure, closed circles = sand temperature, open cirles = air temperature, crosses = air temperature 20cm within the burrow.

For the upper temperature figure, the open circles denote sea temperature at the tide edge.

Arrows indicate the times of sunrise and sunset.


Closed burrows %
60
30
0
Number of crabs
50
0
Tidal Height cm
40
20
0
24
06
12
18
24
06
12
18
Time (h)

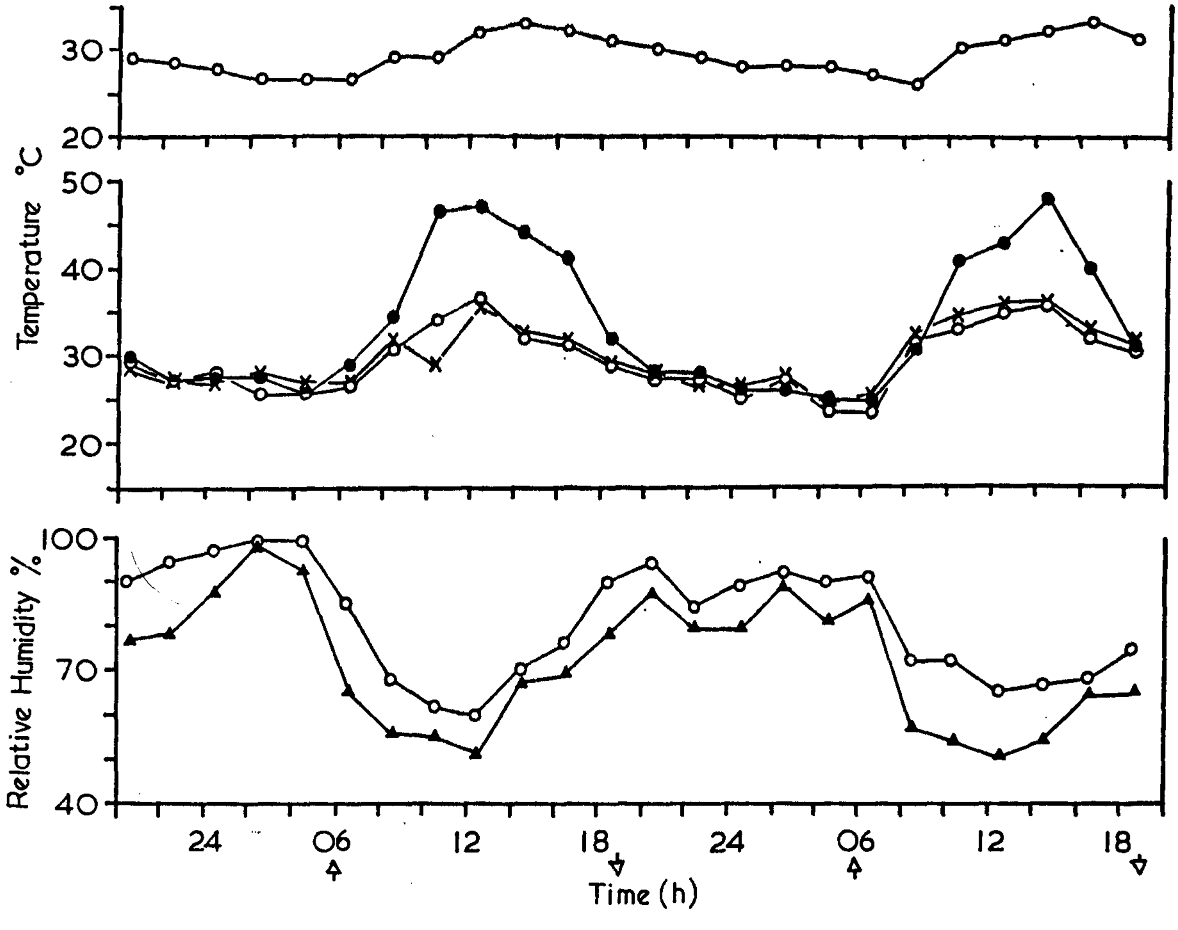
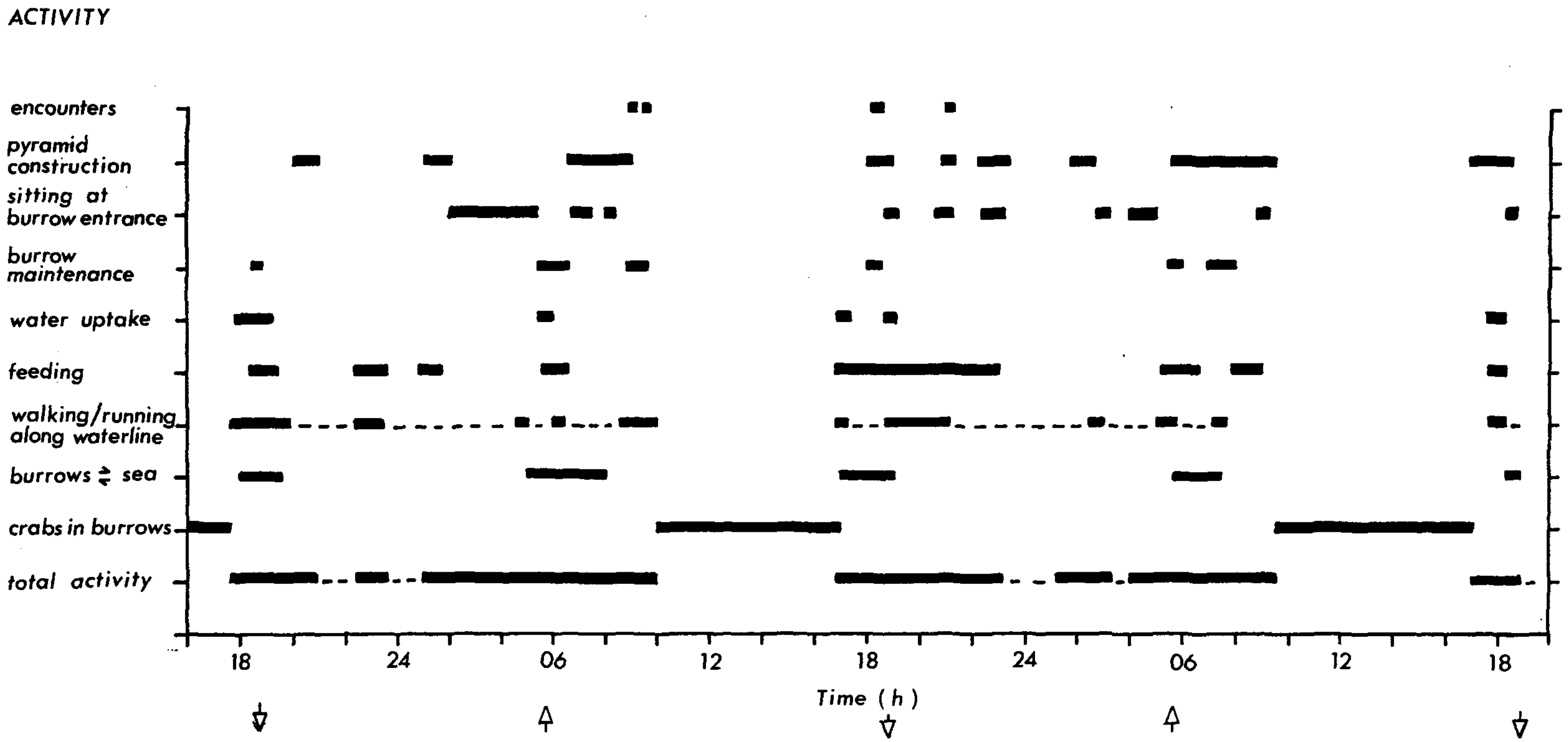
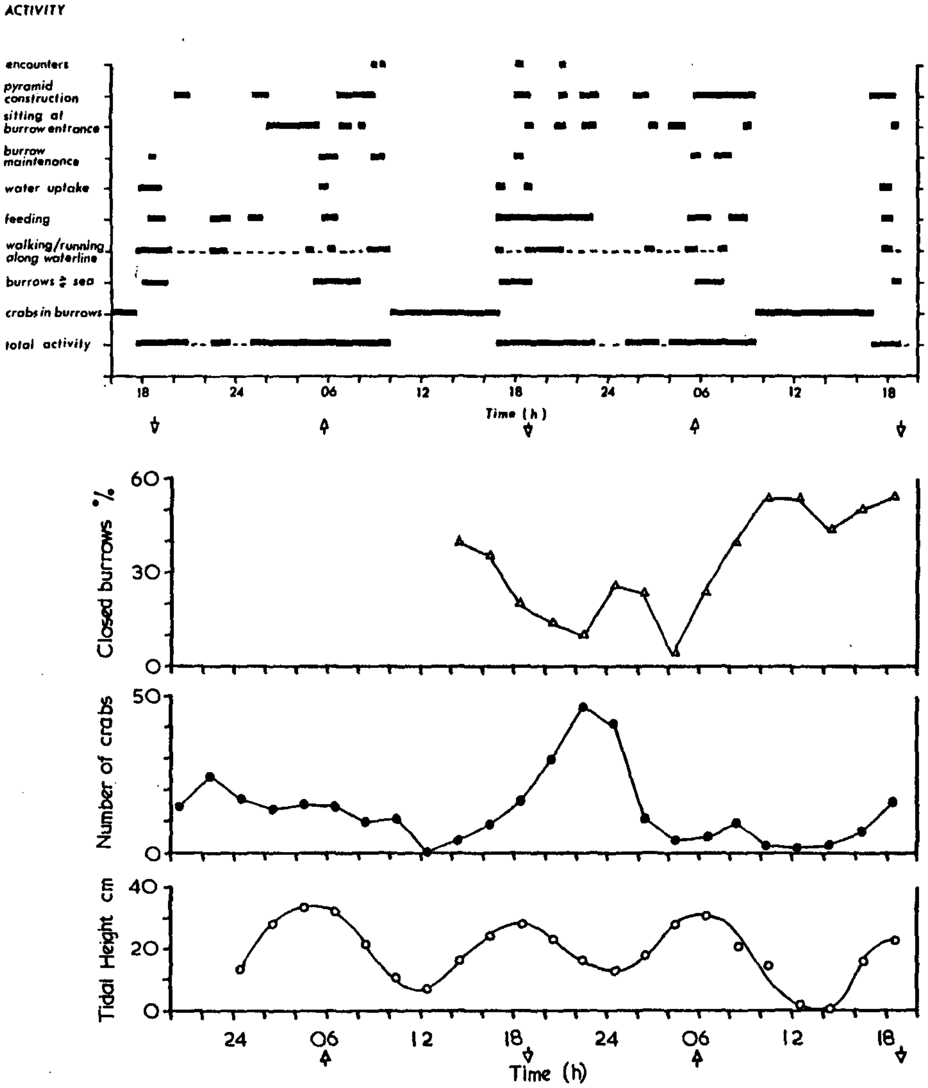

30
20
Temperature °C
50
40
30
20
Relative Humidity %
100
70
40
24
06
12
18
24
06
12
18
Time (h)

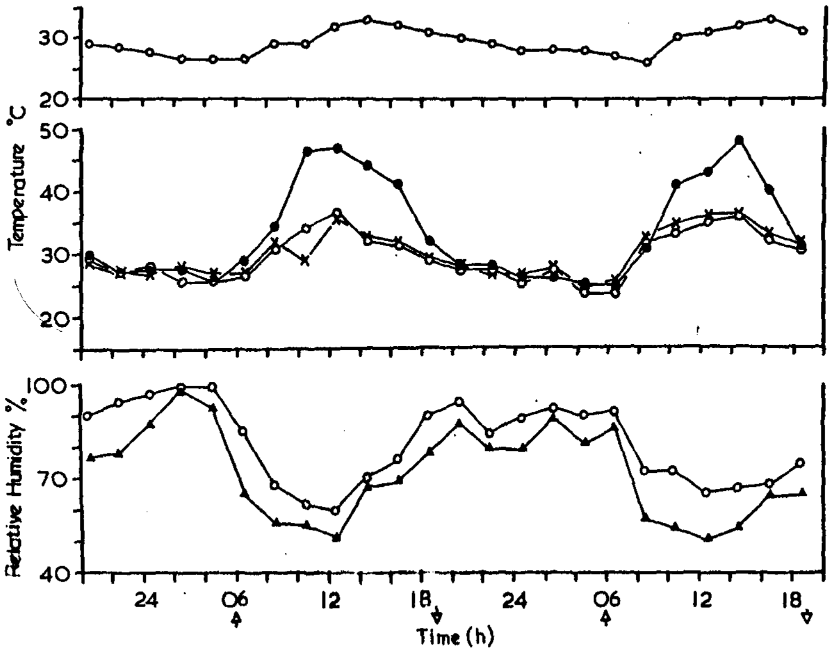
Fig. 4.2. Activities of O. saratan during 2 day field experiment at Sharm Obhor (13th - 15th May 1984). Total activity is derived from pooling the separate activities. Arrows indicate the times of sunrise and sunset.

Figures 4.1. and 4.2. are shown together on the next page.


ACTIVITY
encounters
pyramid construction
sitting at burrow entrance
burrow maintenance
water uptake
feeding
walking/running along waterline
burrows ⇄ sea
crabs in burrows
total activity
18
24
06
12
18
24
06
12
18
Time (h)



ACTIVITY
encounters
pyramid construction
sitting at burrow entrance
burrow maintenance
water uptake
feeding
walking/running along waterline
burrows ⇄ sea
crabs in burrows
total activity
18
24
06
12
18
24
06
12
18
Time (h)
Closed burrows %
60
30
0
Number of crabs
50
0
Tidal Height cm
40
20
0
24
06
12
18
24
06
12
18
Time (h)



30
20
Temperature °C
50
40
30
20
Relative Humidity %
100
70
40
24
06
12
18
24
06
12
18
Time (h)

crabs were observed to visit the sea even during daytime elsewhere on the beach (Fig. 4.2) and there some adult crabs were observed to engage in burrow maintenance also. The majority of the population, however, remained underground. Some of the crabs observed at the tide edge during daytime were making use of the shade provided by a small wrecked boat at the tide edge. The smallest juvenile crabs could not be observed reliably using binoculars so the counts in Fig. 4.1 refer to conspicuous crabs - adults and large juveniles. Small juveniles were reliably observed along the tide edge using the zoom facility of the TV camera by night. By day the camera was overloaded by bright light despite filters and small crabs could not be discriminated. Several walks along the tide edge revealed that some were out of their burrows by day but this technique was not pursued because of the possible interference on the behaviour of those and other crabs.

By night the TV revealed very small O. saratan running and feeding at the tide edge throughout the night as did the adults. The adults often occurred in distinct groups but this did not seem to be the case for the juveniles. Adult and juvenile crabs at the tide edge were seen to engage in a number of activities. Some walked or ran along the tide edge without feeding: this was often a group activity in adults.

Feeding at the tide edge was either by sand pellet feeding, predatory behaviour or general foraging and scavenging along the strand. Feeding is dealt with in more detail in Chapter 5. In the observations reported here sand pellet deposit feeding only occurred around the time of low tide when the narrow damp intertidal sand was exposed. Large crabs could clearly be seen to engage in this activity and small crabs appeared to be doing the same though their size made observations difficult. Adult crabs were observed digging up bivalves at low tide (Mesodesma, probably M. glabratum) and in a number of observations carry them back to their burrows. One adult crab was observed to dig something out from the sand at the water edge at high tide but the identity of the prey (?) item was not determined. Another clearly excavated Mesodesma from near the top of the intertidal zone and carried it to its burrow.

Most of the feeding was by general foraging with crabs of all sizes repeatedly picking up minute objects from the wet sand and various unidentifiable items from the strand. Feeding activity probably continued throughout the night since crabs were observed at the tide edge at all times but the present observations suggested a decline in feeding intensity for several hours in the early morning, picking up again around dawn.

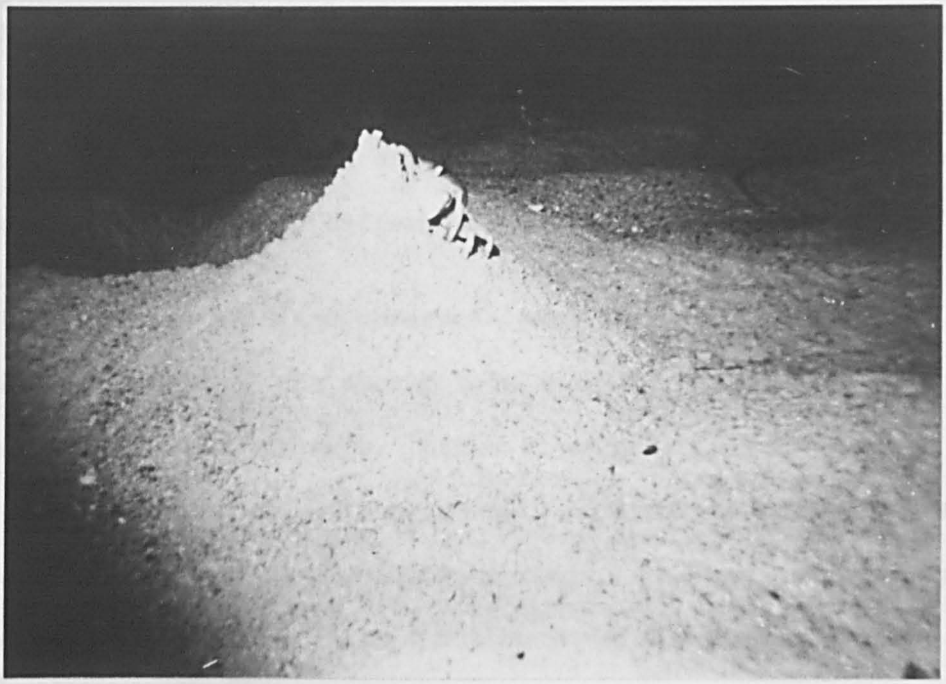
Particularly towards dusk large crabs were seen 'sitting' in the water at the tide edge (Plate 4.3b) or in the adjacent damp sand. This behaviour is associated with irrigating the gills and is detailed in Chapter 7. It also relates to deposit feeding.

Burrowing behaviour was observed throughout the night (Plate 4.3a). Male and female crabs were observed to engage in burrow maintenance, removing sand from their holes. Male crabs added to their pyramids and crabs of both sexes were seen to remain motionless at their burrow entrances for long periods. Some juvenile crabs were also observed burrowing but since the camera was at the lower edge of the pyramid zone it was not well placed to observe juvenile crab burrows near the sea.

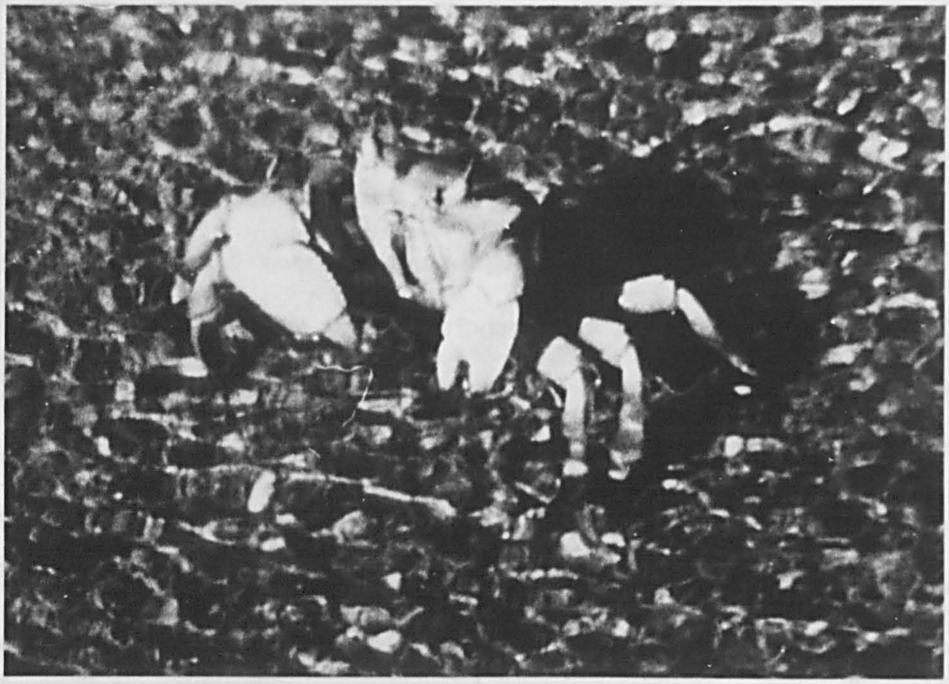
Probably crabs were continuously moving between the burrow zones and the tide edge but such movements were clearly seen around sunrise and sunset. Overall, activity was most intense around sunset and

Plate 4.3. a) Male *O. saratan* at pyramid during darkness.

b) *O. saratan* "sitting" in shallow water at the tide edge.



a



b

sunrise.

Agonistic encounters between male crabs in the pyramid zone are common occurrences and female crabs are attracted to the burrows of males by the pyramids (Linsenmair, 1967 gives details). Several interesting encounters between crabs were observed during the present experiment - each involving different areas under observation.

At 0922h a male crab was observed excavating its burrow. A second crab emerged from the same burrow and both crabs embraced chelae near the burrow entrance. After 10 seconds the crabs disengaged and the previously excavating male entered the burrow while the other crab withdrew to beyond the pyramid. The male then emerged, deposited sand near the entrance and then moved to the top of the pyramid whereupon the other crab ran away. The entire sequence lasted just 1 minute.

At 1809h a crab approached a pyramid and burrow and the resident male emerged and faced the visitor. Both kept chelipeds folded with the chelae directed downwards and the resident pushed the intruder away. This took just 5 seconds whereupon the intruder moved some 30cm from the resident crab which returned to its burrow after 7 seconds, trampled sand at the entrance using its major cheliped and entered the burrow. During the next 3 minutes the crab took three loads of sand to the base of its pyramid, trampling sand at its burrow entrance on each return. It then carried four loads of sand to the top of the pyramid during the next 3 minutes and on returning to its burrow on each occasion it did not trample sand at the entrance. Then the original visiting crab reapproached the burrow as the male emerged. Both crabs faced each other, chelipeds folded as before and the visitor was again pushed away and withdrew. The resident male then entered its burrow and a new visitor entered the burrow from another direction (landwards). One crab emerged 11 seconds later and trampled sand at the entrance with its major cheliped for 2 seconds before re-entering. Six seconds later both crabs emerged and engaged each other face to face as soon as they cleared the entrance. This time chelae were locked and the visiting crab was repeatedly lifted by the original male. After 8 seconds the crabs disengaged and the visitor withdrew. The occupant male recommenced excavation 1 minute later, trampling sand at its burrow entrance.

At 2008h a male crab was observed excavating its burrow when a second crab approached its burrow. The next events happened with great rapidity and both crabs entered the burrow in less than a second. Fifty-six seconds later one crab emerged and moved away and the other, probably the original occupant emerged to deposit sand on its pyramid and then returned to remain at its burrow entrance.

At 0858h a male crab was observed at its burrow entrance and then to enter its burrow. An invader entered the burrow whereupon both crabs emerged and the original occupant appeared to be chased off. The remaining crab then added sand to the pyramid, indicating that it was a male. This entire sequence lasted just 2 min. 34 secs.

The above encounters may have all involved male crabs though according to Linsenmair (1967) visiting females are initially treated as intruders. On a number of occasions crabs were seen moving through the pyramid zone and these may have been males moving to and from the water, males searching for burrows to conquer or females searching for males. The camera position did not allow for sex to be determined visually with certainty unless betrayed by sex specific behaviour, eg. only males build pyramids.

4.3.1.2. 24h field experiment

The week following the 2 day experiment the same area was visited and certain features of crab activity were observed again. This time the tides were neap tides, and the difference in phase from the spring tides resulted in the littoral sand being exposed during the evening and morning and not during the hottest part of the day or the middle of the night. The greatest number of crabs observed at the tide edge was around dusk with numbers remaining high throughout the night and with a slight peak approaching dawn (Fig. 4.3). The greatest numbers of crabs seen at the tide edge during the spring tide observations the previous week was approaching midnight. This was when the tide was out (Fig. 4.1). Thus, these peak numbers of crabs at the tide edge coincided with low tide times during darkness or much reduced light on both occasions. At low tide the crabs on the neap tide cycle were sand pellet deposit feeding, predating Mesodesma and engaged in general foraging as described for the crabs during the spring tide cycle.

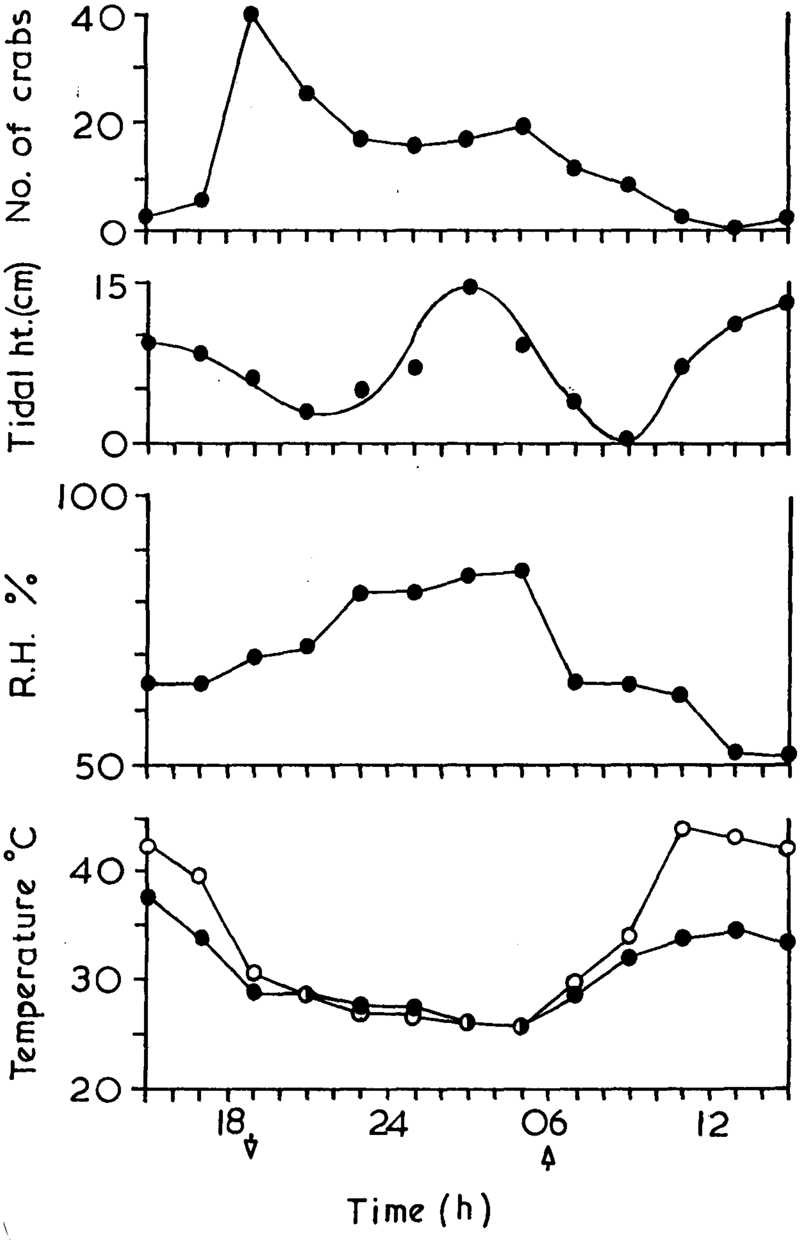
4.3.1.3. General observations

The pattern of crepuscular and nocturnal activity described above was typical of behaviour during most of the year. The shores at King Saud Palace and Sharm Obhor were visited monthly and the beaches were normally worked on from before midday until after sunset. During January and February more crabs were observed out of their burrows during the day though most activity was still towards sunset. During cold winter evenings ($<20^{\circ}$C) few crabs were seen.

4.3.2. Diel patterns of activity under outdoor aquarium conditions

Fig. 4.4 indicates the percentage number of crabs out of their

Fig. 4.3. 24h field experiment at Sharm Obhor during the neap tidal cycle following the 2 day experiment. For the temperature graph, open circles = sand temperature and closed circles = air temperature. Arrows indicate the times of sunset and sunrise.


No. of crabs
40
20
0
Tidal ht.(cm)
15
0
R.H. %
100
50
Temperature °C
40
30
20
18
24
06
12
Time (h)

burrows during a 36h experiment on 16th - 17th June 1984: 16 crabs were known to be in the aquarium. As in the field, crabs remained within their burrows during the warmest part of the day. Emergence was towards late afternoon and crabs remained out of their burrows throughout the night and into the morning with a slight decline in numbers in the middle of the night. There was a clear peak in numbers at the second period of dusk. In the outdoor aquarium there was no tidal influence but crabs were exposed to the natural light/dark cycle. The crabs were nocturnal with an indication of peak activity near dawn and dusk.

Fig. 4.5 presents an analysis of crab activity in the outdoor aquarium on 12th/13th May 1984 based on a videotape record. Feeding, water uptake and burrow maintenance behaviour were all concentrated in the late afternoon just before dusk. All 20 crabs in the tank were at the water edge at 1900h (dusk) and around 14 crabs remained active throughout the night, wandering around the tank and spending most time away from the water.

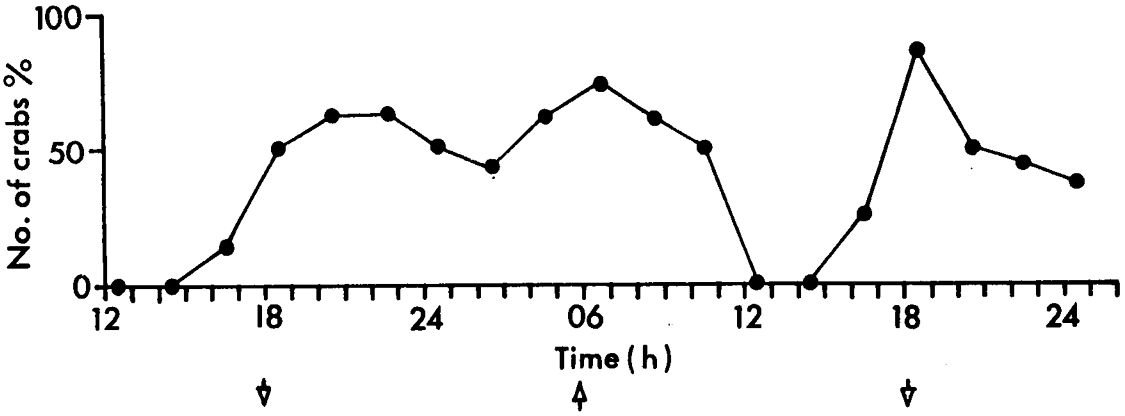
Crabs returned to their burrows at dawn and did not emerge during daytime (observations stopped at 1000h when the equipment was moved to the beach).

4.3.3. Diel patterns of activity under controlled laboratory conditions

Fig. 4.6 illustrates the locomotor activity of 2 male O. saratan held in the same actograph under conditions of dim red light. No clear rhythmicity is evident. This is not surprising given the trauma of capture, handling, packaging and transportation. When a 12:12 LD (light/dark) regime was imposed using the illumination of a 40W bulb alternating with darkness, crabs were most active during the light

Fig. 4.4. Percentage of crabs out of their burrows in the laboratory outdoor crab tank during a 36h period from 16th-17th June 1984. Arrows indicate sunrise and sunset. Based on videotape recording.

Fig. 4.5. Crab activity in the outdoor crab tank on 12th-13th May 1984. The dashed line indicates a reduced level of wandering. The percentage of crabs out of their burrows is indicated by the closed circles and dotted lines. Activities are indicated on the left of the figure.


100
50
0
No. of crabs %
12
18
24
06
12
18
24
Time (h)

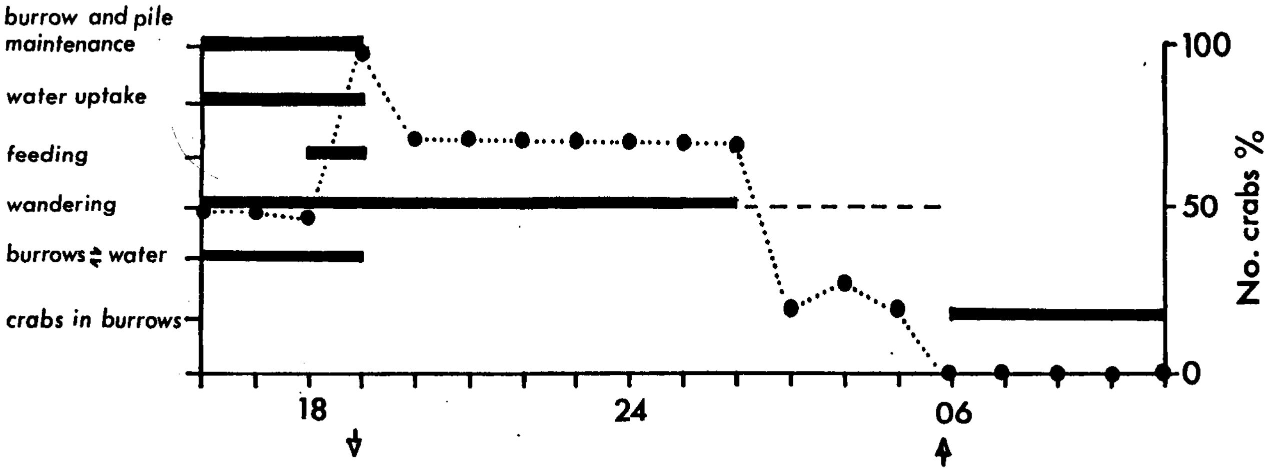
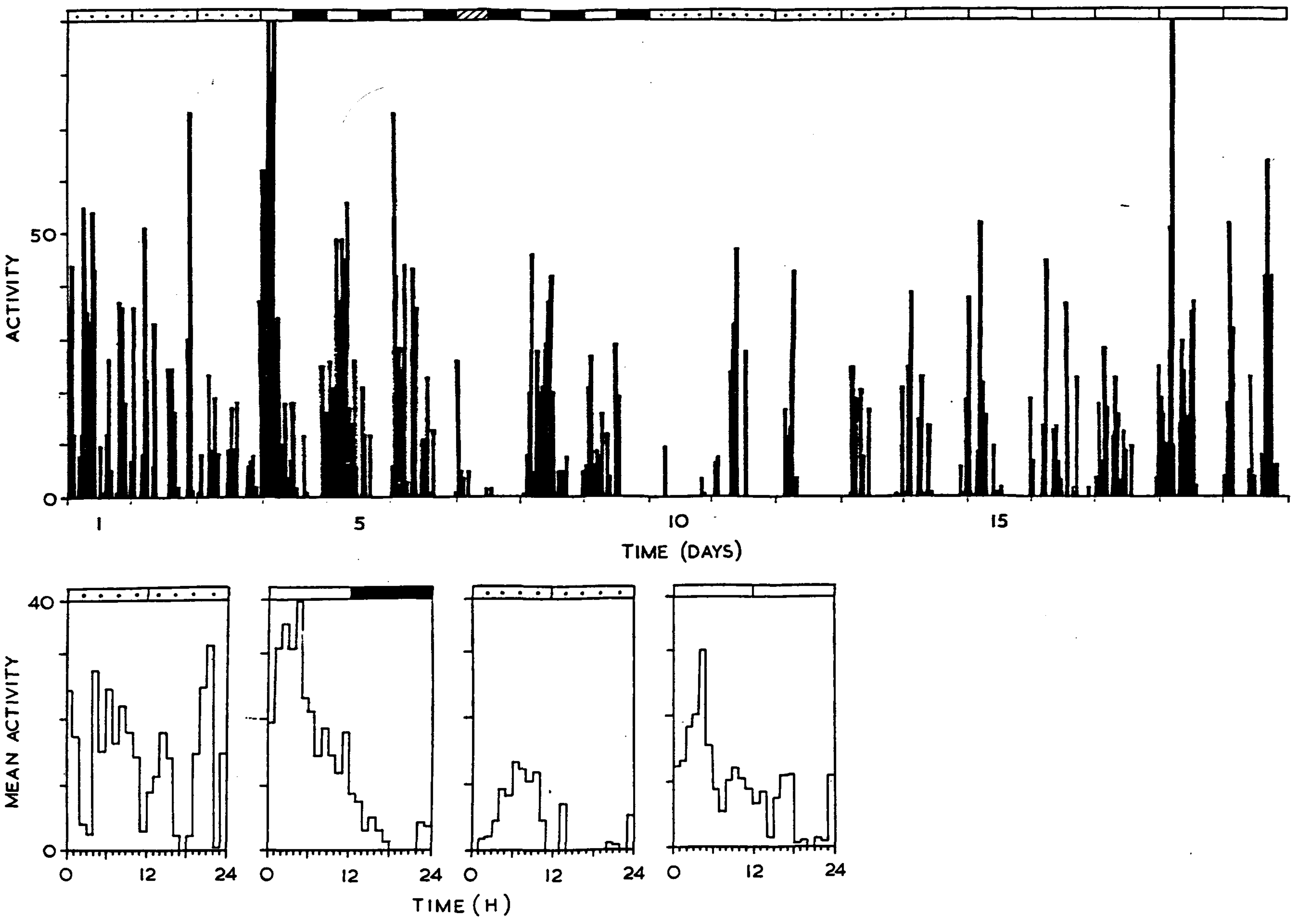

burrow and pile maintenance
water uptake
feeding
wandering
burrows ⇄ water
crabs in burrows
18
24
06
100
50
0
No. crabs %

Fig. 4.6. Locomotor activity of 2 male O. saratan in a laboratory actograph maintained in controlled conditions. The experiment lasted 19 days and activity is plotted hourly. The horizontal bar above each histogram indicates the lighting conditions: stippled = continuous dim red light, white = light (40w), black = darkness. The hatched period indicates bulb failure. The four lower histograms give the mean activity during each successive lighting regime.


ACTIVITY
50
0
1
5
10
15
TIME (DAYS)
MEAN ACTIVITY
40
0
0
12
24
0
12
24
0
12
24
0
12
24
TIME (H)

phase of the cycle. The cycle was out of phase with the natural LD cycle (at Glasgow or Jeddah) with the light period being from 1800h to 0600h. After 6 days entrainment, or perhaps more correctly 5 days since the lights failed during the 4th cycle, conditions of constant dim red light were maintained for 4 days followed by 6 days of constant white light (40W). Locomotor activity peaked during the 'expected' lights-on period and was more strongly expressed under conditions of constant white light than under constant dim red light.

The same result was obtained from a second actograph containing a male crab and a female. O. saratan, therefore, demonstrated an LD -entrained endogenous rhythm of locomotor activity under this particular set of laboratory conditions.

When white light from a 40W bulb was dimmed to around 10W in an alternating 8:16 and 12:12 Bright:Dim regime, activity was more sporadic with a tendency to peak around the times of the light transitions. This was an exogenous response: endogeneity was not investigated due to the declining health of the crabs which also prevented investigation under natural LD entrainment and subsequent constant conditions as originally planned.

4.3.4. Burrowing Activity

Plate 4.4 shows a typical sequence of burrowing activity. It can be seen that the crab emerges from its burrow such that the side with the large cheliped leads. The large bolus of sand is held by both chelipeds and the 2nd and 3rd pereiopods of the trailing side. The obliquely orientated large cheliped supports the sand on the leading side while the small cheliped extends around the front and partly under the bolus, pressing it against the body. On the

Plate 4.4. a-h) Burrowing sequence of _O. saratan_, reproduced from Super 8 movie film.

- a-d) crab emerging from burrow carrying sand.
- e-g) crab discarding sand.
- h) crab returning to burrow.

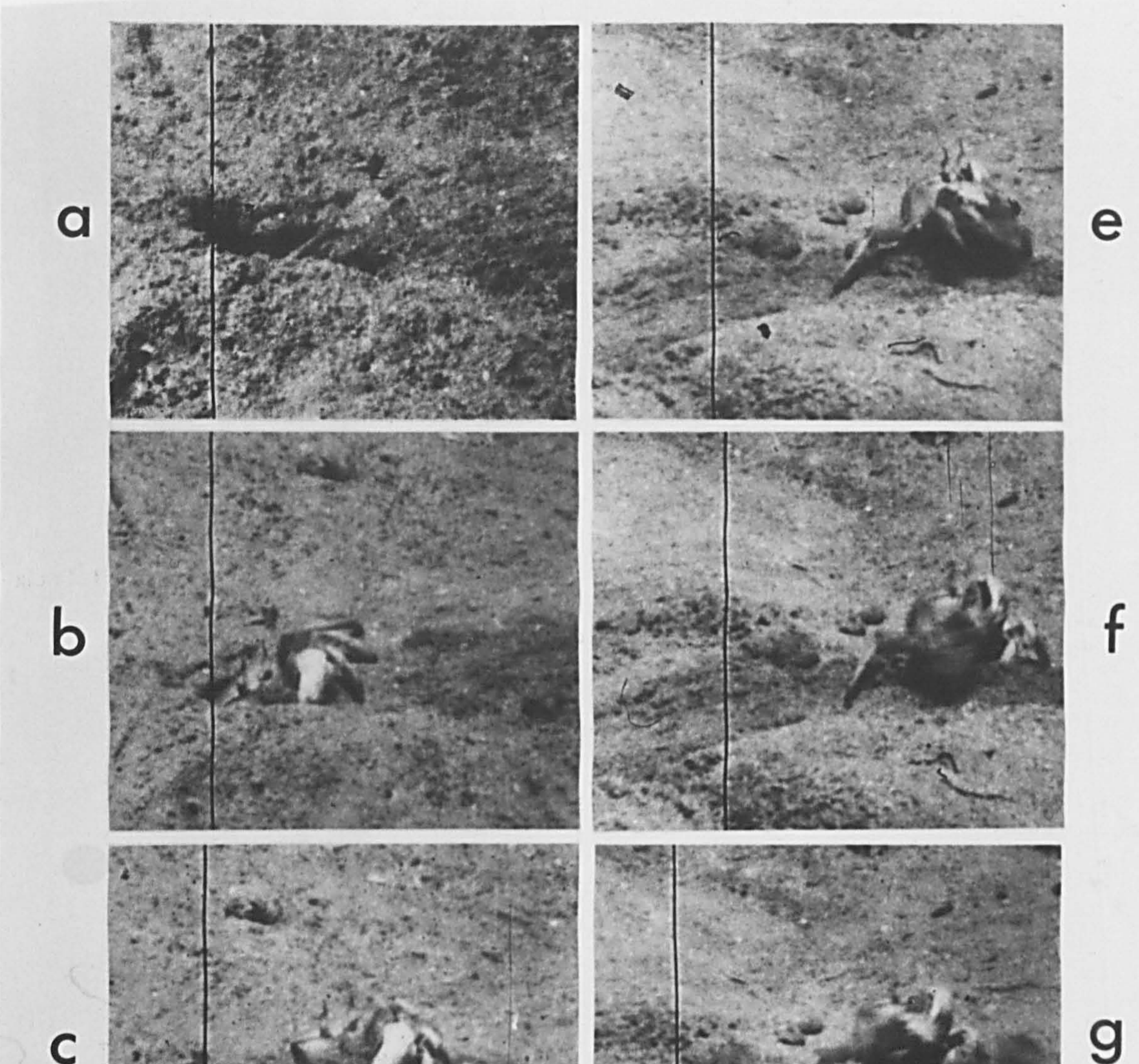
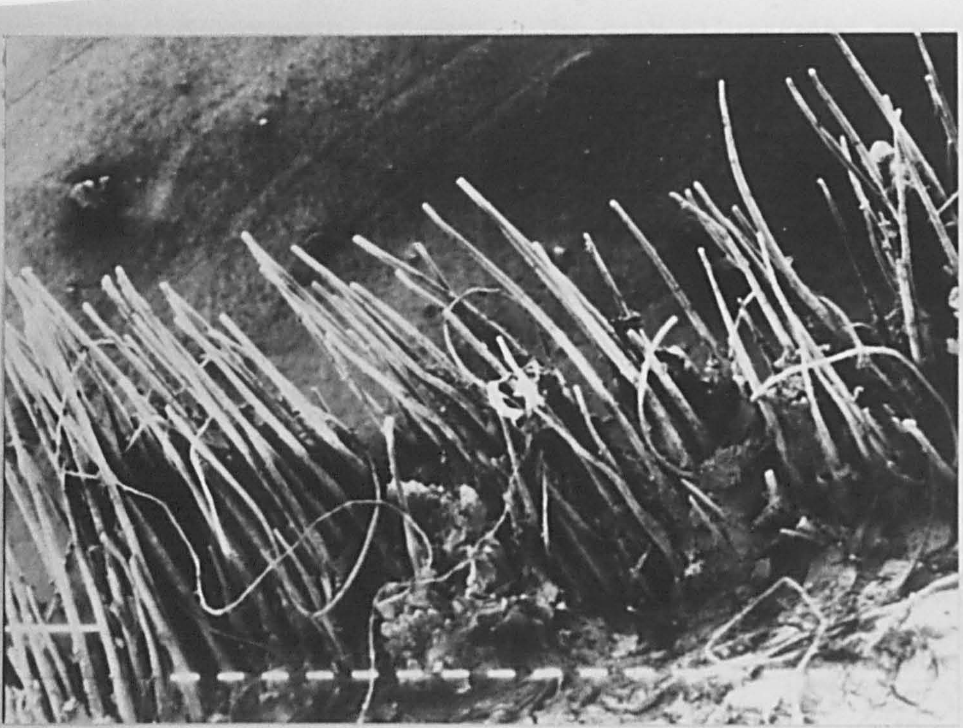
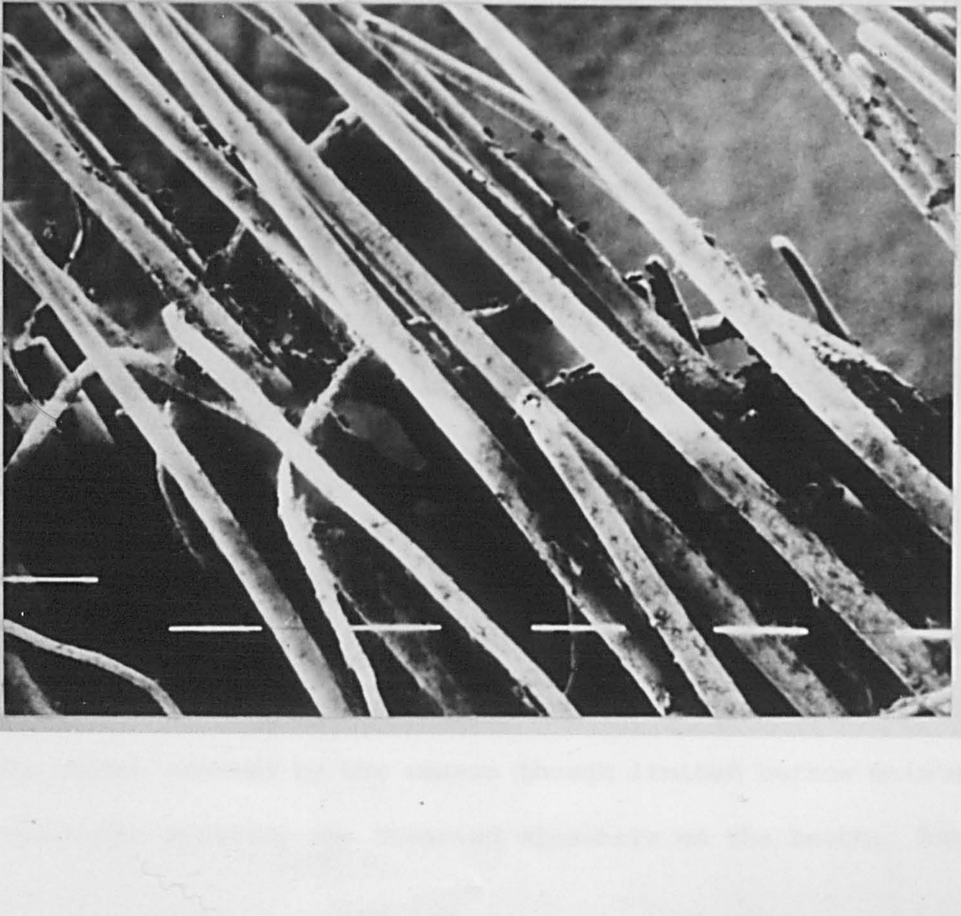

a
b
c
d
e
f
g
h

Plate 4.5. a-b) Detail of the dense simple setae that occur on the propodus of the 2nd pereiopod of O. saratan.

a



b



trailing side the sand bolus is supported by the 2nd and 3rd pereiopods such that the merus of each limb extends over the sand bolus, the carpus and propodus contain it from the side and the dactyl gives lateroventral support. The crab illustrated ejected its sand bolus at the end of a distinct pathway leading from its burrow. Both chelae were raised and the sand was propelled obliquely forwards by the 2nd and 3rd pereiopods in a rapid motion too quick for capture on the 18 frame per second movie film from which the stills were printed.

The crab filmed was not captured but was excavating in the pyramid zone. It was almost certainly a male and having completed the pathway from its burrow it was beginning to establish the base of its pyramid. Such behaviour is described by Linsenmair (1967).

Direct and videotaped records of burrowing in O. saratan conformed to the observations of Linsenmair (1965, 1967) and so to avoid unnecessary duplication, observations of burrowing behaviour were not pursued.

Since it has been implicated in burrowing (Cott, 1929) I here illustrate SEM detail of the setal 'brush' of the propodus of the second pereiopod of O. saratan (Plate 4.5). It is likely, however, that a major function of this brush is for cleaning (Vannini, 1980b).

4.4. Discussion

The present field results support the view that O. saratan near Jeddah are principally nocturnal or crepuscular in their out of burrow activities. No activity was observed between 1000h and 1700h in the region scanned by the camera though limited burrow maintenance and tide edge activity was observed elsewhere on the beach. The crepuscular activity, however, commenced an hour and a half to two hours before sunset and extended for four hours past sunrise. During this period, although the light was bright, temperatures were comparatively low and relative humidities high. Although light conditions undoubtedly influence behaviour (Linsenmair, 1967, for example, suggested that for nocturnal Ethiopian O. saratan the pyramids may have lost their signal function in contrast to the situation with day active Egyptian crabs), and tides may influence behaviour as suggested here for feeding behaviour, I have the strong impression that conditions of temperature and relative humidity are of primary importance in regulating activity. The diurnally active winter crabs also suggest this.

The encounters between crabs were interesting and although agonistic and sexual behaviour were not analysed in this thesis, these limited observations raise some points for discussion. There is little published information on crab encounters in Ocypode spp. in contrast to the wealth of information available for Uca spp. (summarised in Crane, 1975). Schöne (1968) presents information for O. quadrata and presents a drawing of O. saratan in threat posture from a film made by Magnus. This posture is exactly as seen in the present observations; the chelipeds are folded in front of the crab with the chelae tips directed downwards. This display, termed the 'chela down display' by Evans et al. (1976) in his studies of O. ryderi, seems common to the few investigated species of Ocypode (Schöne, 1968; Wright, 1968; Vannini, 1980b). The acrobatic agonistic displays of O. quadrata in which the 2nd pereiopods are raised, all the limbs on one side are raised, or wild chela strikes occur (Schöne, 1968) were not observed here for O. saratan. Linsenmair (1965, 1967), although describing pyramid construction and related territorial and sexual behaviour in O. saratan, did not give details of crab postures during encounters but he did indicate that the pyramid is the motivation for male fights. If two crabs were digging in the same area, fighting did not commence until one built a pyramid (Linsenmair, 1967). He reported observing several hundreds of fights between possessors of burrows and invaders and stated that the possessor defended an area around the pyramid, the "close territory". If this area was infringed, invaders were attacked but he stated that normally this area was protected by the pyramid itself so that policing of the area was not necessary. Also, in the present limited observations, and at other times during the research, agonistic encounters were only observed in the pyramid zone. Vannini (1976, 1980b) indicated that the normally aggressive O. ryderi did not fight when feeding close to each other at the water's edge and Vannini (1980b) cites similar evidence for O. ceratophthalmus (Hughes, 1966), O. quadrata (Cowles, 1908) and O. gaudichaudii (Crane, 1941). O. saratan is therefore similar to these.

It was noted in the present observations of O. saratan that on two occasions crabs locked claws, for 10 seconds one one occasion and for 8 seconds on the other occasion. These encounters did not involve the same crabs. On both occasions an invader had entered the burrow and the claw locking encounter occurred near the burrow entrance following emergence. There was no violent striking of claws as reported for O. quadrata (Schöne, 1968) and on disengagement the visitor moved away from the occupant male. The question raised is was this a more intense male/male encounter or a male/female encounter? Linsenmair (1967) stated that the behaviour of a female near a pyramid was not that different from a male intruder. Also a male with a burrow initially treated a female as an intruder and only the reaction of the female to the male allowed recognition. He did not, however, define these reactions. Linsenmair (1967) indicated that male *O. saratan* did not display to attract females but rather it was the pyramid that attracted them. This is in contrast to *O. ryderi* which engages in a chela waving display to attract females and does not build pyramids.

If the two present observations were male/female encounters why did not the females re-enter the burrows? No copulatory abdominal lowering was noticed and in any case copulation almost certainly occurs within the burrow in *O. saratan*. Linsenmair (1967) caught female crabs approaching pyramids and demonstrated empty or $^{1}/4$ full seminal receptacles whereas those dug out from male burrows had full seminal receptacles. Hughes (1973), however, observed out-of-burrow copulation in *O. quadrata*. The female remained passive and was grasped by the male in a manner which does not conform to the claw locking in my observations and the paired crabs remained together for 25 minutes.

The claw pushing behaviour observed in the other encounters between *O. saratan* in my observations followed 'chela down displays' and similar frontal clashes are reported by Vannini (1980b) for *O. ryderi*. He never observed *O. ryderi* to grab the claws or any other part of the opponent's body with the claws. The 'lateral merus' and 'reverse lateral merus' displays reported for *O. ryderi* (Evans, *et al.*, 1976; Vannini, 1980b) were not seen in my limited observations of *O. saratan*.

'Chela down displays' and frontal pushing was frequently observed under aquarium conditions as well as in the field.

In order to assess the influence of environmental factors on behaviour, crab activities were recorded at the same time as relative humidity and temperature, in addition to tide and light transitions. The absence of crabs at the surface corresponded with outside air temperatures in excess of 30°C and relative humidities below 70% and mostly below 60%.

The frequency of closed burrows was greatest when the relative humidity was lowest and temperature was greatest. Although correlation is no proof of cause and effect it seems to me that the closing of burrows serves to insulate them from unfavourable outside temperatures and especially relative humidities.

In other species, other explanations have been given for burrow closing. For example, Cowles (1908) described O. quadrata closing its burrow after it had stocked it with food and also sometimes when disturbed by other crabs or by man. O. ceratophthalmus closes burrows to seal them from the incoming tide (Barrass, 1963; Hughes, 1966), juveniles do so to escape conflict with conspecifics (Fellows, 1966) and adult males use subsurface plugs to protect mating pairs from disturbance and predation. Linsenmair (1967) described male O. saratan occasionally blocking the burrow of a neighbouring male, presumably for territorial reasons and this has also been seen in O. ceratophthalmus (Lighter, 1974) and a specimen of O. gaudichaudii (sex undetermined) was seen by Crane (1941) to block the burrow of a neighbour. O. ryderi plugged its burrows during the day (Vannini, 1976a), like my O. saratan. Bliss (1968) states that one way of coping with high environmental temperatures is acclimation and another method is burrowing which gives insulation from temperature extremes. Fellows (1973) cites the presence of a surface plug as evidence of predation protection but I believe that in O. saratan it primarily gives added protection from environmental extremes by safeguarding the in-burrow environment. More of this is explained in Chapter 3.

There are a number of detailed descriptions of burrowing behaviour in *Ocypode* species, eg. Cowles (1980) for *O. quadrata*, Cott (1929), Barrass (1963) and Fellows (1966) for *O. ceratophthalmus*, Fellows (1966) for *O. pallidula*, Crane (1941) for *O. gaudichaudii* and Linsenmair (1967) for *O. saratan*. In addition there are many brief references to burrowing behaviour (eg. Milne and Milne (1946) for *O. quadrata*, Rajabai (1972) for *O. macrocera*, and many others). Fellows (1966) indicates that for *O. ceratophthalmus* there are subtle differences in burrowing technique in different populations. This may also be true for *O. saratan* since Al-Kholy (1959) reported that the crabs he observed in Egypt excavated with either side leading. The production of a spiral burrow, however, would seem to demand that the same side leads throughout excavation (see Linsenmair, 1967). Atkinson (1974) reported that in the sublittoral burrowing crab *Goneplax rhomboides*, curved burrows resulted when the crab excavated with the same side continuously leading. When sides were alternated the burrow was linear. This species has equal chelipeds and curved burrows were also observed when one cheliped was missing (Atkinson, pers. comm.). Possibly, in *O. saratan*, the females and juveniles in which the chelipeds were less unequal than in the males, might alternate sides since their burrows are more or less linear. Vannini (1980a) stated that Wolcott had indicated to him that *O. quadrata* would reverse sides periodically and he presumed this was to maintain burrow symmetry. It would be worthwhile investigating this further.

Cott (1929) drew attention to the pointed, flattened, setal-fringed dactyl of each walking leg which he described as an elongated shovel. He stated that the setae (2 rows in this species) along the edge of the propodus of each 2nd and 3rd pereiopod gave a wider supporting surface to the sand load, nearly doubling the width of the legs and thus enabling nearly four times as much sand to be carried as if the legs were bare. He also noted that the merus of the 2nd and 3rd pereiopods was broader than in other pereiopods. This and the presence of 'non-skid' tubercles he considered as adaptations to retain the sand bolus.

I have illustrated the propodal setae of O. saratan which has one row and not two as in O. ceratophthalmus and only on the second pereiopod. They undoubtedly assist in burrowing but are well developed in each side of the crab. It seems likely that they also have a cleaning function since Vannini (1980b) reported O. ryderi cleaning the major claw with the dactylus of the first two pereiopods (no brush on propodus in this species). I have seen O. saratan cleaning the eyestalks using the 3rd maxillipeds as reported for other Ocypode species (Vannini, 1980b).

Cott (1929) clearly exaggerated the importance of these brushes in sand carrying. Species without them transport sand successfully.

The actograph results were surprising and were the opposite to those expected. That the crabs were most active during the light phase of the cycle both during entrainment and subsequent conditions may be a function of experimental conditions in which the light phase of the cycle was several orders of magnitude less in intensity than in the field, or it may be real. Palmer (1971) observed that in Bermuda O. quadrata was predominantly nocturnal though it was occasionally seen during daytime. He placed some of these crabs in tipping carousel actographs in constant temperature conditions and they showed greatest locomotor activity during darkness under natural lighting conditions. This rhythm persisted in constant darkness and constant dim or bright laboratory illumination (5 or 50 ft candles). Laboratory LD cycles successfully entrained the rhythm to a new phase and this persisted in constant conditions.

Jones (1972) observed that in Kenya, adult O. ceratophthalmus were nocturnal and only rarely seen out of their burrows during the day. Jones used tipping box actographs similar to Palmer to record locomotor activity in the laboratory. There was no laboratory entrainment attempted, freshly collected crabs were placed in the actographs and held in constant darkness and relatively constant temperature. Endogenous peaks of activity were centred on the night period and there was no evidence of a tidal component to the rhythm. The activity periods were, however, less clearly defined than those that Palmer (1971) demonstrated for O. quadrata.

Al-Kholy (1959), Magnus (1960) and Linsenmair (1967) report nocturnal activity for O. saratan in Egypt and Ethiopia (though Al-Kholy says 'the crab is not strictly nocturnal as it can be seen wandering by day' and Magnus says 'the main activity is at night ... but also there are many about during the day especially in the afternoon') while Linsenmair (1967) reports predominantly diurnal activity in Egypt. George and Knott (1965) report that O. saratan is day active in Aden. The present results indicate that crabs are active away from their burrows throughout the night and mainly around dawn and dusk but with some activities occurring at reduced level during the day. The middle of the day is avoided except during the winter or unusual weather when temperatures and relative humidity are favourable.

Until experimentation is conducted on fresh unstressed crabs at

Jeddah it would be unwise to deduce too much from the present laboratory results. Under the particular actographic conditions imposed and under conditions of relatively dim laboratory light during LD entrainment, crabs were most active during the light phase and this pattern continued under constant dim red light and white light conditions, ie. LD entrained endogenous locomotor activity was expressed. Actographic design can influence the expression of rhythmicity (Atkinson *et al.*, 1974) and social interactions within actographs can influence the level and precision of activity though apparently not the phase (Atkinson and Naylor, 1973). Also discrepancies between laboratory activity rhythms and field activity patterns are reported for another burrowing decapod, the sublittoral *Nephrops norvegicus* (Atkinson and Naylor, 1973, 1976).

It would clearly be worthwhile to investigate endogenous activity further. It could be that in the field the crabs are potentially active by day but that the expression of this activity is inhibited by high temperatures and low relative humidities. Alternatively, since the crabs constructed burrows in the actographs and there was restricted scope for movement away from these, the expressed rhythm may have been burrow orientated. Thirdly, the expressed rhythm may have been related to transportation stress and/or unnatural entrainment.

CHAPTER 5. FEEDING BEHAVIOUR

5.1. Introduction

There have been many observations on feeding in Ocypode species, especially for O. ceratophthalmus and O. quadrata.

Hughes (1966), working on O. ceratophthalmus, divided feeding behaviour into four categories: foraging, scavenging, sand pellet feeding and predatory feeding including cannibalism. Foraging was taken to include general food searching which was not overtly predaceous and most commonly occurred along the strandline. Scavenging was on a variety of dead animals in various decomposition states, and many of the beach fauna were predated upon. Sand pellet feeding was not observed directly by Hughes (1966) though he saw characteristic pellets. It is described by Crane (1941) and Koepcke and Koepcke (1953) for O. gaudichaudii, by Tweedie (1950) and Braithwaite and Talbot (1972) for O. ceratophthalmus, by Rajabai (1972) for O. macrocera and by Robertson and Pfeiffer (1982) for O. quadrata. Sand is lifted to the mouthparts using the chelipeds and manipulated in the buccal cavity during which process organic material is removed. The sand is formed into a pellet by the endites of the first maxilliped before being discarded. O. gaudichaudii, O. ceratophthalmus and O. macrocera drop the pellet, O. quadrata removes it using its minor chela. Sand pellet feeding is also reported in juvenile O. ceratophthalmus and O. cordimana (Takahasi, 1935 - his Ocypode comments appear to relate to both species but this is not very clear), and in the recently described O. mortoni (George, 1982). Crane (1941) noted that separation was not perfect since sand was found in the alimentary canal as in this study for O. saratan.

It is very clear from the literature that different species of

Ocypode do not all feed in the same way. O. saratan appears very like O. ceratophthalmus in the feeding strategies, showing all 4 types of feeding in both juveniles and adults.

O. occidentalis was reported by Crane (1941) to feed on an 'assortment of seaweed, carrion, amphipods, insects, etc.' and Crane considered it the American west coast equivalent of O. quadrata in its feeding habits. O. occidentalis was not seen to engage in sand pellet feeding. O. quadrata has normally been considered an omnivorous scavenger (Cowles, 1908; Hedgpeth, 1957) but Wolcott (1978) has presented clear evidence that the species is principally a nocturnal predator, at least on North Carolina beaches. Milne and Milne (1946) found no evidence of deposit feeding and Wolcott (1978) makes no mention of it. Robertson and Pfeiffer (1982), however, observed diurnal sand pellet deposit feeding on a barrier beach in Georgia. O. ryderi is reported as being a predator and mainly an omnivorous scavenger (Jones, 1972 - as O. kuhlii: Sakai and Türkay (1976) separated the two species). It was not seen to engage in sand pellet feeding. In contrast, O. cordimana feeds mainly on terrestrial vegetable products such as seeds and leaves (Vannini, 1976a). O. macrocera, however, is mainly a scavenger (Rajabai, 1972) and whereas it also engaged in general foraging amongst the drift and in sand pellet feeding near its burrow, it was not a predator. O. mortoni is a sand pellet feeder for which no other feeding type has been described (George, 1982).

In some species feeding is burrow orientated. O. macrocera engaged in sand pellet feeding within a metre of its burrow (Rajabai, 1972) and in O. ceratophthalmus sand pellets have been found near burrow entrances (Hughes, 1966). Also O. mortoni sand pellet feeds in the immediate vicinity of the burrow (George, 1982). *O. ceratophthalmus* has also been reported to carry prey items up the beach and excavate burrows with the prey item being consumed at the burrow entrance or below ground (Hughes, 1966). In the case of the bivalve prey items *Donax faba* and *D. incarnata*, diurnally active *O. ceratophthalmus* would make short 'foraging trips' from their burrows, excavate *Donax*, and return to the burrow consuming the bivalve at the burrow entrance (Hughes, 1966). Large middens of broken and chipped *D. faba* shells were also reported from the entrances of *O. ceratophthalmus* burrows by Smith (1975). The crabs he observed, however, captured their prey visually in the wash zone about 1 hour before dusk.

There is, in fact, great variation in the time at which *Ocypode* species are reported to feed. *O. quadrata*, for example, feeds as a nocturnal predator on North Carolina beaches (Wolcott, 1978) and deposit feeds by day in Georgia (Robertson and Pfeiffer, 1982). The Indian *O. macrocera* feeds during the day (Rajabai, 1972) and the widely distributed *O. ceratophthalmus* is reported to feed by day and night as adults but by day as juveniles (Barrass, 1963; Hughes, 1966; Jones, 1972). There is an extensive literature on activity cycles and this is examined elsewhere in the thesis (Chapter 4).

There are other feeding differences reported for juveniles and adults. According to Takahasi (1935), *O. ceratophthalmus* only engaged in sand pellet feeding as juveniles in Taiwan though elsewhere it would appear to do so as adults (see Hughes, 1966; Jones, 1972). Crane (1941) has indicated that adult *O. gaudichaudii* feeds almost entirely on microscopic organic matter washed onto the sand by the tide whereas juveniles predated upon amphipods and small insects. On the other hand Rajabai (1972) reported no differences in the diet of adult and juvenile O. macrocera and adult and juvenile O. quadrata appeared to both be predatory (Wolcott, 1978) taking the same prey species (fewer observations were made on juveniles than adults).

Together with their study of feeding behaviour some authors have also considered mouthpart morphology in Ocypode species. Crane (1941) described the mouthparts (and chelae) of O. gaudichaudii and O. occidentalis and drew attention to the longer setae on the mouthparts of O. gaudichaudii which were involved in straining organic material from sand. The whole mouth field was also larger in O. gaudichaudii and this Crane (1941) attributed to being an adaptation for manipulating large quantities of sand. Jones (1972) describes some of the mouthparts (maxillipeds) of O. ceratophthalmus and O. ryderi (as O. kuhlii) and found both species very similar to each other, differing only in minute detail. Of these two, only O. ceratophthalmus had been observed to engage in sand pellet feeding.

Detailed studies of mouthpart morphology and setation have been made for other decapods, including the crayfish, Austropotamobius pallipes (Thomas, 1970), the Norway lobster, Nephrops norvegicus (Farmer, 1974), larval American lobster, Homarus americanus (Factor, 1978), hermit crabs (Roberts, 1968; Schembri, 1982b, c) and brachyuran crabs, eg. Carcinus maenas (Borradaile, 1922), Ebalia tuberosa (Schembri, 1980, 1981b, 1982a), Uca spp. (Altevogt, 1955a, b, 1957, 1976; Miller, 1961; Crane, 1975) and Dotilla spp. (Vogel, 1984).

Against this background, observations on feeding behaviour, diet and mouthpart morphology are made for O. saratan.

5.2. Material and Methods

Observations of feeding behaviour were carried out on captive

O. saratan maintained in a large outdoor tank in which beach conditions were simulated. This arrangement is detailed in Chapter 4. Again observations were either direct or using closed circuit television in continuous or time-lapse mode.

Field observations were carried out at the Sharm Obhor site, mostly by direct visual observations but supplemented by closed circuit television recordings.

In the field during each monthly distribution study, several crabs were caught and immediately killed by formalin injection. Formalin and carmine was injected into the stomach and stomach contents were later examined under a binocular microscope (Wild and Zeiss) and dietary components identified. Identifications were confirmed by Dr A. Bodoy and Dr S. Beltagi of the Faculty of Marine Science, King Abdul-Aziz University, Jeddah.

To investigate the structure of the mouthparts, animals were killed by low temperature (fridge) and fixed in 70% ethanol. Gross morphology was studied by dissection of decalcified specimens by leaving the crabs in a 3% solution of concentrated nitric acid in 70% ethanol. Individual mouthparts were dissected out, stained overnight in a 1% aqueous solution of lignin pink, and mounted in a 50:50 mixture of glycerol and 70% ethanol. They were then examined under a stereomicroscope.

Mouthparts were photographed using facilities in the Faculty of Engineering, King Abdul-Aziz University, and were also examined using stereoscan electronmicroscopy (SEM) using the Cambridge 600 SEM in the Faculty of Science, King Abdul-Aziz University. Further SEM studies were carried out at the Zoology Department, University of Glasgow using a Philips SEM 500 instrument. Material to be examined was fixed using 25% glutaraldehyde, transferred to sodium cacodylate buffer, transferred to 2% osmium tetroxide, critical point dried and sputter coated with gold (20-50nm). The samples were mounted on aluminium stubs using conductive silver paint.

Mouthpart terminology follows McLaughlin (1980, 1982) who has attempted to standardize terminology throughout the Crustacea. Setal terminology mostly follows Thomas (1970) and Factor (1978). Factor's scheme is simpler than that of Thomas but does not cover all the setal types. In fact, in reviewing the setal literature it is clear that a standardized overview is needed. Each author, although conforming to certain basic terms tends to erect his own terminology or conforms to the terminology of the nearest similar setae in the literature even though there may be clear differences in detail. For example, Roberts (1968) erected his own scheme for hermit crabs, based on light microscope studies; Thomas (1970) undertook a remarkably detailed study of the setae of a crayfish, the more impressive because it relied on light microscopy. In lobster studies, Farmer (1974) followed Thomas but was more general and Factor (1976) adapted Thomas's scheme in a study of larval mouthparts in a lobster and used SEM techniques. Schembri (1982a, b) uses Factor's scheme and extends it in leucosid crab and hermit crab studies. The ocypodids *Uca* and *Dotilla*, however, have some setal types completely different from those reported in the above literature requiring new terminology, eg. spoon-tipped setae (Miller, 1961; Vogel, 1984). Because of the difficulties of standardization the terms used here are the ones for which there is general agreement: plumed setae comprising plumose setae (two opposite rows of narrow setules as in a feather) and pappose setae (narrow setules come off shaft in any place); serrate setae (rows of toothlike setules along distal half of shaft); serrulate setae (like small serrate setae with finer setules and a subterminal pore); plumodenticulate setae (combinations of plumed and serrate setules with the latter being distal on the shaft); simple setae (long, narrow, rod like, no setules); cuspidate setae (short, robust, conical, often curved, few or no setules). Thomas (1970) and others point out that there is considerable variation within setal types and gradations between them. Although a general approach has been taken it has still been necessary to devise some new terminology to describe two setal types encountered - scopulodenticulate (L. scopula = small brush; denticulus = little tooth) setae and spatulopectinate (L. spatula = spoon; pecten = comb) crooked (end curled over) setae. These names were decided on following advice from Dr P.G. Moore (Millport).

5.3. Results

5.3.1. Behavioural observations

Feeding behaviour was observed both in the field and in the laboratory. The most detailed observations resulted from laboratory observations. The crabs in the simulated environment of the outside aquarium demonstrated all types of feeding behaviour, sand pellet deposit feeding, general foraging, scavenging and predatory behaviour.

To encourage sand pellet, ie. deposit feeding at the water's edge, the aquarium sand was organically enriched by mixing in Artemia eggs and a commercial pelletized fish food. The deposit feeding behaviour was similar to that reported by earlier workers on other species (eg. Tweedie, 1950; Crane, 1941; Robertson and Pfeiffer, 1982).

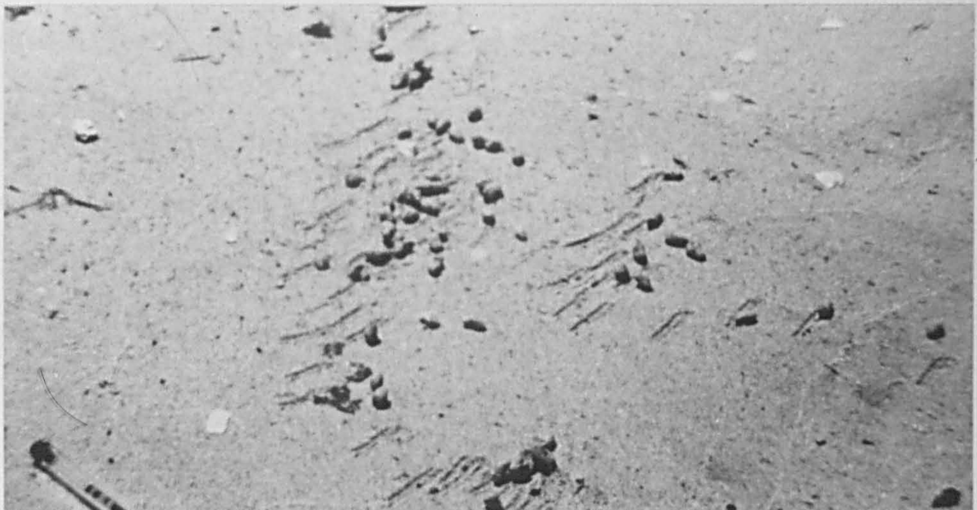
O. saratan scooped damp sand towards the mouthparts using their chelipeds. The small or minor cheliped was used more than the large or major one. Initially, the claw tips are pressed superficially

Plate 5.1. a) Sand pellets indicative of deposit feeding by O. saratan. Note the marks left in the sand by the minor cheliped.

b) As above except that here there are indications of occasional use of the major cheliped in addition to the minor one.

a

b



into the sand with the dactyl slightly open. The cheliped is then scooped backwards, raking through the sand. Scoopmarks in the sand indicate that the dactyl is sometimes brought a little closer to the pollex during this motion. This raking has the effect of pushing sand on to the concave chela surface. This is then conveyed to the mouth to complete the scooping motion. The manipulation of the sand in the mouthparts is very difficult to observe but the food particles mixed with inorganic small particles appear to be sorted from coarser particles in the buccal cavity by the maxillipeds and conveyed to the mouth. The rejected material is accumulated as a ball but I was unable to observe the details of this. It is then brushed away using the small cheliped. Characteristic sand pellets accumulate near the edge of the water and a typical field example is illustrated in Plate 5.1. Here not only can the pellets be seen but the details of the claw action can be observed in the marks in the sand. In Plate 5.1a it appears that the minor cheliped has been used and in Plate 5.1b both chelipeds, but mainly the minor one.

This form of feeding in the field and in the laboratory is mainly crepuscular and nocturnal but in the field there is a tidal correlation with peak feeding at low tide (see Chapter 4). Pellets were always in the wet sand near the waterline and were not associated with burrows, with the possible exception of some juveniles whose burrows occurred in the damp sand near the waterline (Plate 5.2a).

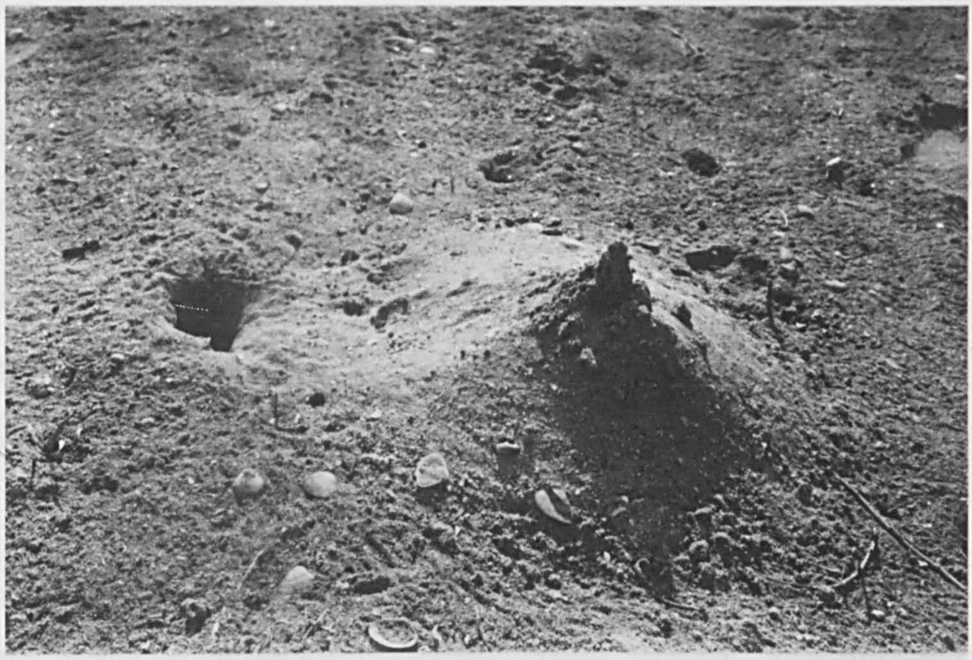
In both aquarium and field observations crabs investigated strandline material and were frequently observed to feed on it. Food items taken were both animal and plant remains, the former including any available food items including picnic refuse and the latter including macroalgal and seagrass fragments. In the field and aquarium various food items were placed on the sand and behaviour

Plate 5.2. a) Juvenile O. saratan burrow near waterline. In addition to excavated sand there are feeding pellets in the vicinity of the burrow and claw scrape marks. Other feeding pellets can be seen in the damp sand along the strand.

b) Male O. saratan burrow. Note the Mesodesma shells around the burrow.

a

b



observed. Large items, eg. dead fish were accepted eagerly and repeatedly visited by the crabs with some crabs taking pieces to their burrows. Smaller food items were either consumed on site or carried to the burrow.

During feeding excursions along the strandline and along the damp sand near the waterline, crabs used especially their minor chelipeds with great rapidity, transferring tiny food items to the mouth.

Predatory behaviour including cannibalistic behaviour was observed in the aquarium and in the field. Crabs used either one or both chelipeds to catch prey and convey it to the mouthparts. Several strategies were used. In the aquarium a form of predatory feeding was observed that was not seen in the field. Crabs would enter the water and for long periods hunt insect larvae that abounded under laboratory conditions. In both aquarium and field observations crabs were seen to hunt insects on the sand with success and large O. saratan were seen to sieze and capture juvenile crabs of the same species, crushing them with the major chela.

Crabs were frequently observed in the field probing the sand at the water's edge and capturing the bivalve Mesodesma (probably M. glabratum, A. Ansell, pers. comm.). In an aquarium experiment, a number of shells were buried 2 to 7cm beneath the sand at the water's edge. When a crab moved over the location where the shells were buried it would suddenly stop and after a pause probe the sand with both chelipeds and brush the sand with the first walking legs. Then the crab dug rapidly using both chelipeds until the bivalve was captured. Sometimes it would be eaten on the spot but often the bivalve would be taken to the crab's burrow and the crab would crush and consume it at the burrow or carry it within. Many of the burrows investigated in the field had shell remains inside that probably reflect this mode of feeding. Shells around a male crab's burrow are shown in Plate 5.2b.

In the field, as well as feeding near the water's edge, crabs at Sharm Obhor were observed foraging along the base of the low limestone cliff at the top of the shore. The shape of the beach limited crabs to the shore at Sharm Obhor but at King Saud Palace some tracks extended as far as 100 metres inland behind the dunes and this probably represents nocturnal foraging.

5.3.2. Stomach contents

Of 40 crabs whose stomach contents were examined microscopically, only 2 (5%) had completely empty stomachs (Table 5.1). The stomachs of the remainder all contained recognizable fragments though in most cases a proportion of the stomach contents were too digested for identification. Of the 38 crabs with filled stomachs, 35 (92%) contained sand, 20 (53%) contained diatoms, 18 (47%) contained foraminiferans and 6 (16%) contained mud in their stomachs. This is indicative of deposit (sand pellet) feeding.

Twenty-six crab stomachs (68%) contained bivalve remains, mostly those of *Mesodesma* sp., probably *M. glabratum*. Fifteen stomachs (39%) contained crustacean remains which were too broken up for unequivocal identification. It is likely that much of it was amphipod material, 2 stomachs (5%) contained clearly identifiable amphipod fragments, probably talitrids, eg. *Talorchestia* sp. Six stomachs (16%) contained the remains of juvenile *O. saratan* and some of the unidentified crustacean muscle may also have belonged to *O. saratan*. This indicates predatory behaviour.

Table 5.1. Stomach Contents Analysis

Carapace width (cm)	1.1	1.1	1.3	1.3	1.6	1.8	1.9	1.9	2.0	2.1
Crab sex	?	?	?	?	♂	♂	♀	?	♂	♂
Month	Apr	Aug	July	Dec	Dec	Oct	Jan	Sept	Mar	Apr
Mud	+	+								
Sand	+	+	+	+	+	+	+	+	+	+
Diatoms	+						+	+	+	
Macroalgal fragments	+	+	+		+	+	+	+	+	+
Sea grass fragments		+						+		
Foraminifera		+				+		+		
Sponge fragments						+				
Coral fragments		+								
Amphipod fragments							+			
Unidentified crustacean remains	+		+	+					+	
Juvenile *Ocypode* remains									+	
Bivalve remains, usually *Mesodesma*		+	+	+	+	+		+		+
Crinoid and/or Ophiuroid arm fragments				+						
Unidentified eggs										
Gastropod egg capsules										
Nematodes										
Insect fragments										
Sea Urchin spines										

Table 5.1. cont'd

Carapace width (cm)	2.1	2.1	2.2	2.3	2.3	2.3	2.3	2.5	2.5	2.7
Crab sex	♀	♀	♀	♂	♂	♀	♂	♀	♀	♀
Month	Apr	May	Feb	Feb	Mar	Aug	Sept	Feb	Mar	Feb
Mud				+						
Sand		+	+	+	+	+	+	+	+	
Diatoms			+	+	+		+		+	
Macroalgal fragments		+	+	+	+		+	+	+	
Sea-grass fragments								+		
Foraminifera			+	+	+		+		+	
Sponge fragments			+							
Coral fragments										
Amphipod fragments										
Unidentified crustacean remains				+						
Juvenile *Ocypode* remains										
Bivalve remains, usually *Mesodesma*		+		+		+	+		+	
Crinoid and/or Ophiuroid arm fragments										
Unidentified eggs										
Gastropod egg capsules						+	+			
Nematodes										
Insect fragments										
Sea Urchin spines										

Table 5.1. continued

Carapace width (cm)	2.7	2.8	3.1	3.1	3.2	3.2	3.4	3.6	3.7	3.8
Crab sex	♀	♂	♂	♀	♀	♀	♀	♀	♂	♂
Month	Feb	Oct	Aug	Dec	Jan	May	Sept	July	Mar	June
Mud	+								+	
Sand		+	+	+	+	+	+	+	+	
Diatoms	+				+	+	+	+	+	+
Macroalgal fragments			+	+	+	+	+	+		+
Sea-grass fragments			+					+		+
Foraminifera	+					+	+	+	+	+
Sponge fragments		+								+
Coral fragments										
Amphipod fragments										
Unidentified crustacean remains	+					+	+		+	
Juvenile *Ocypode* remains				+	+					
Bivalve remains, usually *Mesodesma*		+		+	+	+	+	+		
Crinoid and/or Ophiuroid arm fragments		+					+	+		+
Unidentified eggs										
Gastropod egg capsules							+			
Nematodes				+	+					
Insect fragments										
Sea Urchin spines										

Table 5.1. cont'd

Carapace width (cm)	3.9	3.9	4.0	4.0	4.1	4.1	4.1	4.2	4.2	4.3
Crab sex	♀	♂	♀	♀	♂	♀	♀	♂	♀	♂
Month	Apr	Oct	Mar	June	Dec	Mar	Aug	Jan	Dec	July
Mud	+									
Sand	+	+	+	+	+	+	+	+		+
Diatoms		+	+		+	+				
Macroalgal fragments	+	+		+	+	+	+		+	+
Sea-grass fragments		+		+			+			+
Foraminifera	+	+		+		+				
Sponge fragments	+	+								
Coral fragments			+			+	+			
Amphipod fragments									+	
Unidentified crustacean remains	+	+		+	+		+	+		
Juvenile *Ocypode* remains					+			+	+	
Bivalve remains, usually *Mesodesma*	+	+			+	+	+	+	+	+
Crinoid and/or Ophiuroid arm fragments				+			+		+	
Unidentified eggs	+									
Gastropod egg capsules				+						
Nematodes								+	+	
Insect fragments				+						
Sea Urchin spines							+			

Table 5.1. continued

Summary

	Number of stomachs	% (n = 38)
Mud	6	16
Sand	35	92
Diatoms	20	53
Macroalgal fragments	31	82
Sea-grass fragments	10	26
Foraminifera	18	47
Sponge fragments	6	16
Coral fragments	4	11
Amphipod fragments	2	5
Unidentified crustacean remains	15	39
Juvenile *Ocypode* remains	6	16
Bivalve remains, usually *Mesodesma*	26	68
Crinoid and/or Ophiuroid arm fragments	8	21
Unidentified eggs	1	3
Gastropod egg capsules	4	11
Nematodes	4	11
Insect fragments	1	3
Sea Urchin spines	1	3

The remainder of the stomach contents seem to indicate general foraging and scavenging behaviour. For example, 31 (82%) of stomachs contained macroalgal fragments and 10 (26%) contained sea-grass fragments. In addition to those plant fragments characteristic of the strandline, there are other strandline items, eg. echinoderm remains in 9 stomachs (24%), sponge fragments in 6 stomachs (16%) and gastropod egg capsules in 4 stomachs (11%).

Most crabs' stomachs (32, 84%) contained food items indicative of deposit feeding combined with either scavenging or herbivorous feeding. The smaller crabs appear more dependent on deposit feeding and have a less varied diet than larger crabs. Large O. saratan demonstrate cannibalistic feeding on small O. saratan.

No sexual differences are apparent and little seasonal variation is evident despite the fact that the heat-induced mortalities in shallow water and emersed sublittoral areas in summer must enhance the scavenging mode of feeding. On one occasion at Sharm Obhor in July 1984, in a small area I counted 3 pufferfish, 20 sea urchins, 45 brittle stars, 8 large bivalves, 4 squid, 10 swimming crabs and much seaweed, all dead on the lower shore and emersed reef platform opposite the Ocypode burrows. Similar mortalities were seen in August when 45 mostly small and medium sized O. saratan were seen feeding on the dead animals in the evening.

5.3.3. Morphology of the mouthparts

The mouthparts of O. saratan are illustrated in Plates 5.3 - 5.13.

Mouth

The mouth is located behind and between the mandibles and anterior to it is the labrum. This is shaped like a triangle, the apex directed downwards between the mandibles and its lobed frontolateral margins are shaped to fit within the inner face of the mandible head. Posterior to the labrum (ie. approximately below it) is the metasoma with its forwardly directed lobes, the paragnaths, which wipe against the lower face of the heads of the mandibles. The paragnaths are provided with a fringe of pappose setae.

Mandibles (Plate 5.3a, b)

The mandibles are the strongest of the mouthparts. They are smooth and robust with a well developed incisor edge and a conspicuous 3-segmented mandibular palp which is shown in a typical orientation in Plate 5.3a. The Plates show left and right mandibles from their inner face and in Plate 5.3b the palp has been removed to display the cutting edge. The palp is provided with cuspidate, pappose and plumodenticulate setae. When the mandible is held against the labrum, the palps appear to occupy a groove in its surface. Sparse serrate setae are also found on the lower outer surface of the mandible head.

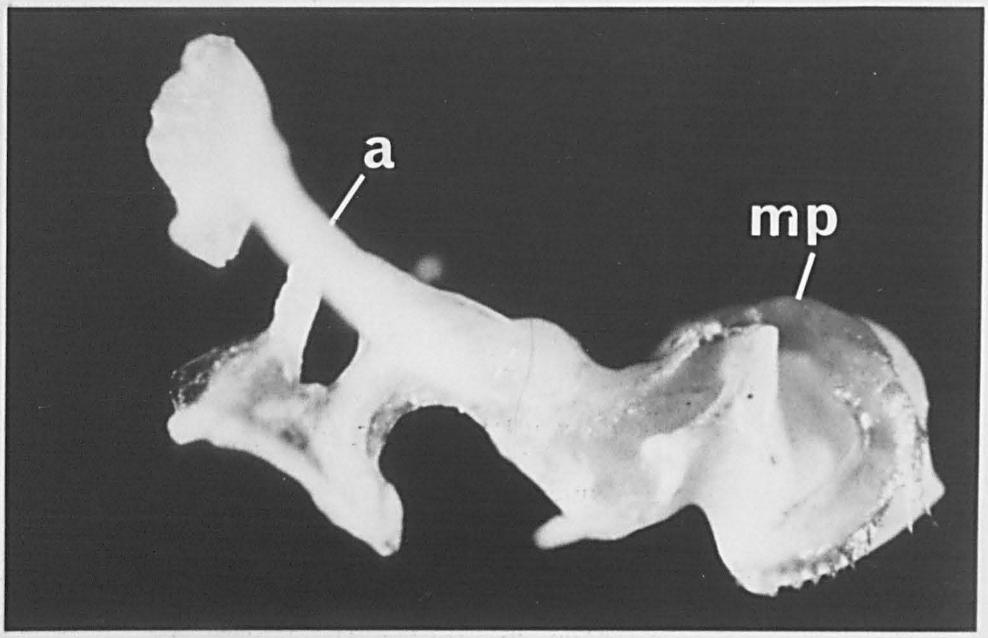
1st Maxillae (Maxillules) Plates 5.4a, b, c, 5.5a)

These are small mouthparts composed of two well developed endites and an endopod. The endopod is extended laterally and divided into two segments. The distal segment is covered distally by dense plumose and plumodenticulate setae and the proximal segment is more flattened and less setose. The basal endite is flattened and its medial edge is provided with a fringe of cuspidate and rod shaped setae (Plate 5.4c). The coxal endite is similar but has a denser field of cuspidate setae around its medial edge, bordered by rod shaped setae (Plate 5.5a).

Plate 5.3. a) Left mandible of O. saratan. mp = mandibular palp, a = apophysis.

b) Right mandible of O. saratan. The palp has been removed to display the head (h).

a



b

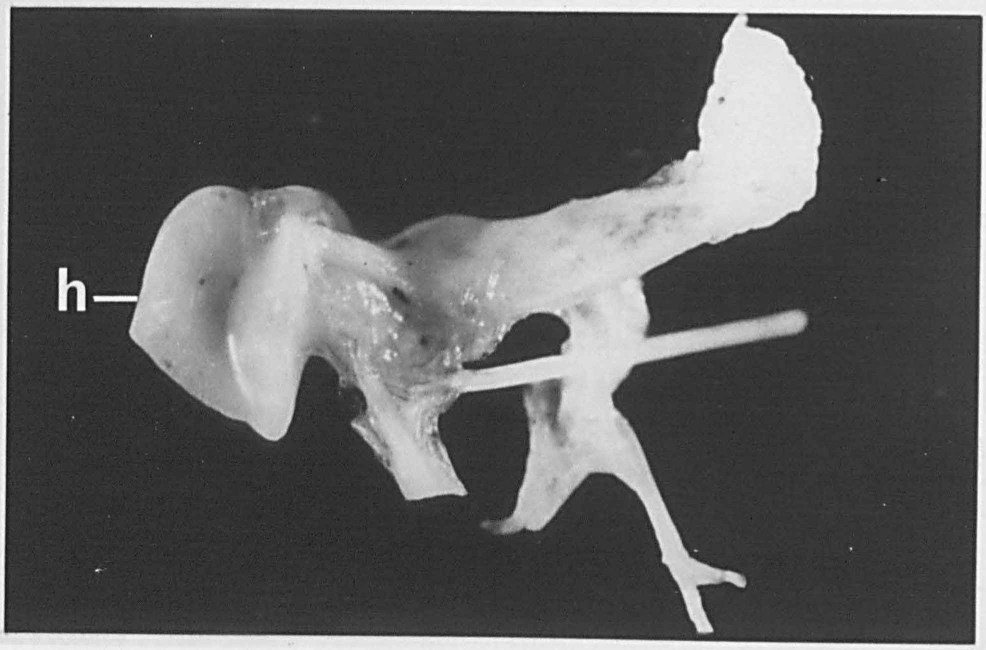


Plate 5.4. a) First maxilla (maxillule) of O. saratan. Inner view; in life the endopod is dorsal. et = endites, en = endopod.

b) As (a) but outer view. The strong setation of the basal endite can be seen.

c) The strong cuspidate and simple setae of the basal endite. The scale bar is 100μm (S.E.M.).

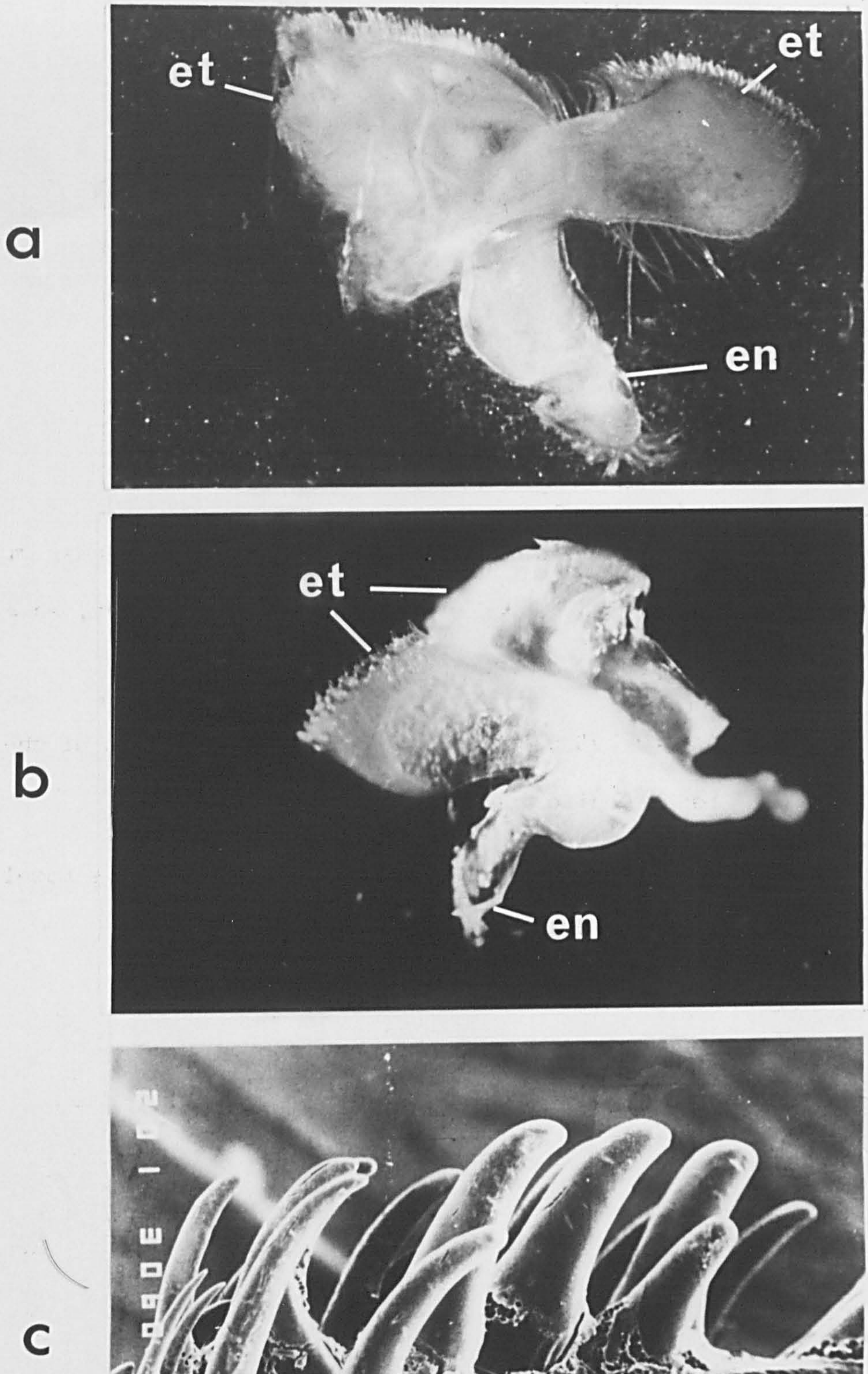

a
et
et
en
b
et
et
en
c

Plate 5.5. a) Setation of the coxal endite of the maxillule of *O. saratan*. Scale bar = 10μm (S.E.M.).

b) Second maxilla of *O. saratan* (outer view). The exopod is the scaphognathite (sc), en = endopod, et = endites.

c) First maxilliped of *O. saratan* (outer view). en = endopod, ex = exopod, et = endites, ep = epipod.

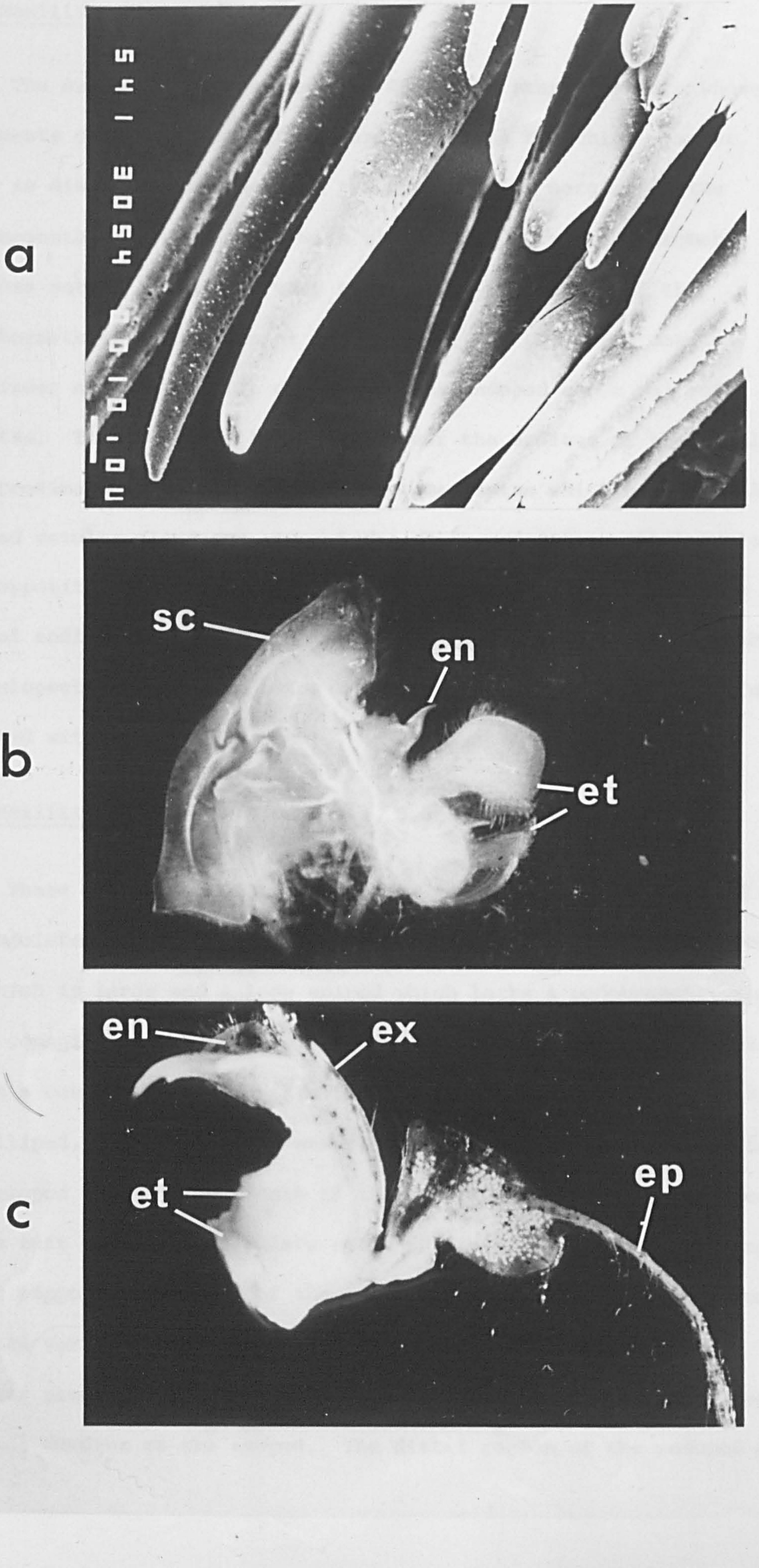

a
0.01MM 4504 145
b
sc
en
et
c
en
ex
et
ep

Plate 5.6. a) First maxilliped of O. saratan (inner view).

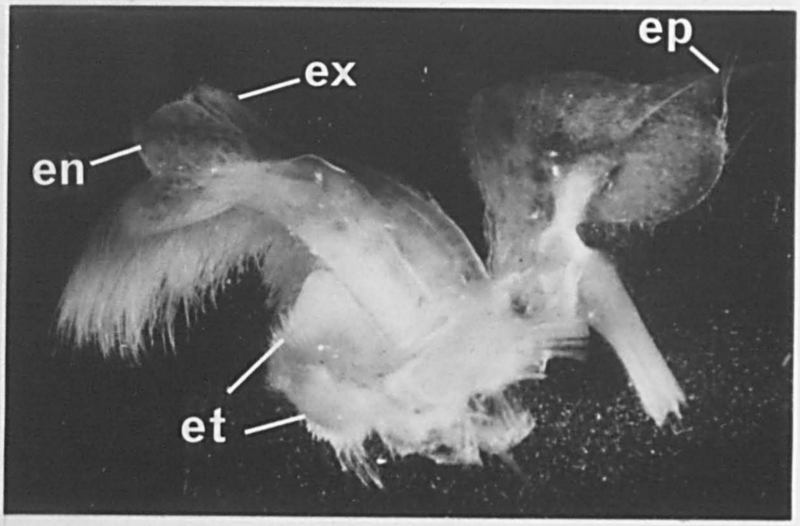
en = endopod, ex = exopod, et = endites, ep = epipod.

b) Second maxilliped of O. saratan (outer view).

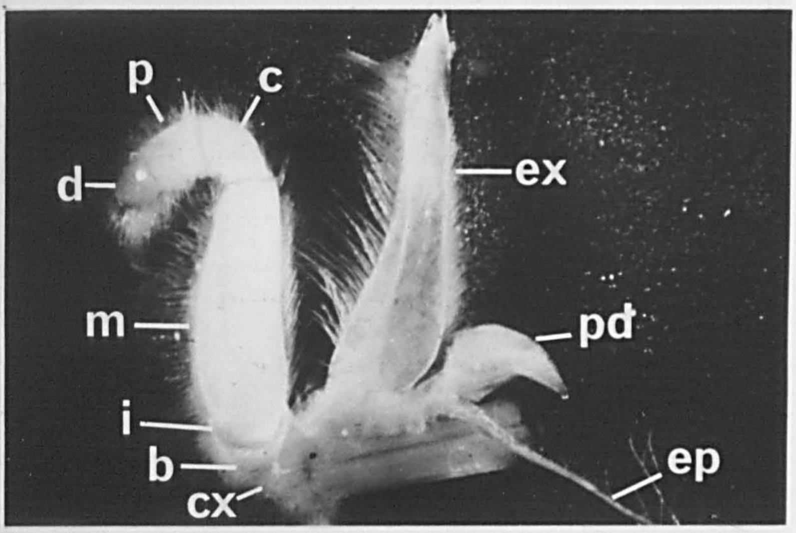
d = dactylus, p = propodus, c = carpus, m = merus, i = ischium, b = basis, cx = coxa, ex = exopod, pd = podobranch, ep = epipod.

c) Third maxilliped of O. saratan (outer view). Labelling as (b), f = flange of coxa.

a



b



c

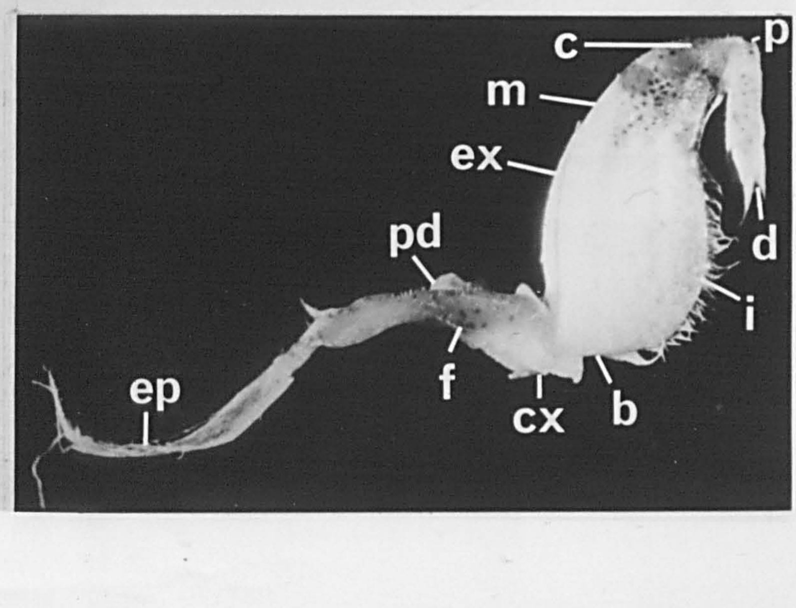


Plate 5.7. a-c) First maxilliped of <u>O. saratan</u> (S.E.M.).

a) setation of distal portion of endopod (right) and exopod (left). Scale bar = 1000μm.

b) Setal tuft from distal region of exopod.

c) Detail of plumodenticulate setae from setal tuft illustrated in (b).

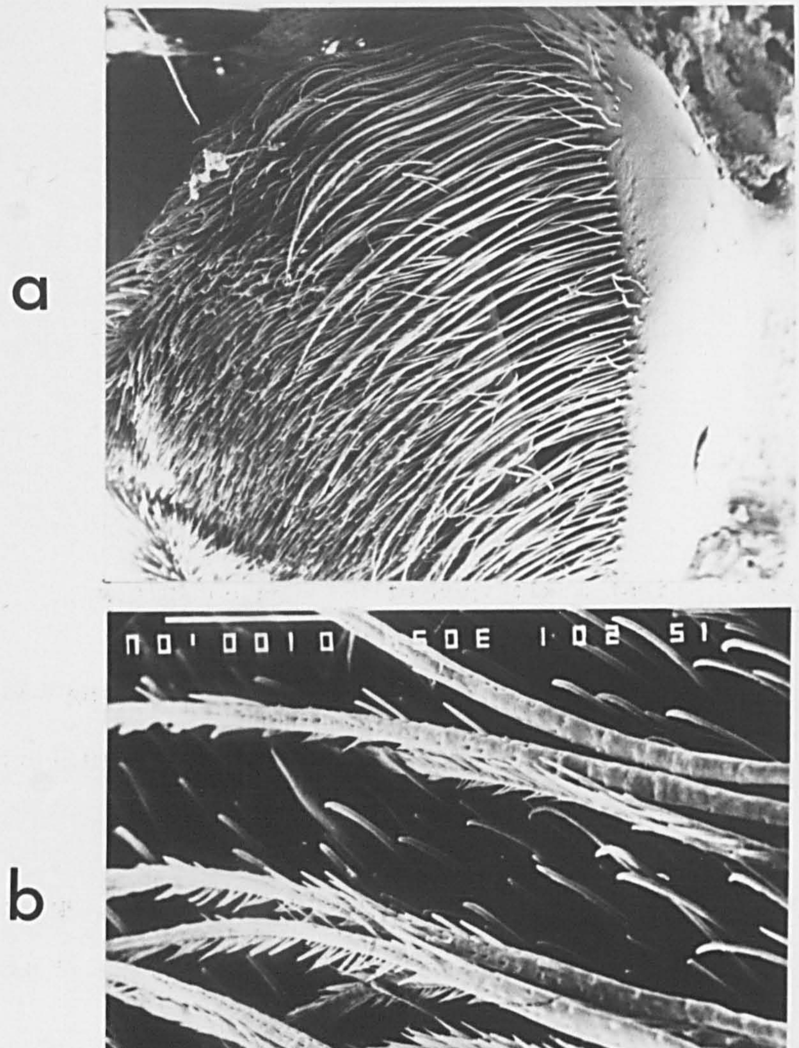

a
15 200 3054 1000.0U
b
c

Plate 5.8. a–c) First maxilliped of O. saratan (S.E.M.).

a) Setal fields on the endopod overlapping the setose distal endite. The proximal endite is just visible (lower left).

b) Detail of pappose endopod setae overlapping the spatulopectinate crooked setae of the distal endite. Scale bar = 100µm.

c) Detail of a spatulopectinate crooked seta.



a
b
c

Plate 5.9. a-c) First maxilliped of O. saratan (S.E.M.).

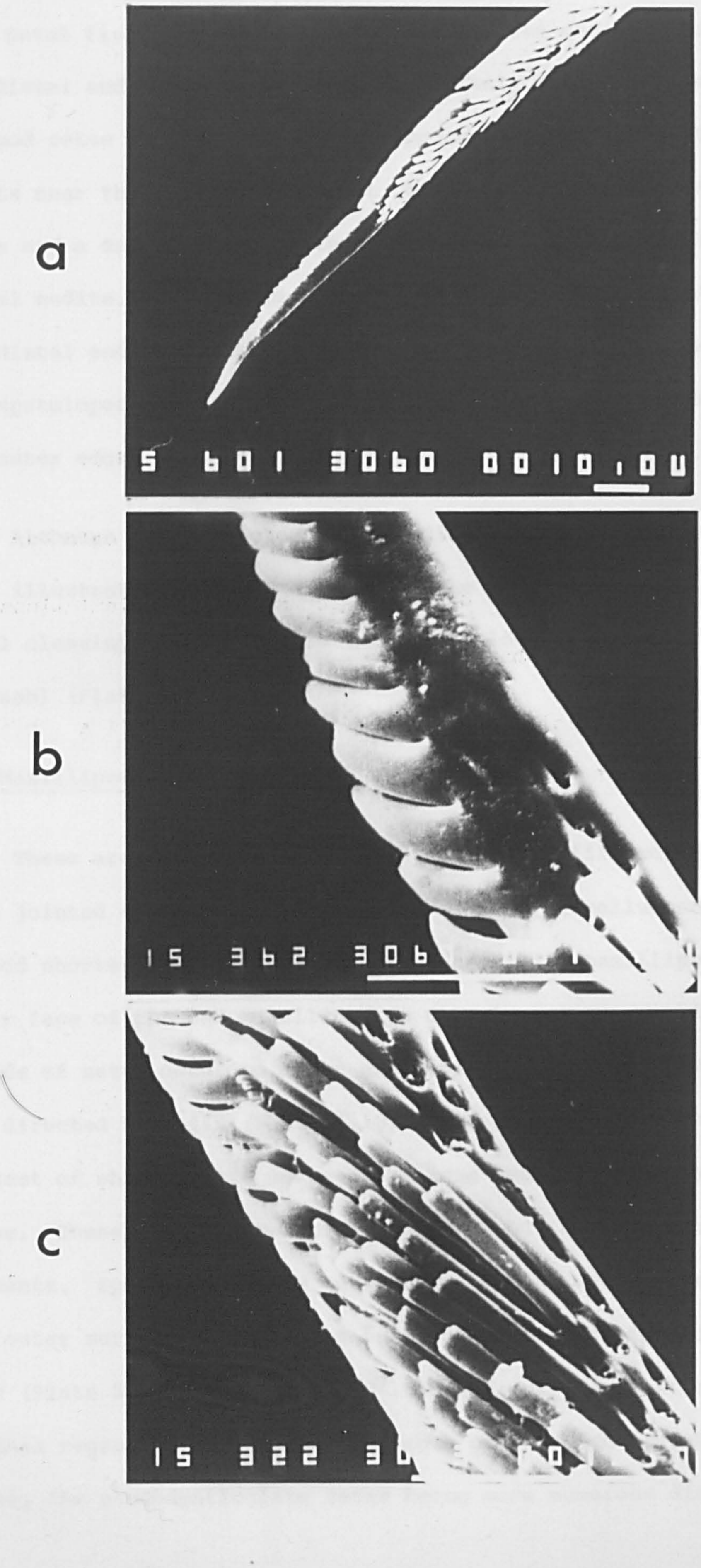
a) Scopulodenticulate seta of epipod. Scale bar = 10μm.

b) Detail of distal region showing denticulations.

Scale bar = 10μm.

c) Detail of setal shaft showing brush-like surface.

Scale bar = 10μm.


a
5 601 3060 0010 10U
b
15 362 306
c
15 322 30

bears a dense margin of similar setae.

Setal fields from the endopod overlap the endites, particularly the distal endite which is large and densely setose (Plate 5.8). The endopod setae in this region are pappose with relatively spine free shafts near their bases. Amongst these are spatulopectinate crooked setae and a dense forest of these occurs on the outer surface of the distal endite. The proximal endite is orientated at right angles to the distal endite and bears dense relatively short pappose setae and spatulopectinate crooked setae. Its setae are most dense along its outer edge.

Although not connected with feeding, the setae of the epipod are also illustrated. From their brush-like appearance and function (gill cleaning) I have called these scopulodenticulate setae (scopula = brush) (Plate 5.9).

2nd Maxillipeds (Plates 5.6b, 5.10, 5.11)

These are smaller than the 1st and 3rd maxillipeds. Each consists of a jointed endopod, a large exopod with no flagellum and an elongate epipod shorter than that of the first and third maxillipeds. The outer face of the 2nd maxilliped is densely setose; particularly dense fields of setae occur on outer and medial surfaces of the endopod and are directed medially (Plate 5.10). All the endopod segments, the largest of which is the merus, bear long medially directed serrate setae. These are triserrate on the merus but biserrate on the distal segments. Spatulopectinate setae occur on the merus (Plate 5.11a). The outer surface of the merus bears pappose setae towards the lateral edge (Plate 5.11) and simple rod-like and cuspidate setae also occur in this region. The exopod bears rows of plumodenticulate and pappose setae, the plumodenticulate setae being more numerous distally and

Plate 5.10. a-c) Second maxilliped of O. saratan (S.E.M.).

a) Overall view of outer surface. Scale bar = 1000µm.

b) Setae of the merus.

c) Detail of (b) showing triserrate shafts.

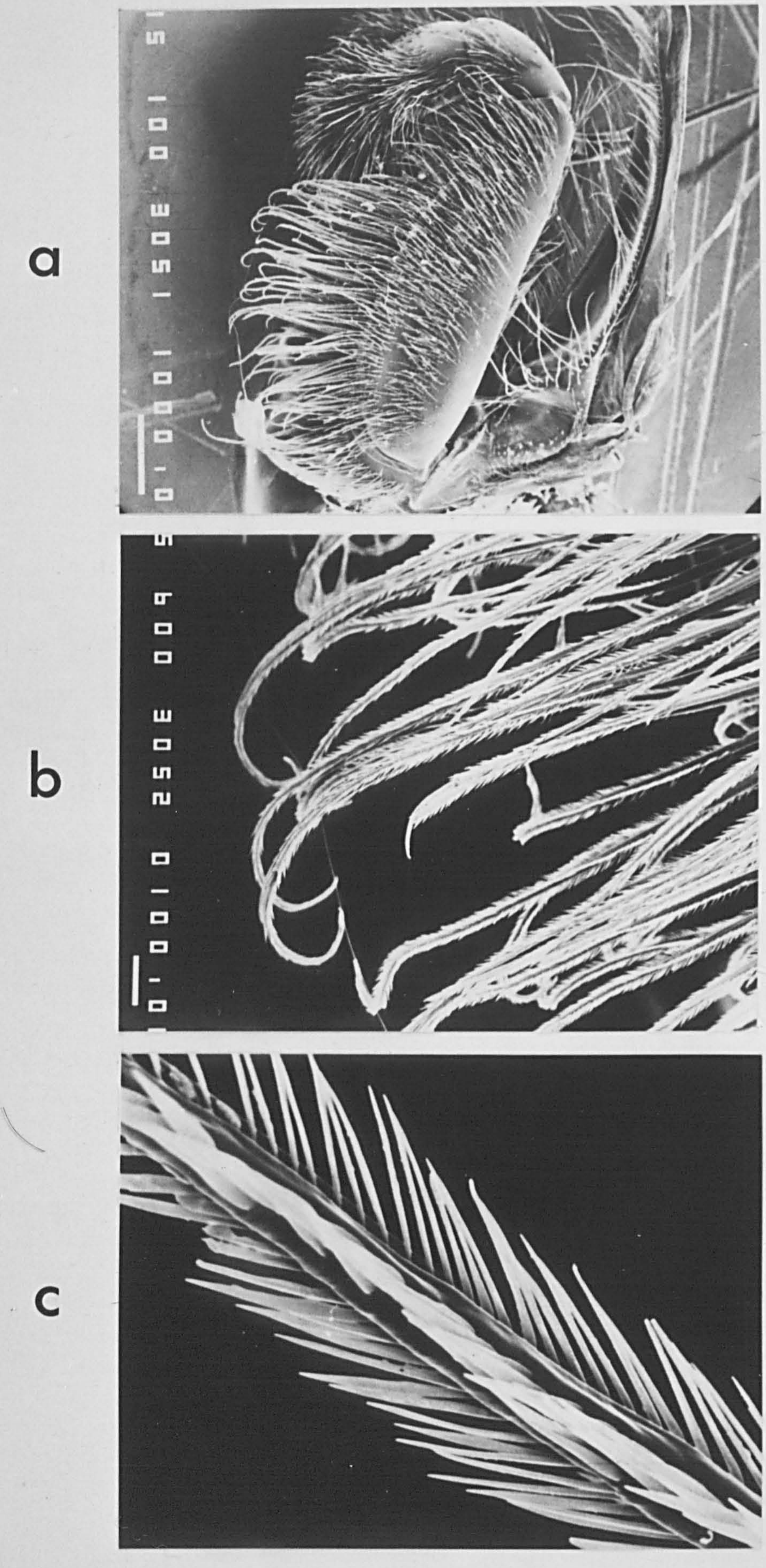
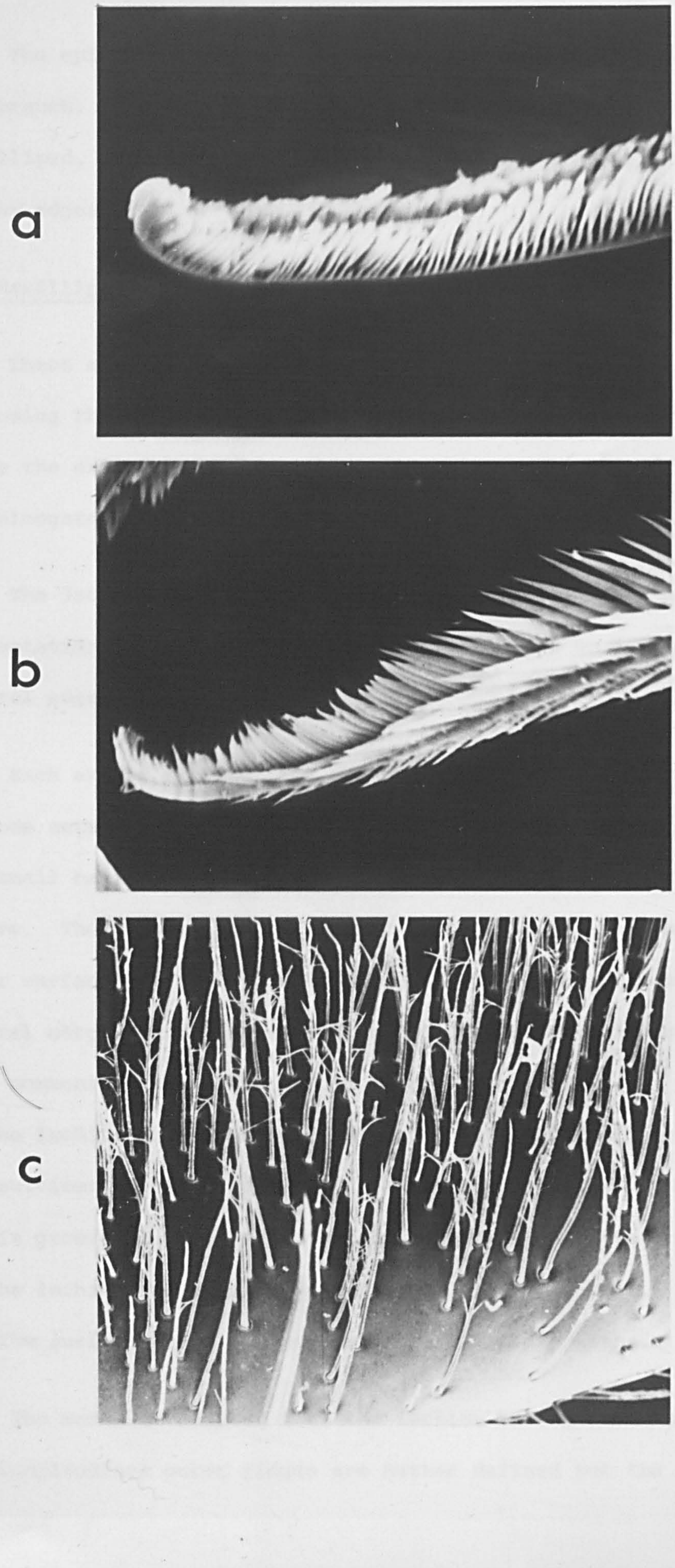

a
15 100 3051 1000,0
b
5 600 3052 0100,01
c

Plate 5.11. a-c) Second maxilliped of O. saratan (S.E.M.).

a) Spatulopectinate crooked seta from merus.

b) Biserrate tip of the setal type shown in Plate 5.10c.

c) Pappose setae on the outer lateral edge of the merus.


a
b
c

the pappose setae more numerous on the proximal lateral edge.

The epipod extends from the fused coxa and basis and bears a podobranch. The epipod setation is similar to that of the first maxilliped, ie. long scopulodenticulate setae extending from its narrow edges.

<u>3rd Maxillipeds</u> (Plates 5.6c, 5.12, 5.13, 5.14)

These are the largest of the mouthparts and are the outermost, enclosing the others. The segmented endopod is large and flattened while the exopod is small with no flagellum. The epipod is large and elongate and bears a small podobranch.

The 3rd maxillipeds are less setose than the other maxillipeds but setation is well developed on the medial and to a lesser extent lateral edges (Plate 5.12).

Each exopod extends from the outer side of the basis and bears pappose setae particularly at its apex. The coxa articulates with the small basis which is fused to the ischium though marked by a groove. The ischium is the largest segment and has a tuberculate outer surface. A poorly defined ridge occurs near the medial and lateral margins and here cuspidate and simple rod-like setae occur more commonly than in the middle of the outer face. The medial edge of the ischium is densely setose with long and short triserrate setae and multiserrate setae (Plate 5.13). The lateral edge is not setose but is grooved to receive the margin of the exopod which is parallel to the ischium and extends only fractionally beyond it. The inner ischium surface bears sparse, probably serrulate setae.

The merus is shorter than the ischium but is structurally similar. The longitudinal outer ridges are better defined but the setation is

Plate 5.12. a-c) Third maxilliped of O. saratan (S.E.M.).

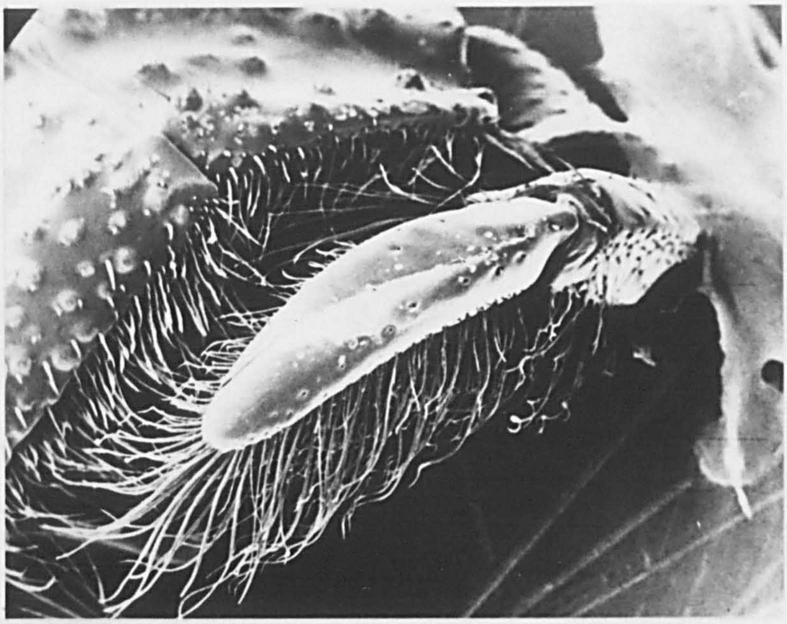
a) Distal segments of maxilliped.

b) Setation of dactylus.

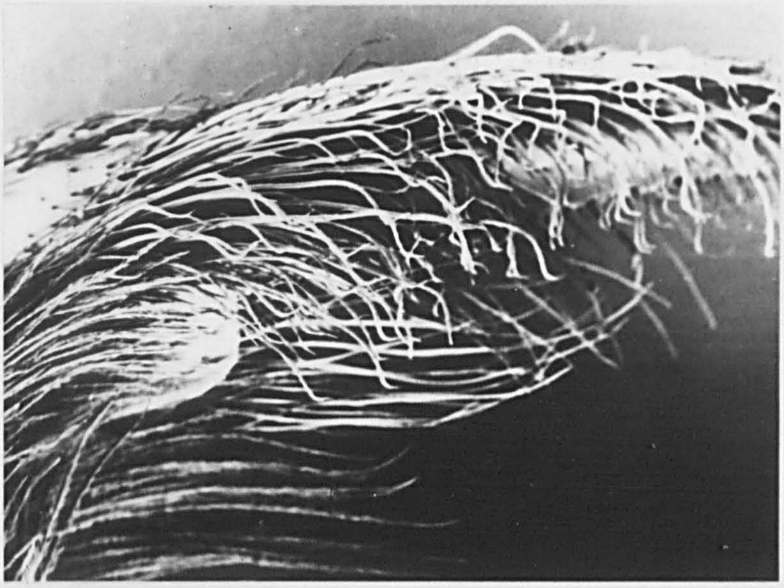
c) Detail of serrate setae from dactylus.

Scale bar = 1μm.

a



b



c

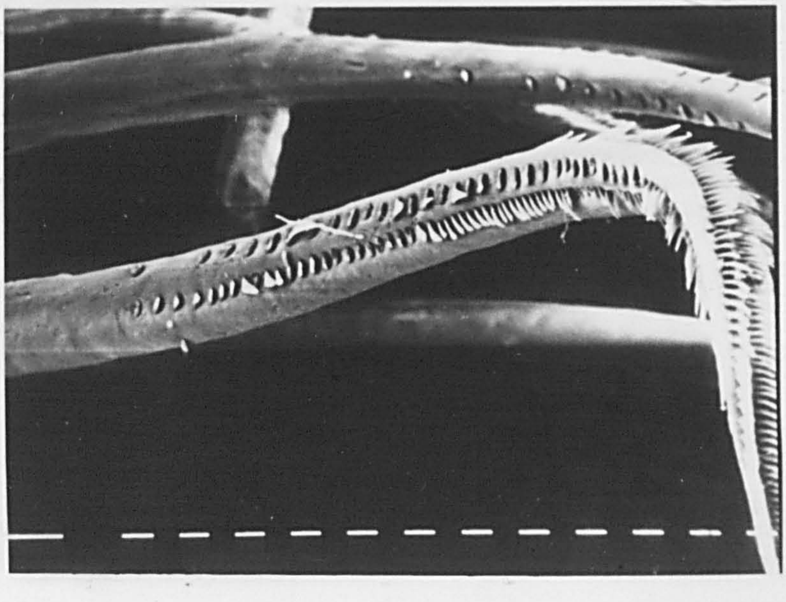


Plate 5.13. a-c) Third maxilliped of O. saratan (S.E.M.).

a) Serrate setae of the medial edge of the ischium. Scale bar = 100µm.

b) Detail of short triserrate and cuspidate setae from region shown in (a). Scale bar = 100µm.

c) Detail of elongate triserrate and multiserrate setae from region shown in (a). Scale bar = 10µm.


a
b
c

Plate 5.14. a-c) Third maxilliped of O. saratan (S.E.M.).

a) Flange region extending from coxa. The podobranch can be seen (centre left) and the epipod (upper left).

b) Pappose setae from the flange region. Scale bar = 100µm.

c) Simple setae from the flange edge. Scale bar = 100µm.


a
b
c

similar to that of the ischium on all surfaces other than the lateral edge where, beyond the exopod there are plumodenticulate setae and some serrate setae. The distal edge of the inner face of the merus is bordered by dense plumodenticulate setae.

The carpus articulates obliquely with the merus and its setation is similar to the merus. Short serrulate seta occur on its inner surface and plumodenticulate setae fringe its distal inner margin. Simple rod-like setae occur on the lateral surface while the medial surface bears long plumodenticulate setae.

The propodus is bordered by plumodenticulate setae and triserrate setae. Cuspidate and simple rod-like seta occur on its outer surface and a brush of triserrate setae along its inner surface.

The dactyl is bordered by triserrate setae with long naked shafts and short curled triserrate tips (Plate 5.12). Other triserrate setae were like those on the propodus, ie. straighter with the setules extending further down the shafts which were nevertheless still naked for most of their length. Triserrate setae extend partly on to the inner surface of the dactyl but its outer surface bears only sparse cuspidate setae.

The epipod is joined to the coxal flange and its setation is the same as that of the other epipods. Its flattened 'blade' is bordered by scopulodenticulate setae. The setation of the coxal flange is illustrated in Plate 5.14. It bears simple rod-like, serrate and plumodenticulate setae.

5.3.4. Morphology of chelae (Plate 5.15)

Plate 5.15 illustrates the inner face of the large and small chelae of a male and female crab; both are left handed. The

Plate 5.15. Chelae morphology of <u>O. saratan</u>. Top - male crab (4.2cm carapace width): bottom - female crab (4.2cm carapace width). Both crabs were 'left-handed' ie. major cheliped was on the left. The inner surface of the chelae are illustrated. The stridulating ridges can be seen on the major chelipeds.


½ mm
1
2
3
4
5
6
7
8

stridulating ridge can be clearly seen and is larger in the male. In the male illustrated the stridulatory ridge is composed of 77 striae bordered on the distal side by dense setae. In the female illustrated there are 69 striae and the setal field though present is much less developed. The striae are shorter and do not extend as far dorsally as in the male.

Both chelae of both sexes are curved such that the outer face is convex and the inner face is concave. On the larger claw the opposing faces of the pollex and the dactyl are both provided with a continuous row of robust, blunt teeth. In both sexes the teeth of the minor chela are triangular and relatively small and sharp (see Plate 5.15).

Feeding observations indicate that O. saratan uses its large chela to crush Mesodesma shells and the small chela is used as a forceps to pick up material from the sand and strand. Both are used in deposit feeding.

5.3.5. Morphology of Stomach (Plate 5.16a, b, Fig. 5.1)

The stomach of crabs is divided into a cardiac and pyloric region with an extensive system of supporting ossicles to which muscles are attached. Within the cardiac region of the stomach some of these ossicles connect with three tooth bearing ossicles which constitute the gastric mill (Pearson, 1908).

The powerful gastric mill of O. saratan reflects its varied diet. The urocardiac ossicle is smooth walled and terminates in a robust dorsal tooth. It lies between the two complex zygocardiac ossicles which show a gradation of teeth. In dorsal view these are large, blunt and molar like anteriorly, grading to small sharp teeth posteriorly (Fig. 5.1a) while in ventral view a separate row of teeth

Fig. 5.1. Teeth of the zygocardiac and urocardiac ossicles of the gastric mill of O. saratan. Anterior is downwards.

a) dorsal view of zygocardiac ossicles either side of urocardiac ossicle. The direction of movement of the urocardiac ossicle is indicated by the arrow.

b) ventral view of teeth of zygocardiac ossicle.

c) inner face of zygocardiac ossicle.

d) lateral view of dorsal (median) tooth of urocardiac ossicle. This moves up and down the inner face of the zygocardiac ossicle.

e) outer face of zygocardiac ossicle.

The scale bar = 1mm.

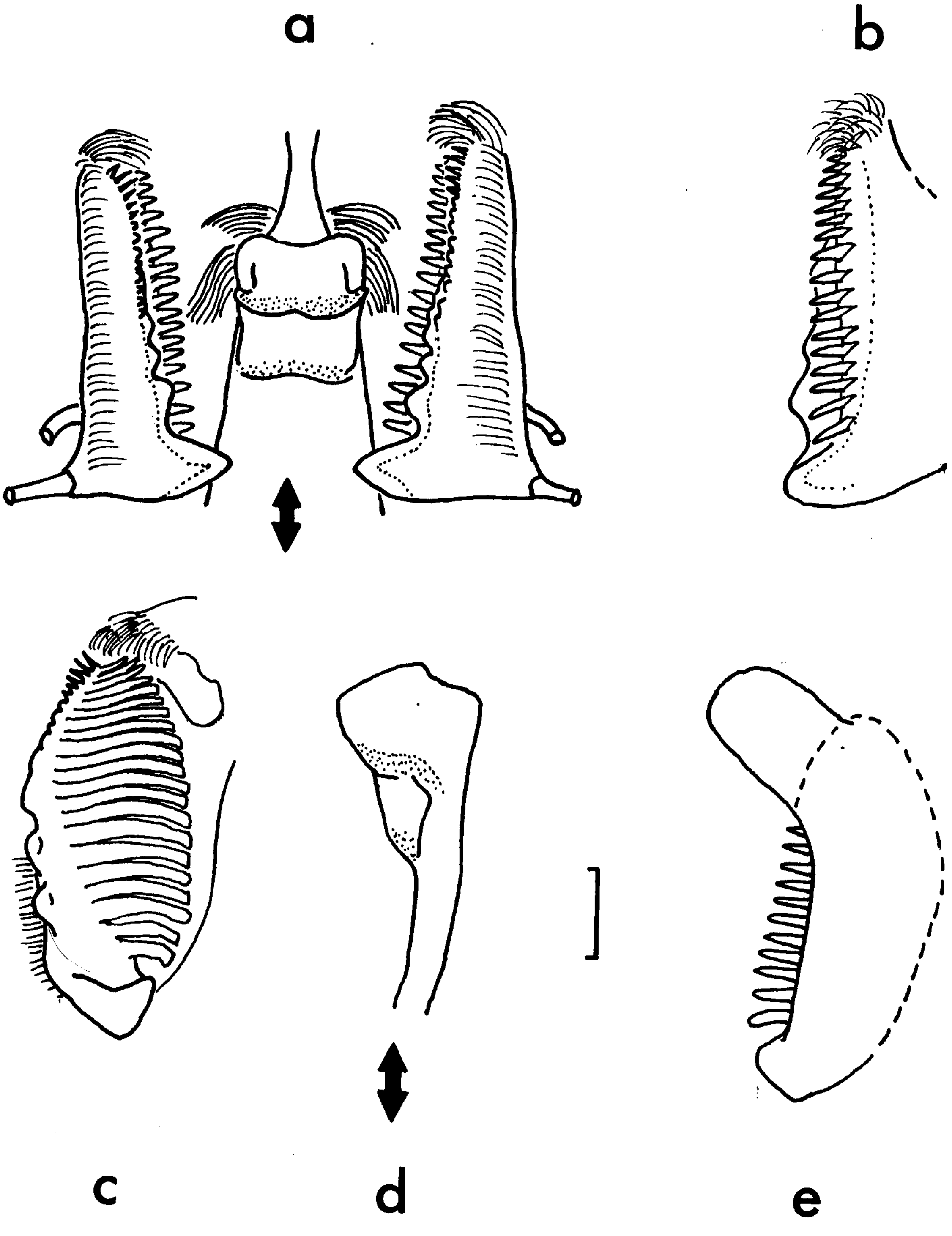

a
b
c
d
e

Plate 5.16. The stomach of O. saratan.

a) Posterior view of stomach. The pyloric region has been removed to reveal the gastric mill and the cardiac region of the stomach with its supporting ossicles. The width of the stomach illustrated is 16mm.

b) Detail of the gastric mill viewed posteriorly showing the teeth of the zygocardiac ossicles. The urocardiac ossicle is also visible (top centre).

a

b

is evident (Fig. 5.1b). These comb-like teeth are continuations of transverse ridges occupying the inner face of the zygocardiac ossicle (Fig. 5.1c). In side-view, the dorsal tooth of the urocardiac ossicle can clearly be seen (Fig. 5.1d). Comparing Figs 5.1c and 5.1d, it can be seen how this tooth makes contact with the teeth of the zygocardiac ossicle as it moves backwards and forwards.

Plate 5.16ashows a general posterior view of the stomach showing the supporting ossicles. Plate 5.16b shows the gastric mill whose urocardiac and zygocardiac ossicles are also detailed in Fig. 5.1.

According to Warner (1977) the effective stroke of the dorsal tooth of the urocardiac ossicle is from posterior to anterior, past the graded teeth of the zygocardiac ossicles such that the event sequence is straining and tearing followed by crushing and chewing.

5.4. Discussion

O. saratan is a generalised opportunistic feeder, employing all the methods described for other Ocypode species. In this respect it is probably closest to O. ceratophthalmus though few species have been subject to detailed feeding studies. This conclusion is supported by laboratory and field behavioural observations, stomach contents analysis, mouthpart and cheliped morphology and stomach morphology.

A number of interesting points arise from the behavioural observations. The deposit feeding technique used by O. saratan shares common features with both O. gaudichaudii and O. ceratophthalmus, and the somewhat different O. quadrata in the manner that the sand is gathered to the mouth and also in the way it is ejected. Crane (1941) for O. gaudichaudii and Tweedie (1950) for O. ceratophthalmus both describe the chelipeds as acting as rakes and Robertson and Pfeiffer (1982) draw a distinction between this and the method employed by

O. quadrata by saying that the articulating function of the chelipeds is not used in the first two species. That is certainly the case for O. gaudichaudii since Crane (1941) specifically mentions it saying that the chelae are held almost closed. Tweedie (1950) states that O. ceratophthalmus is similar to Crane's O. gaudichaudii, leaving similar marks in the sand to that figured by Crane (1941). It is difficult to distinguish detail in Crane's photographs but there are places where the bifid traces left by the slightly open dactyl and pollex can be seen. Also, Braithwaite and Talbot (1977) report that in O. ceratophthalmus the chelae are used to scrape the surface forming pairs of short parallel furrows. This is similar to the situation in O. saratan but here there is clear evidence in some, though not all sand traces, that the dactyl is brought slightly towards the pollex at the start of the sweep. In these cases the trace left in the sand is not as dramatic as that figured by Robertson and Pfeiffer (1982) for O. quadrata where the dactyl is widely extended and pinches up sand during the scooping motion. O. gaudichaudii and O. ceratophthalmus drop the pellet of rejected material from the mouthparts. O. quadrata flicks it away with the small cheliped and this action has been observed for O. saratan though I cannot be certain that this occurred on every occasion.

The fine details of deposit feeding cannot be deduced from the information given for O. macrocera (Rajabai, 1972) and O. mortoni (George, 1982).

No-one has yet worked out the manner in which the sand is sorted by the mouthparts. The sand appears to be gathered from the chelipeds by the distal segments of the third maxillipeds (Crane, 1941) and formed into a pellet posteriorly (Crane, 1941; Rajabai, 1972). Crane (1941) states that the endites of the 1st maxilliped are orientated 'exactly like a pair of butter-ball paddles' and the inference is that the sand bolus is produced in this region. Tweedie (1950) states that 'the maxillipeds could be seen vibrating with a semi-liquid mass of sand in a state of suspension between them.' Possibly the curious distal flanged shape of the first maxillipeds is responsible for retaining sediment and transferring it proximally for sorting, assisted by the distal segments of the second and third maxillipeds.

Sorting is undoubtedly related to mouthpart setation. Crane (1941) states that 'there are no pectinated spoon-tipped hairs, so characteristic of most fiddler crabs, on the second maxilliped (of O. gaudichaudii or O. occidentalis); in both, however, there is a row of short, thickened hairs on the inner (dorsal) side of the merus and a cluster of similarly thickened and slightly concave hairs among the normal ones on the tip of the palp.' Robertson and Pfeiffer (1982) also reported no spoon-tipped setae but pointed out that deposit feeding was up to 90% as efficient as in Uca pugilator which relies primarily on deposit feeding. Using SEM I have examined the small ocypodid Dotilla sulcata which has spoon-tipped setae (see Vogel, 1984) and certainly such setae do not occur in O. saratan. The elongated spatulopectinate crooked setae that occur particularly on the third maxilliped in O. saratan are, however, rather similar to some of them. They are particularly dense on the endites of the third maxillipeds of O. saratan, especially the distal endite. Because of their small size their structure is not very apparent without SEM and so they are easily overlooked. I do not think that Crane (1941) observed these setae. Crane's description, particularly of the row of short thickened hairs, corresponds to cuspidate setae in my observations; they are similar to the H2 setae of Factor (1978), ie.

they have sparse setules on the shaft. The slightly concave similar setae Crane described from the tip of the palp of the second maxilliped may have referred to serrate setae since some of these are robust and appear concave due to the arrangement of the setules. I think it is likely that the spatulopectinate crooked setae seen here in *Ocypode saratan* perform a fine sediment sorting function and the clue to this comes from *Uca* spp., particularly *U. pugilator*. In *Uca* spp. it is clear from Miller (1961) that 'shallowly cupped hairs' occur on the endites of the first maxillipeds and on the second maxillipeds. These are probably synonymous or at least similar to my spatulopectinate crooked setae judging from Miller's statement and low power light microscope photographs. In *Uca* the spoon-tipped setae remove coarse material and the first and second maxillipeds work together to accumulate the finer material for ingestion. *U. pugilator* which inhabitats sandy areas had more numerous and better developed spoon-tipped hairs than the mud dwelling *U. minax* and *U. pugnax*. The sand dwelling *Dotilla* spp. have spoon-tipped setae and so does the sand dwelling *Scopimera globosa* (Ono, 1965). Thus, it is strange that the sand dwelling *Ocypode* do not have similar spoon-tipped setae and clearly more detailed study of the feeding mechanism is necessary.

A further point on deposit feeding is that the sand in the mouthparts appears fluid. Tweedie (1950) drew attention to this. Robertson and Pfeiffer (1982) noticed that *O. quadrata* rested its setal tufts on the wet sand during feeding and this may be to replenish water diverted to the mouthparts during feeding. The use of water to sort particles is well established for *Uca* spp. (Altevogt, 1957; Miller, 1961). This replenishment of branchial water was also seen in *O. saratan* though its frequency was not investigated and related to feeding. Methylene blue taken into the branchial chamber from the setal leg tufts (see Chapter 7) was found in the stomach of O. saratan.

Crane (1941) and Tweedie (1950) speak of Ocypode deposit feeding in this way to obtain plankton stranded on the sand. Robertson and Pfeiffer (1982) attribute O. quadrata's feeding in this way to the presence of local dense patches of benthic diatoms which seems a better explanation. Nevertheless, Braithwaite and Talbot (1972) described O. ceratophthalmus as feeding by rushing down the beach between the swash to collect organic particles carried by the swash and deposited as the water drains through the surface. This was separate from their observations of sand pellet feeding but indicated the validity of stranded plankton as a food source.

Crane (1942) described O. gaudichaudii as unique amongst Ocypode spp. in feeding exclusively by deposit feeding when adult. Crane (1941) and Koepcke and Koepcke (1953) however, showed that juveniles were scavengers and predators. From the information on O. mortoni it appears that this species may be principally (probably exclusively) a deposit feeder (George, 1982). Some species are specifically mentioned as not deposit feeding, eg. O. occidentalis (Crane, 1941) and O. ryderi (Vannini, 1976a). For many Ocypode species there is no description of feeding. General foraging, often in the strand, scavenging and predatory behaviour are probably common to most species though descriptions are limited to a few.

Vannini (1976a) summarises much of the available information and it is clear that there are differences in dietary preferences with age and also geographical variations. An example of the former has already been given (O. gaudichaudii): geographical variation is exemplified by O. ryderi which included insects in its varied diet in

Somalia (Vannini, 1976a) but not in Kenya where the only predatory behaviour observed involved locating and excavating bivalves (Jones, 1972). Also *O. quadrata* was 90% predatory on North Carolina beaches and the remainder of its feeding did not involve deposit feeding (Wolcott, 1978) whereas Robertson and Pfeiffer (1982) observed deposit feeding in Georgia. Previously the species had been regarded as mainly a scavenger (eg. Cowles, 1908). Such differences seem to reflect different local conditons and, perhaps, lack of detail in early observations of *O. quadrata* such that the extent of predatory behaviour was overlooked.

Clear accounts of foraging and scavenging behaviour occur for several species, eg. *O. ceratophthalmus* (Tweedie, 1950; Hughes, 1966; Jones, 1972), *O. macrocera* (Rajabai, 1972), *O. ryderi* (Vannini, 1976a), *O. quadrata* (Cowles, 1908). *O. saratan* engages in similar behaviour, mostly amongst the strand.

Ocypode spp. include skilled predators. Predatory behaviour can be divided into several categories. Firstly, there is the location and capture of relatively immobile species such as bivalves (*Donax*, *Mesodesma*) and mole crabs (*Hippa*, *Emerita*). For example, Tweedie (1950), Hughes (1966) and Smith (1975) describe *O. ceratophthalmus* digging *Donax* spp. out of the sand and Wolcott (1978) reports this for *O. quadrata*. Smith (1975) showed that predation was selective with respect to *Donax* colour morphs. Vannini (1976a) reported apparent predation on *Hippa ovalis*, Koepcke and Koepcke (1953) reported juvenile *O. gaudichaudii* feeding on *Emerita* sp. and Fales (1976) and Wolcott (1978) reported nocturnal predation by *O. quadrata* on *E. talpoida*. Graham and Turner (1984) showed variations in the nutritional quality of *Donax* and *Emerita* which was reflected in the hepatopancreatic composition of *O. quadrata*. These are its main food items in nature (Wolcott, 1978), Emerita having the higher calorific content.

Secondly, there is the capture of more active prey, eg. baby turtles (O. cordimana; Tweedie, 1950 re-interpreting an observation by Gibson-Hill, 1947), newly hatched terns (O. quadrata; Fales, 1976), other large species of semiterrestrial and aquatic crabs (O. ceratophthalmus; Hughes, 1966), insects (O. ryderi and O. cordimana; Vannini, 1976a) amphipods and isopods (O. quadrata; Cowles, 1908; Wolcott, 1978).

Thirdly, there is cannibalism, eg. in O. ceratophthalmus (Fellows, 1966; Hughes, 1966) and O. quadrata (Cowles, 1908).

Therefore, O. saratan fits into all of these predation categories. Indeed, O. saratan was seen to employ all the feeding strategies described for other species though it did not seem to engage in extensive landward migrations but rather migrated towards the sea, feeding at the tide edge at low tide. Vannini (1976a) pointed out that this behaviour was only shared by O. ceratophthalmus, eg. (Hughes, 1966) though it seems to me that the diurnal O. gaudichaudii is also in this category (Crane, 1941). It must also be remembered that the behaviour of many species is undescribed.

O. saratan is, therefore, mainly supralittoral moving seawards to feed. There is a gradation of habitat preference within Ocypode species and some, like O. africana, O. cordimana and O. pallidula may be regarded as extralittoral (Gauld and Buchanan, 1956; Fellows, 1966, 1973, 1975; Vannini, 1976a). Of these, O. cordimana at least is known to feed mainly on terrestrial insects and vegetation (Vannini, 1976a; George, 1982) behind the beach, which is an area infrequently visited by O. saratan in my observations.

The chela morphology of *Ocypode* spp. is very similar between species. As has been seen, several species undertake sand pellet feeding but only adult *O. gaudichaudii* have chelae with truncated tips to facilitate sand gathering (Crane, 1941). It would be interesting to compare the dactyl and pollex of *Ocypode* species. Crane (1941) states for *O. gaudichaudii* that the inner surfaces of both dactyl and pollex are slightly concave. This is in addition to their longitudinal inwards curvature. *O. saratan* lacks truncated claw tips but the dactyl and particularly the pollex are slightly concave in each chela. It is impossible to assess this feature in the literature for other species and I have not had the opportunity to examine a species range of museum material. Deposit feeding and non-deposit feeding species may show differences in this feature. It would also be interesting to know whether the setation distal to the stridulating ridge on the large chela helps to protect this from sand abrasion during feeding and whether its development is correlated at all with deposit feeding. The length and width of the pollex of the large chela also seem variable between species. For example, the long thin pollex of *O. madagascariensis* represents one extreme (Crosnier, 1965) and the broad short pollex of *O. mortoni* represents the other (George, 1982). Most other *Ocypode* spp., including *O. saratan* are intermediate between these. There is too little information in the *Ocypode* literature on the structure of the small chela yet it is clear that there are specific differences. In *O. mortoni*, which deposit feeds, although the tips of the large chela are not truncated those of the small chela are. Yet this species is said to gather sand using 'the lower toothed knife edge of the chelipeds' (George, 1982) which is not the technique reported for other species.

A detailed study of the functional morphology of the chelae of Ocypode spp. would seem to be worthwhile.

The gastric mill of the stomach also indicates varied diet in O. saratan. Comparing it with those figures for various crabs by Warner (1977), its zygocardiac ossicles have common features with those of the predatory Callinectes sapidus (which has sharp posterior teeth and pronounced blunt anterior ones) and those of a deposit feeding Uca sp. (which has grinding teeth in transverse ridges). Similar transverse ridges are also a feature of the zygocardiac ossicles of herbivores (Warner, 1977). The urocardiac ossicle of O. saratan is relatively simple, however, and lacks transverse ridges like those found in Uca and the vascular plant herbivore Aratus pisoni. It would be interesting to compare the gastric mills of different Ocypode species to see if dietary differences are reflected in structural differences.

Finally, little quantitative work has been done on the ecological rôle of Ocypode spp. Vannini (1976a) has constructed a food web for O. ryderi but does not consider energetics. Cowles (1908), of O. quadrata said 'Ocypodas are great scavengers and keep the beach almost free from decomposing animal and vegetable matter'. Wolcott (1978), however, showed that O. quadrata on a North Carolina beach was the top predator in a simple filter-feeding based food chain. It derived most energy from predating the mole crab Emerita talpoida and consumed most of the production of this species and of the bivalve Donax variabilis. An equivalent study of O. saratan would be valuable as would the study of situations where several species occur in the same general area but are zoned and show dietary differences (eg. O. cordimana, O. ceratophthalmus and O. mortoni in

Hong Kong (George, 1982), *O. cordimana* and *O. ceratophthalmus* in in many places (Vannini, 1976a), *O. africana* and *O. cursor* in W. Africa (Gauld and Buchanan, 1956)).

DIVISION 3. PHYSIOLOGY

SUBDIVISION A. RESPIRATION

CHAPTER 6. BRANCHIAL MORPHOLOGY

6.1. Introduction

Diaz and Rodriguez (1977) remarked that adaptive responses to different environments could be functional, structural, behavioural or a combination of these. Bliss (1963) stated that 'associated with the evolution of terrestrial life in brachyuran crustaceans are striking modifications in their physiology and morphology, particularly of their respiratory organs'. Pearse (1929a, b) noted that in *O. quadrata* the number and volume of gills was reduced in comparison with aquatic crabs. Compared with aquatic forms, terrestrial or semiterrestrial crabs have gills of reduced number, volume and surface area per unit weight (Gray, 1957; Edney, 1960; Bliss, 1963; Griffin, 1971; Hawkins and Jones, 1982). The gill lamellae of terrestrial crabs are modified to prevent collapse in air (Harms, 1932; von Raben, 1934; Storch and Welsch, 1975; Greenaway, 1984). The lamellae are wider spaced than in aquatic crabs (Greenaway, 1984), sclerotised and spaced out by projections (von Raben, 1934; Storch and Welsch, 1975; Greenaway and Farrelly, 1984).

Renewed interest in gill areas of land crabs is seen in work on *O. platytarsis* (Veerannan, 1974) and *Holthuisana* spp. (Greenaway, 1984). Hawkins and Jones (1982) have also recently investigated gill area in two mud crabs, *Helice crassa* and *Macrophthalmus hirtipes*, both of which are littoral but the former extends into semiterrestrial conditions and the latter remains immersed.

Pearse (1929a, b) reported that in O. quadrata the number of gills was reduced to 12 with two of the gills 'fused into a great gill which is provided with two pairs of longitudinal vessels'. That Ocypode spp. have 12 gills is perpetuated in the subsequent literature (eg. Ayers, 1938; Gray, 1957; Bliss, 1963; Rao, 1968a). In fact, it has 14 gills as correctly tabulated by Calman (1909) and reiterated for O. cordimana by Greenaway and Farrelly (1984) in independent observations concurrent with this study of O. saratan. The 'great gill' is produced by the interfoliated lamellae of the anterior and posterior arthrobranchs of the fourth thoracic somite (gills 5 and 6).

Not only the gills, however, are modified in terrestrial and semiterrestrial crabs. The branchial chambers may be enlarged and have modified vascularised walls (Bliss, 1963, 1968). Pearse (1929b) describes 'irregular rows of respiratory tufts along the blood vessels on the membranous lining of the branchial cavity' of O. quadrata. The respiratory function of these branchial tufts in O. quadrata is again stated by Ayers (1938) and is clearly shown by Diaz and Rodriguez (1977) who present evidence on the respiratory function of the lining of the branchial chamber in seven semiterrestrial branchyuran species from marine, estuarine and freshwater habitats. Diaz and Rodriguez (1977) also compared the shapes of the branchial chambers of these species and determined branchial volumes. The enlarged and vascularised epibranchial chambers of terrestrial and semiterrestrial crabs are often referred to as 'lungs' (see Jobert, 1876; Semper, 1878; Borradaile, 1903; Bliss, 1968; Diaz and Rodriguez, 1977; Greenaway and Farrelly, 1984) though some authors (Diaz and Rodriguez, 1977) restrict this term to the perforated branchial chambers of pseudothelphusids. Such paired lungs which are formed from the branchiostegites and lateral thoracic body walls have recently received renewed attention in freshwater/ land crabs of the genus *Holthuisana* (Greenaway and Taylor, 1976; Taylor and Greenaway, 1979; Greenaway *et al.*, 1983a, b; Greenaway, 1984) and also in *Ocypode* species (Storch and Welsch, 1975; Greenaway and Farrelly, 1984).

Carli (1969) briefly described the branchial walls of *O. saratan* noting that they were folded and vascularised as in *O. quadrata* and *O. ceratophthalmus*. The present work describes the morphology of the branchial chamber and gills of *O. saratan* in detail and presents data on gill area and branchial volume. Brief comment is made on two other crab species that were exposed to semiterrestrial conditions at Sharm Obhor.

6.2. Material and Methods

The branchial morphology of *O. saratan* was investigated using a number of techniques. Both freshly killed and preserved crabs were dissected under a stereomicroscope and the branchial morphology was examined and photographed. Gills, scaphognathite, branchial wall sections and setal tufts at the limb bases were removed from fresh crabs and prepared for scanning electron microscopy (SEM). The SEM methodology is given in Chapter 5.

Sections of gills were also prepared for standard microscopical examination and photographed using an Olympus AO11 photomicroscope. Sections were stained with either standard haemaloxylin-eosin or with Mallory triple stains.

Further information on the structure of the epibranchial chamber was obtained from an examination of the shape and surface characteristics of paraffin wax and polyester resin casts (see below).

An attempt was made to locate the respiratory sites by following the technique used by Diaz and Rodriguez (1977). A 1.5mg/l solution of methylene blue was prepared in boiled distilled water and reduced with hydroquinone or sodium sulphite. From 1 to 5μl were injected into living crabs either into the branchial veins, or into the heart or into the limb bases. Oxidation of the methylene blue at the sites of oxygen uptake was reported by Diaz and Rodriguez (1977), producing dark blue/black staining. The technique consistently failed to work even when crabs were preflushed with nitrogen and then held in an atmosphere of oxygen. The technique was modified with the methylene blue prepared according to the nerve staining method of Pantin (1969) and reduced with sodium hydrosulphite which gave reliable reoxidation results on the bench but unfortunately not in the crab. Correspondence with Rodriguez did not shed any new light on the problem so the attempt was abandoned.

For the determination of the number of gill lamellae and of gill area, the method followed was similar to that used by Gray (1957). Live crabs were wiped with tissue paper to remove excess water and then weighed. Carapace width and sex were also recorded. The crabs were then sacrificed by killing them at low temperature (fridge) following which the gills were removed from the right branchial chamber in each case and placed singly in labelled petri dishes containing seawater. The length of each gill was measured using digital precision callipers. Following this, the number of gill lamellae per millimetre was determined using the ocular micrometer of a dissecting microscope. Several regions of the gill were examined and knowing the total length of the gill and the number of gill lamellae per unit length, the total number was then determined by multiplication. To account for the differing size of the gill lamellae both along the length of the gill and either side of the midline, the gill was examined distally, proximally and at the midpoint and one pair of opposed lamellae was examined from each of these regions (except in the case of the smallest gills when just the midpoint was considered). In this way the overestimations of gill area implicit in just using the lamellae at the middle of the gill (see Gray, 1957; Veerannan, 1974) are avoided.

The removed lamellae were mounted in seawater on a slide and using a dissecting microscope with a camera lucida (Wild), their outlines were drawn. Lamellar area was determined from the weight of the drawing paper since it had been determined that gill area (mm^2) = paper weight (g) x 5.91 (area in $mm^2 \equiv 1g$). The gills from the left branchial chamber were assumed to have the same area as those from the right.

It should be noted here that Gray (1957) used the term platelet. Hughes (1983) explains that Gray used this word to include the lamellae on both sides of a given gill axis (ie. 1 platelet = 2 lamellae in Gray's work). Hughes (1983) continues Gray's usage for American species but he adopts the more familiar term lamella for British species. I have used the word lamella(e), ie. there is a row of lamellae on each side of the gill axis.

The volume of the branchial chamber was measured in O. saratan employing 3 methods, two of which proved successful. Initially, the method of Diaz and Rodriguez (1977) was followed in which specimens were killed by immersion in 10% formalin and weighed after the removal of surplus fluid from the body and gill chamber. As with Diaz and

Rodriguez (1977) the pereiopods were removed prior to weighing, this removing variability caused by specimens that had autotomised limbs. Melted paraffin wax was syringed into Milne-Edwards opening until the gill chamber was filled. This was checked by cutting a small 'window' in the roof of the gill chamber through which any necessary topping-up of the wax could be achieved. The resulting cast perfectly represented the shape of the chamber and its volume was determined from the weight of the cast and the density of the wax. In each crab used, both branchial chambers were cast with wax and the mean branchial volume was taken. A total of 32 crabs were used.

As an alternative to paraffin wax, polyester resin was also employed to cast the branchial chamber and branchial volume was similarly obtained from cast weight and resin density. Although the resulting cast was durable the resin proved difficult to use and after 3 trials this method was abandoned.

The above methods both had the disadvantage of not penetrating the smallest interstices of the branchial chamber, air traps could form in the branchial chamber which were difficult to clear and the resulting paraffin wax casts were very fragile and easily damaged on removal.

It was decided to use another method in an attempt to reduce the variability in the results caused by these factors.

Forty-four crabs were killed in low temperature (fridge), surplus water was removed from the body surfaces and branchial chambers and the crabs were measured and weighed. All the crabs had a full complement of fully formed limbs so pereiopods were not removed. All inhalent and exhalent openings were closed using cyanoacrylate glue and a small hole was drilled on the dorsal side of each branchial chamber. Using a scaled burette, each branchial chamber was carefully filled with water and the volume noted from the burette. The mean branchial volume was thus determined for each crab. This appeared to be a more satisfactory technique, reducing variability in the data.

Since the ocypodid crab Dotilla sulcata was common at Obhor, living in the sand strip along the water's edge, this was briefly examined in order to compare its branchial morphology and hydrophilic setal tufts with those of O. saratan. The littoral grapsid Metopograpsus messor which is amphibious and common in the rocky areas of Red Sea beaches was also similarly examined, in each case using SEM techniques similar to those described previously.

6.3. Results

6.3.1. Prebranchial chamber

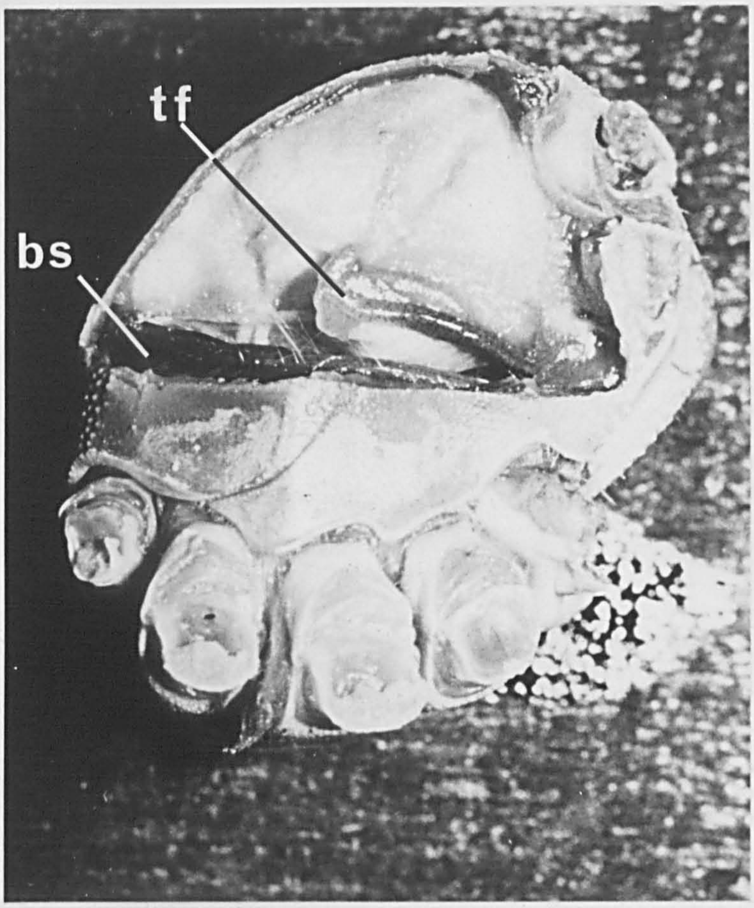
The paired prebranchial chambers are situated at each side of the mouth. Each is anterior to and connected to the branchial chamber of the same side and is formed by the ingrowth of the inner edge of the anterior part of the subbranchial region of the carapace (Pearson, 1908). Each prebranchial chamber opens anteriorly to the outside and posteriorly into the branchial cavity with which its walls are continuous (see Plates 6.1 and 6.2).

A scaphognathite (exopod of second maxilla) occupies each prebranchial chamber (Plate 6.2a). The scaphognathite may be regarded as a pump, the prebranchial chamber, the pump house. The undulatory movements of the scaphognathite are responsible for creating the respiratory current. Scaphognathite function has been described in some detail for the shore crab Carcinus maenas (see Hughes et al.,

Plate 6.1. a) Lateral view of epibranchial chamber of O. saratan. The carapace has been removed to illustrate the branchiostegal shelf (bs) and the thoracic fold (tf). The crab is orientated in its natural position. The pyramid-like shape of the epibranchial chamber can be seen.

b) Dorso-lateral view of epibranchial chamber and branchial chamber of O. saratan. The branchiostegal shelf can be seen partially covering the gills (g). The thoracic fold can also be seen.

a



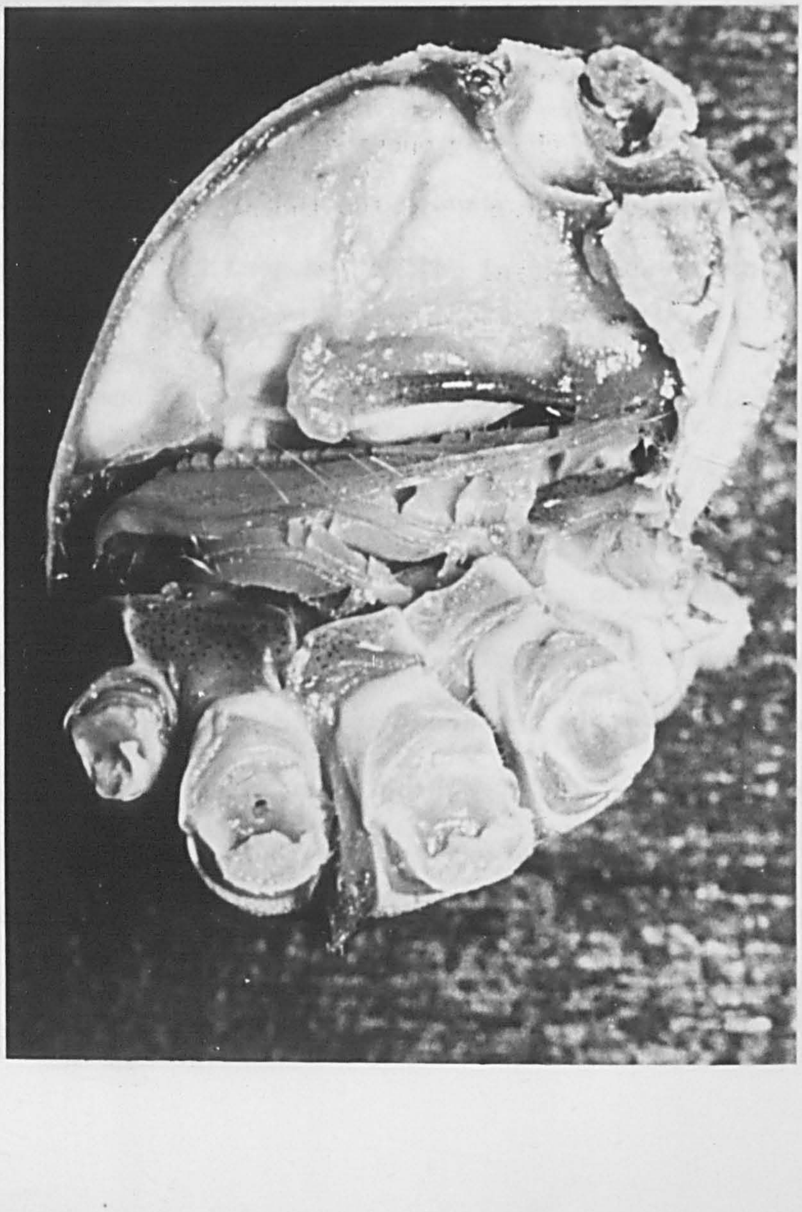
b

Plate 6.2. a) Scaphognathite of O. saratan.

b) Dissected branchial chamber of O. saratan. Note the gills beneath the branchiostegal shelf and the setal tufts between pereiopods 3 and 4. The branchial chamber opens anteriorly into the epibranchial chamber which contains the scaphognathite. Compare with Plate 6.1a.

a

b



1969; Young, 1975) and it is capable of pumping forwards, or backwards as first noted in Corystes cassivelaunus by Garstang (1896). Its rôle in O. saratan is discussed in Chapter 7 but it is noted here that the scaphognathite is robust and its long edge bears very short plumed setae. The scaphognathite fits closely against the smooth walls of the prebranchial chamber.

6.3.2. Branchial chamber

6.3.2.1. General structure

The branchial chambers of O. saratan are modified for aerial respiration and each contains both a gill chamber and a 'lung'. Seven pairs of gills occupy the lower part of each branchial chamber and a soft flap of tissue from the base of the branchiostegite partly separates the gills from the dorsal expanded epibranchial space (see Plates 6.1 and 6.2). This feature has previously been noted in O. gaudichaudii by Koepcke and Koepcke (1953), in O. quadrata by Diaz and Rodriguez (1977) and in O. cordimana by Greenaway and Farrelly (1984) who termed it the branchiostegal shelf. A horizontal flap of similar tissue is also present on the thoracic side of the branchial chamber. In addition to this horizontal division of the branchial chamber, there is a vertically aligned flap of tissue adjacent to the inner (thoracic) wall of the epibranchial chamber and which partly divides this chamber into an inner and outer region (see Plates 6.1 and 6.2). This feature was also noted in O. cordimana by Greenaway and Farrelly (1984). The walls of the epibranchial lungs are formed from the inner surface of the branchiostegite and on their inner side by the thoracic body wall and are conspicuously folded and extensively vascularised.

Plate 6.3. Casts of epibranchial chamber of *O. saratan* using polyester resin (left) and paraffin wax (centre and right).

a - lateral view, b - posterior view, c - anterior view, d - ventral view of right epibranchial chamber - note impressions of gill lamellae, e - corresponding ventral view of left epibranchial chamber, f - dorsal view of left epibranchial chamber, g - corresponding dorsal view of right epibranchial chamber, h and i - respectively left and right dorsal views of reduced epibranchial space of crab with ripe gonads. For d to i anterior is to the top. For a, anterior is to the right. (cf. Plates 6.1 and 6.2).

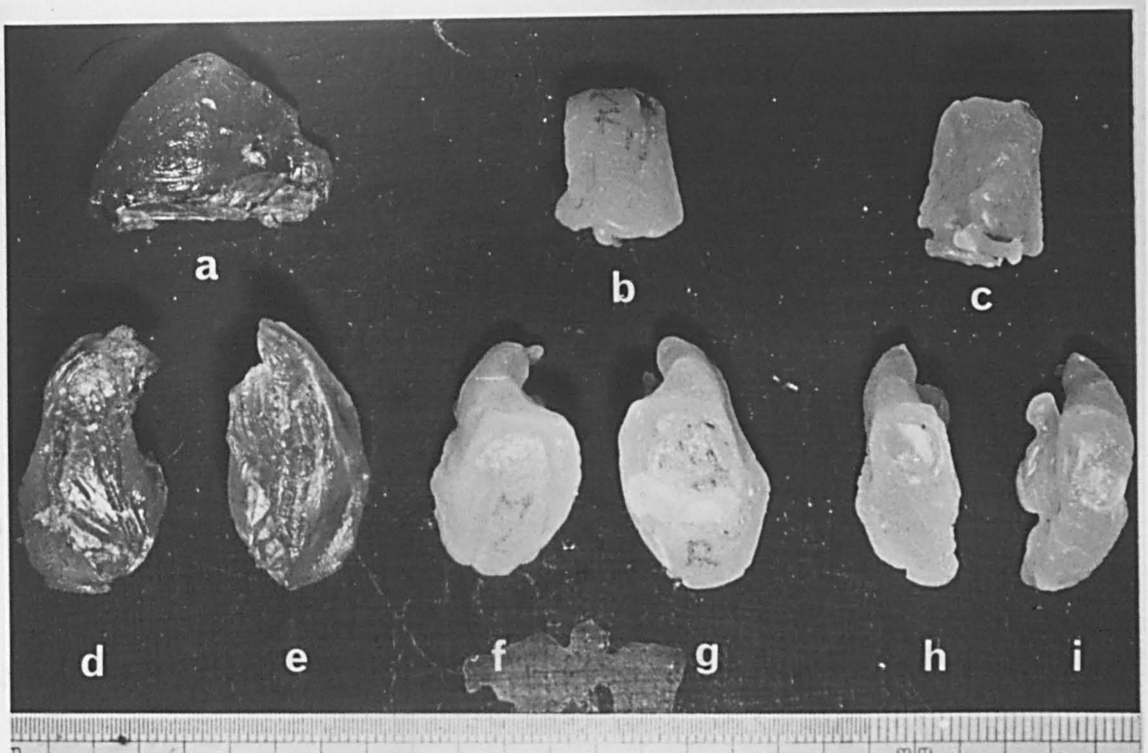
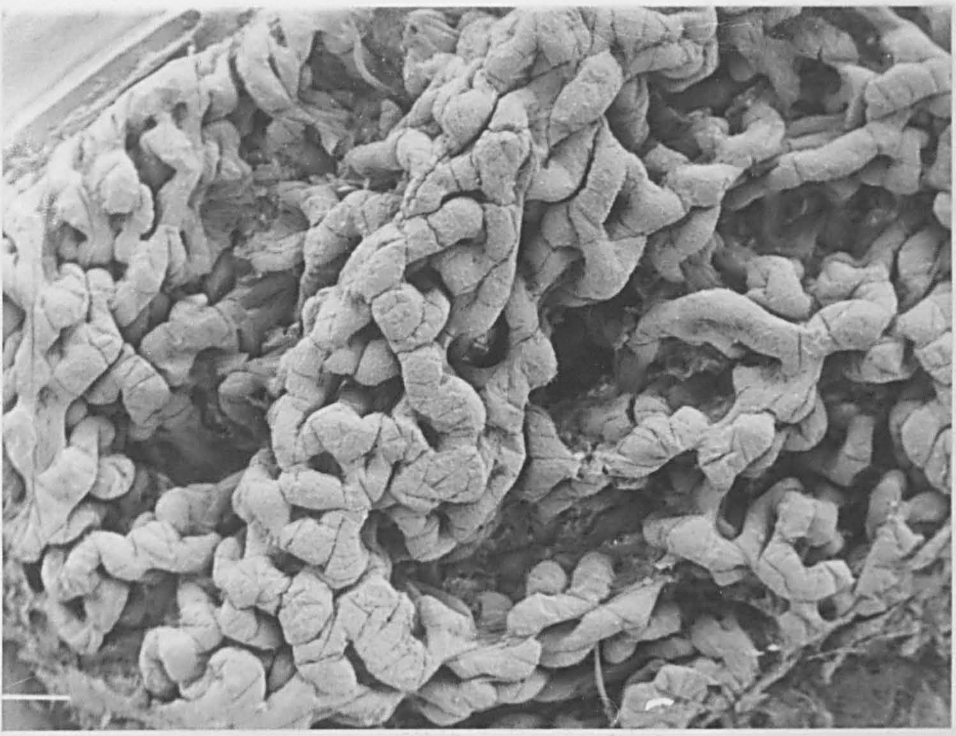

a
b
c
d
e
f
g
h
i
Made in England
Nº 34R

Plate 6.4. a-b) Detail of epibranchial wall of O. saratan (S.E.M.).

Scale bars = 1µm.

a



b

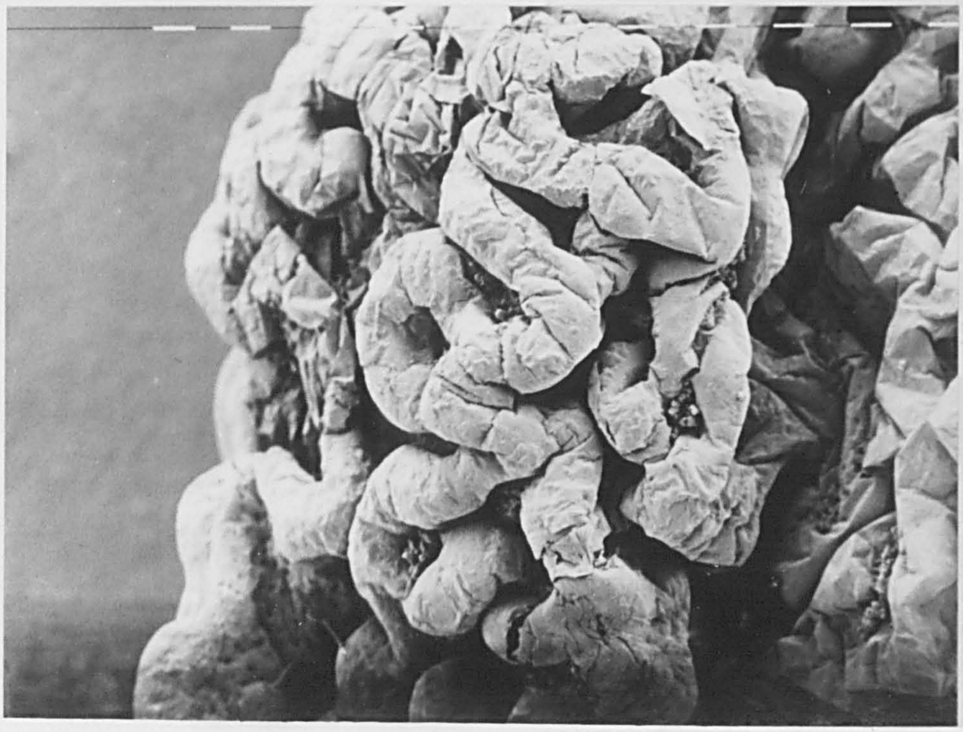
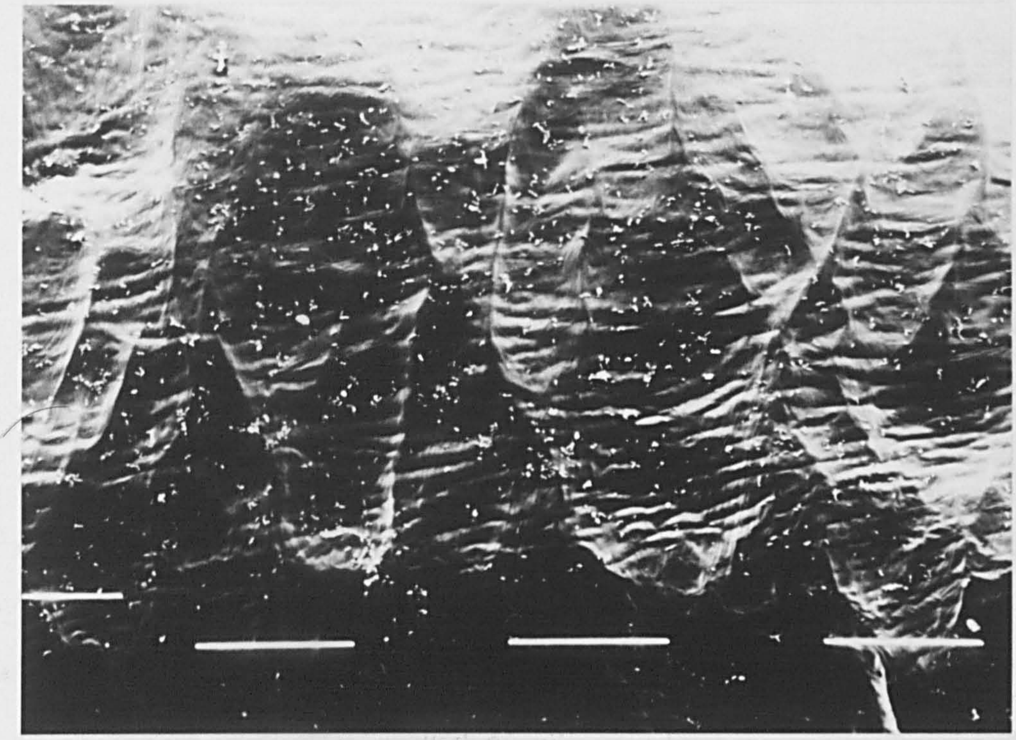


Plate 6.5. a) Branchiostegal shelf of O. saratan. Scale bars = 1μm.

b) Nematodes infecting epibranchial walls of O. saratan. The damaged branchial walls contrast with those shown in Plate 4. Scale bars = 1μm.

a



b

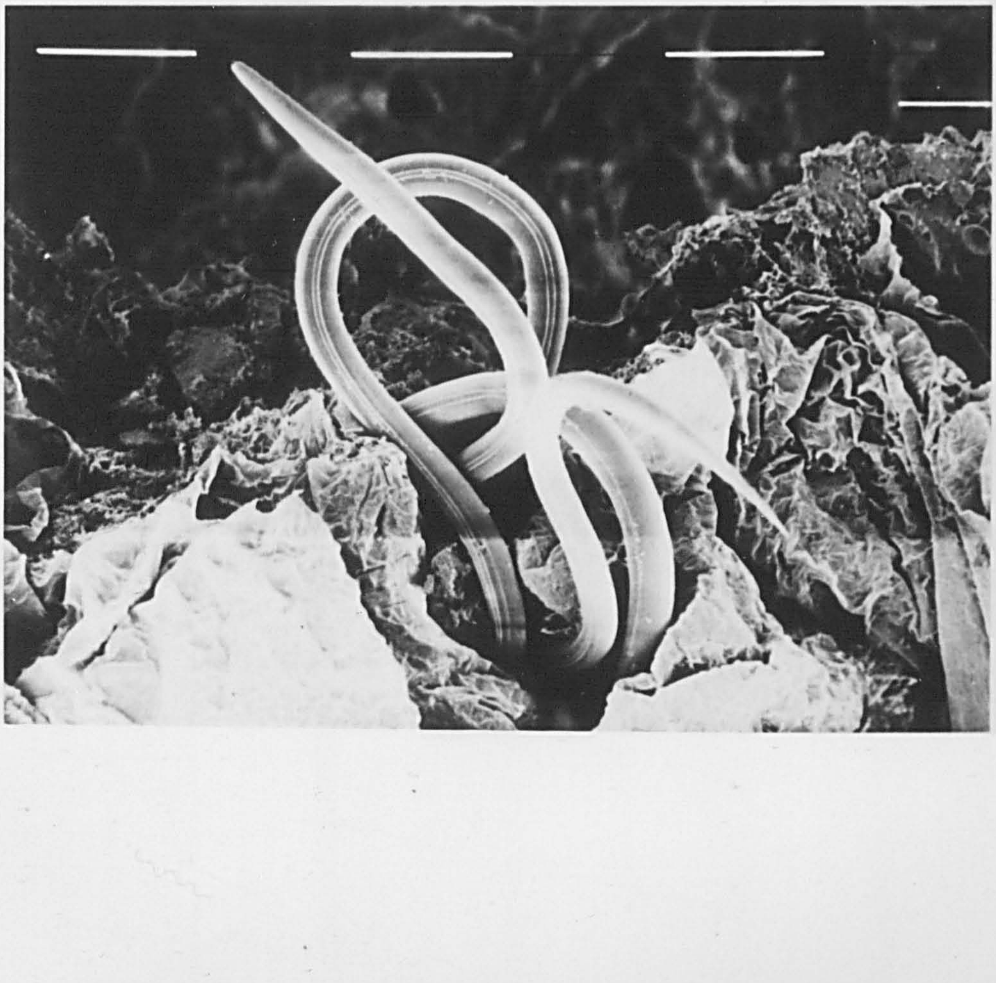


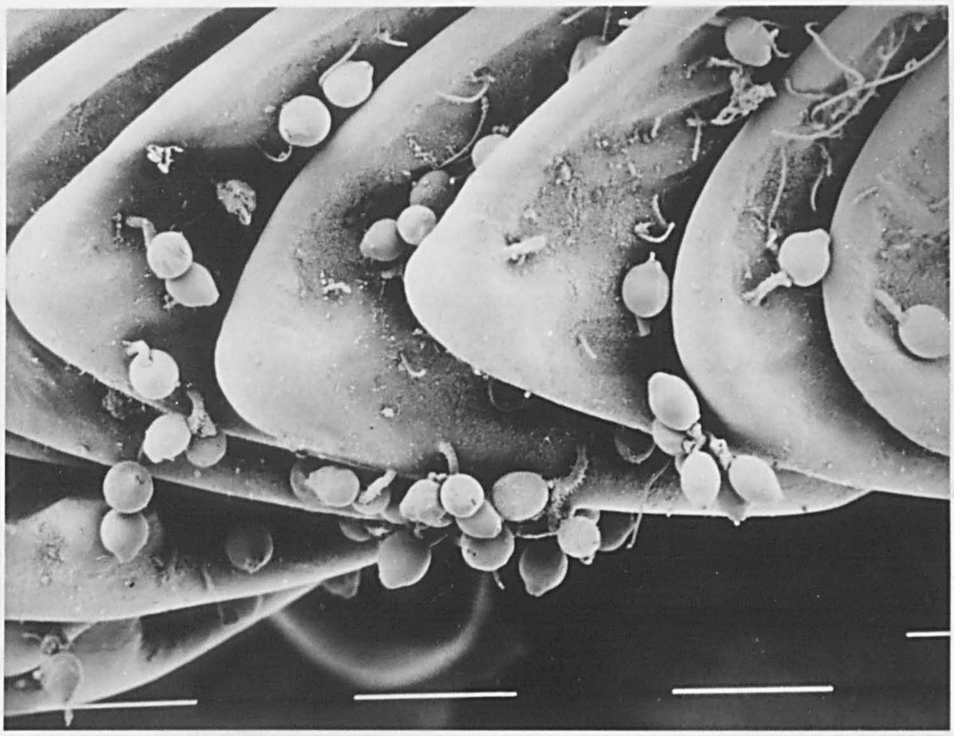
Plate 6.6. a) Gill lamellae of O. saratan colonised by an ecto-commensal ciliate, Epistylis sp. (S.E.M.).

Scale bars = 1µm.

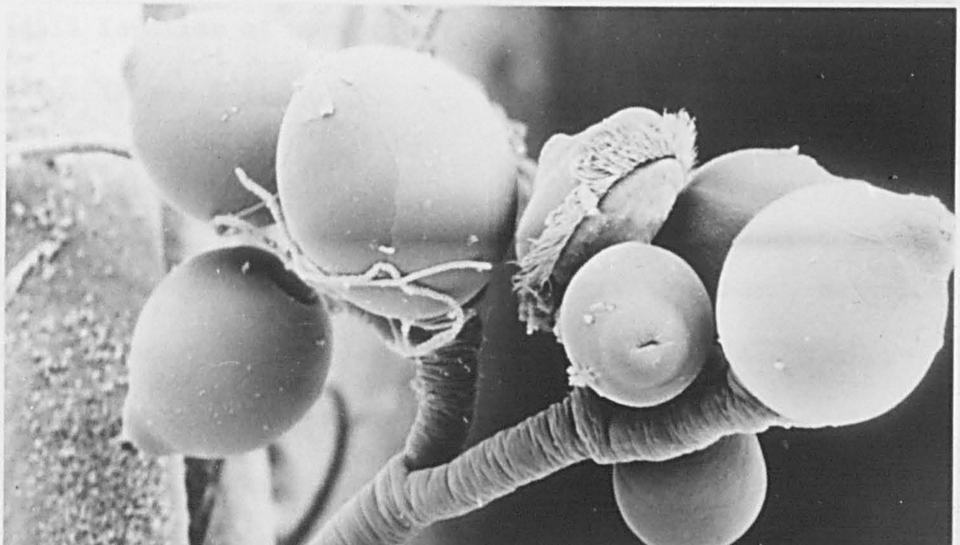
b) Detail of Epistylis sp. (S.E.M.).

a

b



a



b

The shape of the lung portion of the branchial chamber is seen in Plate 6.3 which shows paraffin wax and polyester resin casts of epibranchial chambers. The impression of the folded walls or 'respiratory tufts' (Pearse, 1929b) and also the impressions of the gill lamellae can be seen in the casts. The branchial walls are shown in far greater detail in Plate 6.4 which is a scanning electron micrograph of the branchial wall. Examination of the dorsal and lateral branchiostegite walls and the thoracic wall of the 'lung' all revealed the same folded structure. In contrast, the branchiostegal shelf was comparatively smooth (Plate 6.5a). The thoracic fold was also less corrugated than the thoracic wall.

Some SEM preparations showed damaged branchial walls and in these preparation nematodes were abundant in the branchial chamber walls (Plate 6.5b).

The gill lamellae of many crabs contained a commensal ciliate, Epistylis sp. (Plate 6.6).

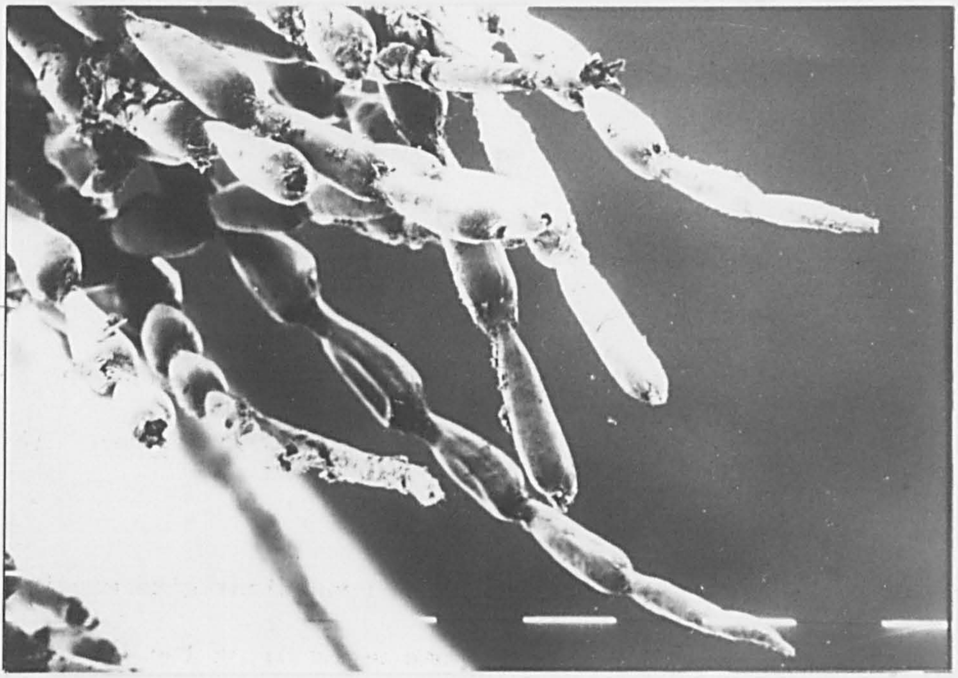
6.3.2.2. Branchial apertures

There are three openings into the branchial chamber. Anteriorly, the branchial chamber communicates with the prebranchial chamber which in turn opens to the exterior. At the base of each cheliped is the large 'Milne Edwards' opening which constitutes an anterior aperture to the branchial chamber and between the third and fourth pereiopods is a posterior aperture surrounded by setal tufts (Plate 6.2b) which is sometimes called Müller's opening (Little, 1983; Stebbing, 1893 summarises Fritz Müller's description). The hydrophilic nature of these tufts has been demonstrated for O. quadrata by Wolcott (1976, 1984) and those of O. saratan are shown in Plate 6.7a. These annulated setae are the main setal type in the leg tufts though

Plate 6.7. a) Detail of setae from the branchial inhalent aperture between pereiopods 3 and 4 of <u>O. saratan</u>. (S.E.M.) Scale bars = 1µm.

b) Setal detail from the branchiostegite margin. Note the delicate pappose setae along the inner margin and the rows of simple and cuspidate guard setae outside them. (S.E.M.) Scale bars = 1µm.

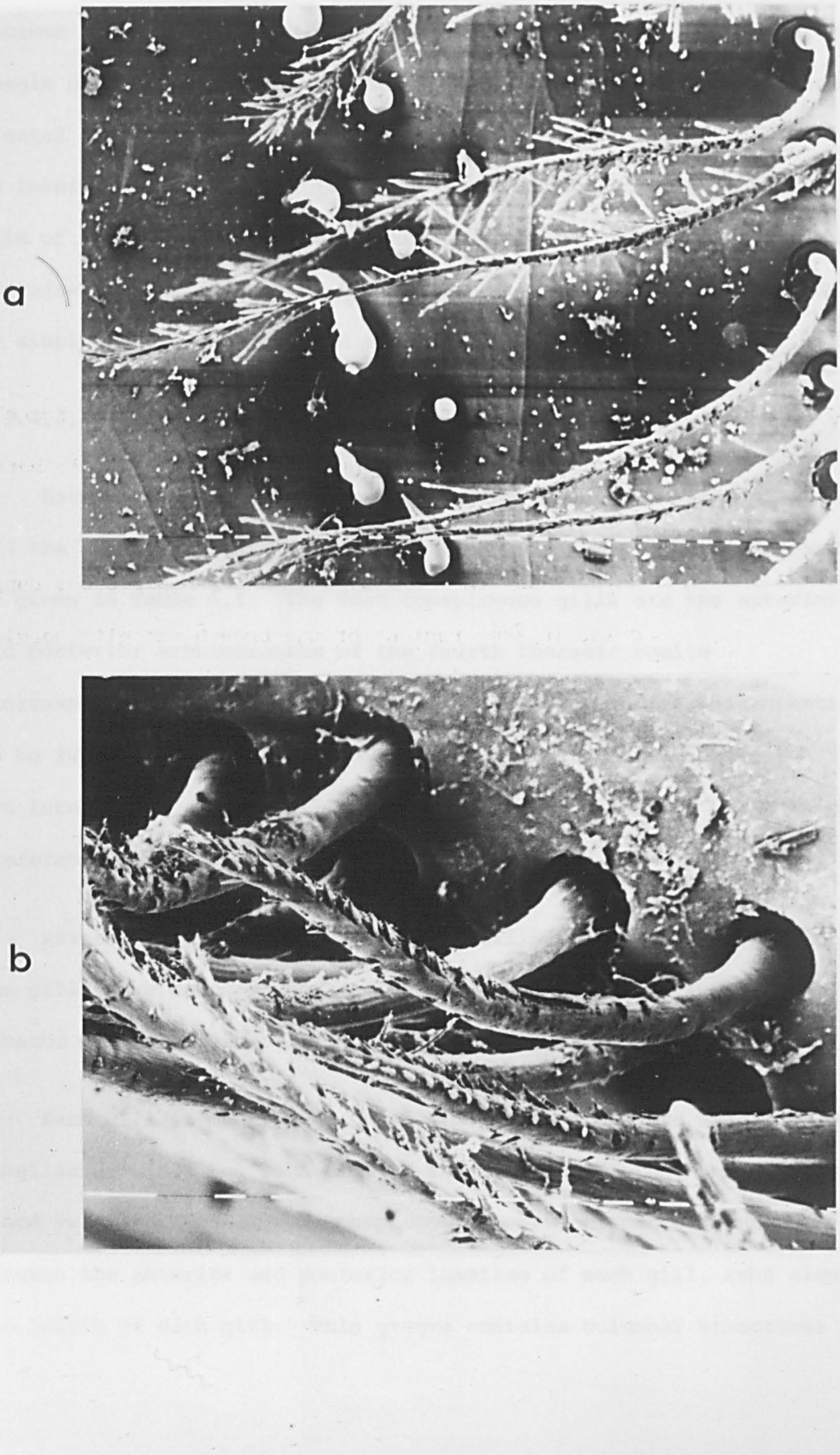
a



b

Plate 6.8. a) Detail of the pappose and guard setae of the branchiostegite margin of <u>O. saratan</u>. (S.E.M.) Scale bars = 1μm.

b) Details of denticulate setae which replace the pappose setae in some regions of the branchiostegite margin. (S.E.M.) Scale bars = 1μm.


a
b

as in O. quadrata (Wolcott, 1984) some spined and plumose setae also occur. The bases of the third and fourth pereiopods are normally held in such a position that the setal tufts are closely apposed to enclose a channel leading into the branchial chamber. Elsewhere the margin of the branchiostegite lies closely against the body and has a setal fringe bordering the epimera of the legs (Plate 6.7b). This is interpreted by Wolcott (1984) as a gasket, trapping a capillary film of water and sealing the branchial chamber. The setal fringe contains both pappose setae and denticulate setae and is protected by simple and cuspidate guard setae (Plate 6.8).

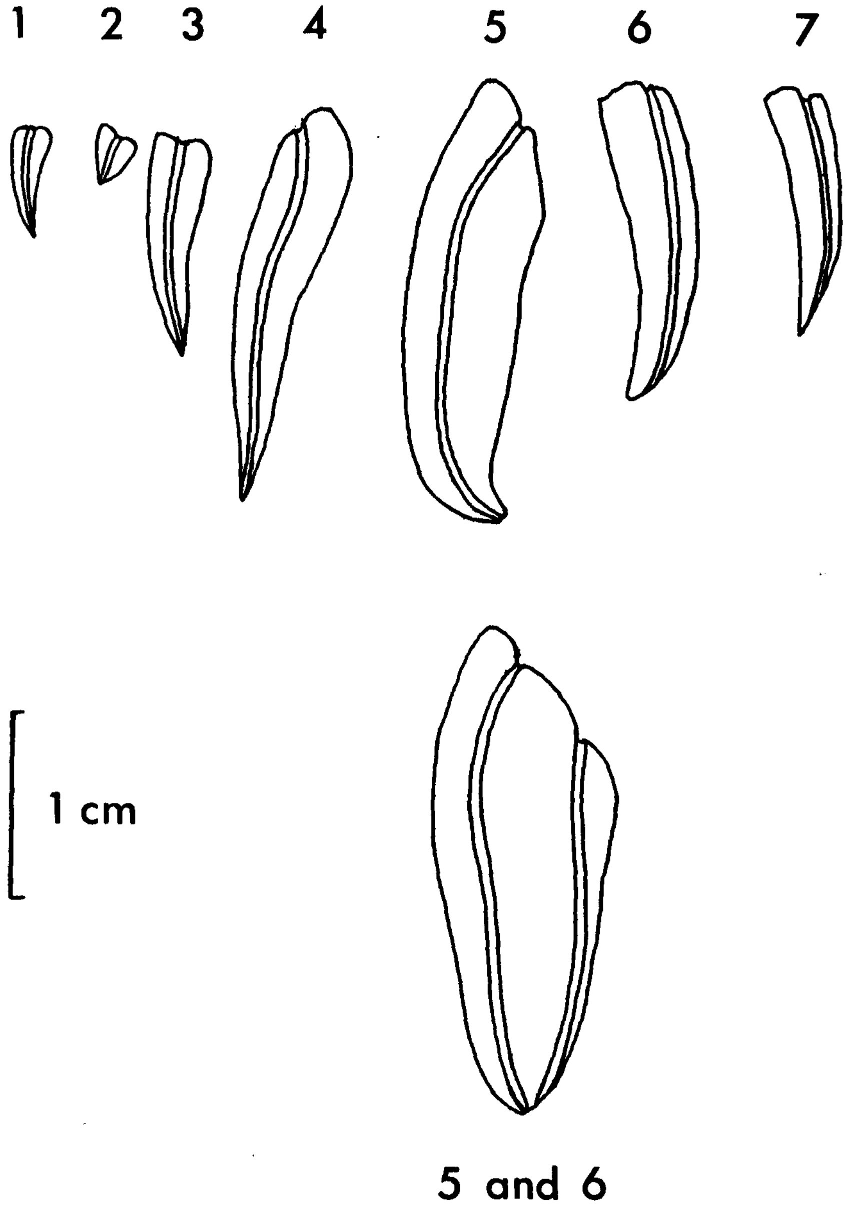
6.3.2.3. Gill morphology

Each branchial chamber contains seven phyllobranchiate gills and the three elongate epipods of the maxillipeds. The gill formula is given in Table 6.1. The most conspicuous gills are the anterior and posterior arthrobranchs of the fourth thoracic somite (corresponding to cheliped). These gills appear on first examination to be fused along their length but they are not, their lamellae are interleaved and the gills can be separated with care using forceps, preferably while the gills are immersed.

Plates 6.1 and 6.2 illustrate the gills in situ and in Fig. 6.1 the gills have been removed and the anterior and posterior arthrobranchs of the 4th thoracic somite have been separated.

Each gill is of typical phyllobranchiate structure with the lamellae set in a row each side of the central afferent and efferent blood vessels. Dorsally a conspicuous groove, formed by a space between the anterior and posterior lamellae of each gill, runs along the length of each gill. This groove contains columnar structures in

Fig. 6.1. Outlines of the gills of O. saratan. Gills 5 and 6 appear to be a single unit (lower figure) but can be separated (top).


1
2
3
4
5
6
7
1 cm
5 and 6

gills 3, 4 and 5 (see Plate 6.9). The corresponding lamellae each side of the gill are often unequal in area (Table 6.2).

Table 6.1. Gill formula of Ocypode saratan

	Thoracic somites and associated appendages							
	1	2	3	4	5	6	7	
	(maxillipeds)			(cheliped)	(pereiopods)			Total
Gill type								
podobranch	-	1	1	-	-	-	-	2
anterior arthrobranch	-	-	1	1	-	-	-	2
posterior arthrobranch	-	-	1	1	-	-	-	2
pleurobranch	-	-	-	-	1	-	-	1
epipod	(1)	(1)	(1)					(3)
Total	(1)	1(1)	3(1)	2	1	-	-	7+(3)

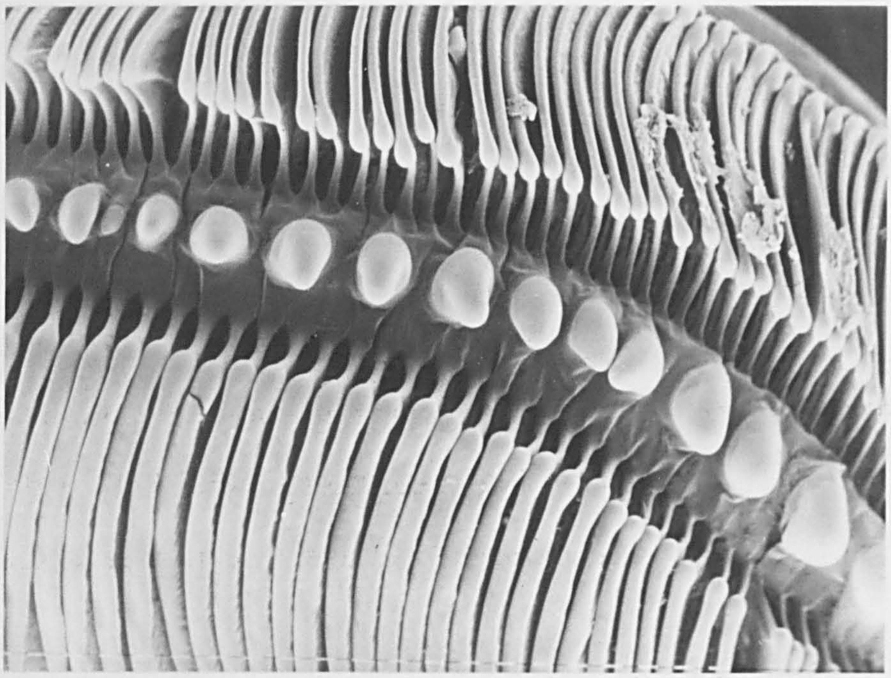
Gill areas are examined in section 6.3.3 but it suffices here to note from Table 6.2 that the difference in area of opposing lamellae is least in the podobranch of the second thoracic somite (gill 1) and greatest in the posterior arthrobranch of the 4th thoracic somite (gill 6) and the podobranch of the third thoracic somite (gill 2). It can be seen that the shape of the lamellae either side of the mid-line of the gill may be constant along the length of the gill as in the posterior arthrobranch of the 3rd somite (gill 4) and the pleurobranch of the 5th thoracic somite (gill 7) or may vary along the length of the gill, eg. the anterior arthrobranch of the third thoracic somite (gill 3).

Gills 5 and 6 have interfoliated lamellae which has created the false impression that they are fused together. This feature is

Plate 6.9. a) Columnar structures in the dorsal interlamellar space of gill 3 of O. saratan. (S.E.M.) Scale bars = 1µm.

b) Same feature in gill 5. Scale bars = 1µm.

Note the reinforced lamellar margins, with their nodular dilations which serve to keep the lamellae apart.

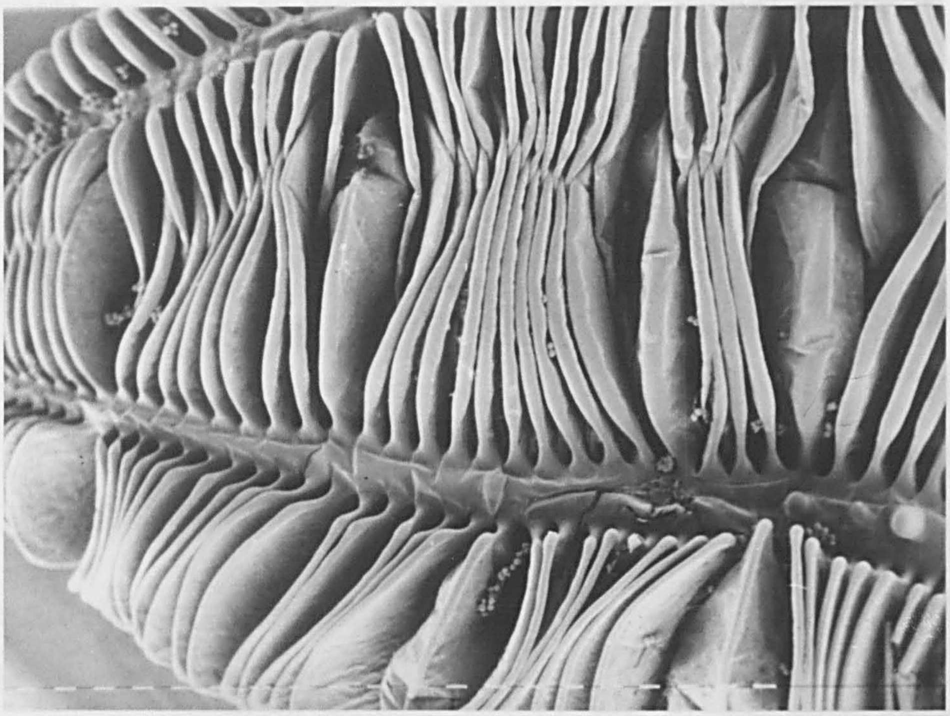


a

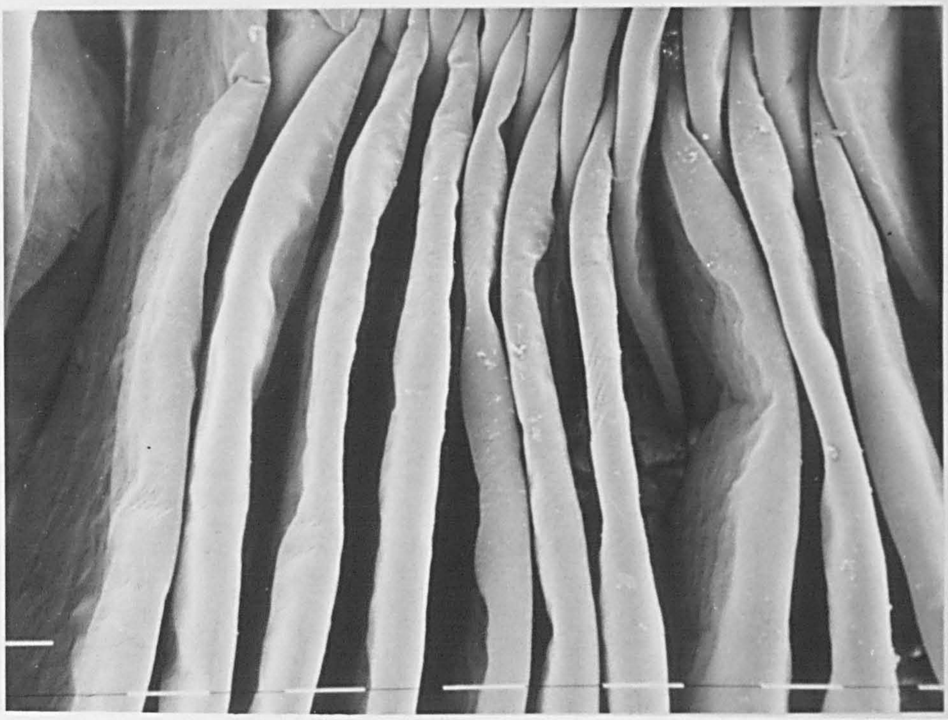
b

Plate 6.10. a–b) Interfoliated lamellae of gills 5 and 6, making them appear to be a single structure, the 'great gill'. Scale bars = 1µm.

a



b



illustrated in Plate 6.10.

Lamellar structure is also illustrated in Plate 6.11 where the interfoliated gills 5 and 6 have been sectioned. The robust lamellar walls and the lamellar haemolymph space crossed by the pillar cells can be clearly seen.

Fig. 6.2 indicates the total number of lamellae $.g^{-1}$ wet body weight plotted against wet body weight.

Table 6.2. Relative areas of gill lamellae (mm^2)

Gill No.	Gill length	Area of inner lamellae			Area of outer lamellae			Ratio		
Site		1	2	3	1	2	3	$^{1}/1$	$^{2}/2$	$^{3}/3$
1	3	-	0.33	-	-	0.36	-	-	0.92	-
2	2	-	0.07	-	-	0.43	-	-	0.16	-
3	7.5	0.2	0.7	1.1	0.6	1.1	1.4	0.4	0.6	0.8
4	14	0.5	1.8	2.0	0.6	2.2	2.6	0.8	0.8	0.8
5	14.5	1.6	3.6	3.2	2.1	4.8	6.6	0.8	0.8	0.5
6	12	1.1	1.8	1.9	2.4	6.0	6.1	0.5	0.3	0.3
7	8	0.5	1.0	1.2	0.7	1.1	1.3	0.7	0.9	0.9

carapace width 2.68cm
wet weight 11.6g. Male

Site 1 is near tip of gill, Site 2 is in the middle and Site 3 is near the base of the gill.

Plate 6.11. Longitudinal section through the 'great gill' (gills 5 and 6) of _O. saratan_. The interfoliated lamellae of the two gills can clearly be seen. The larger lamellae are those of gill 5.

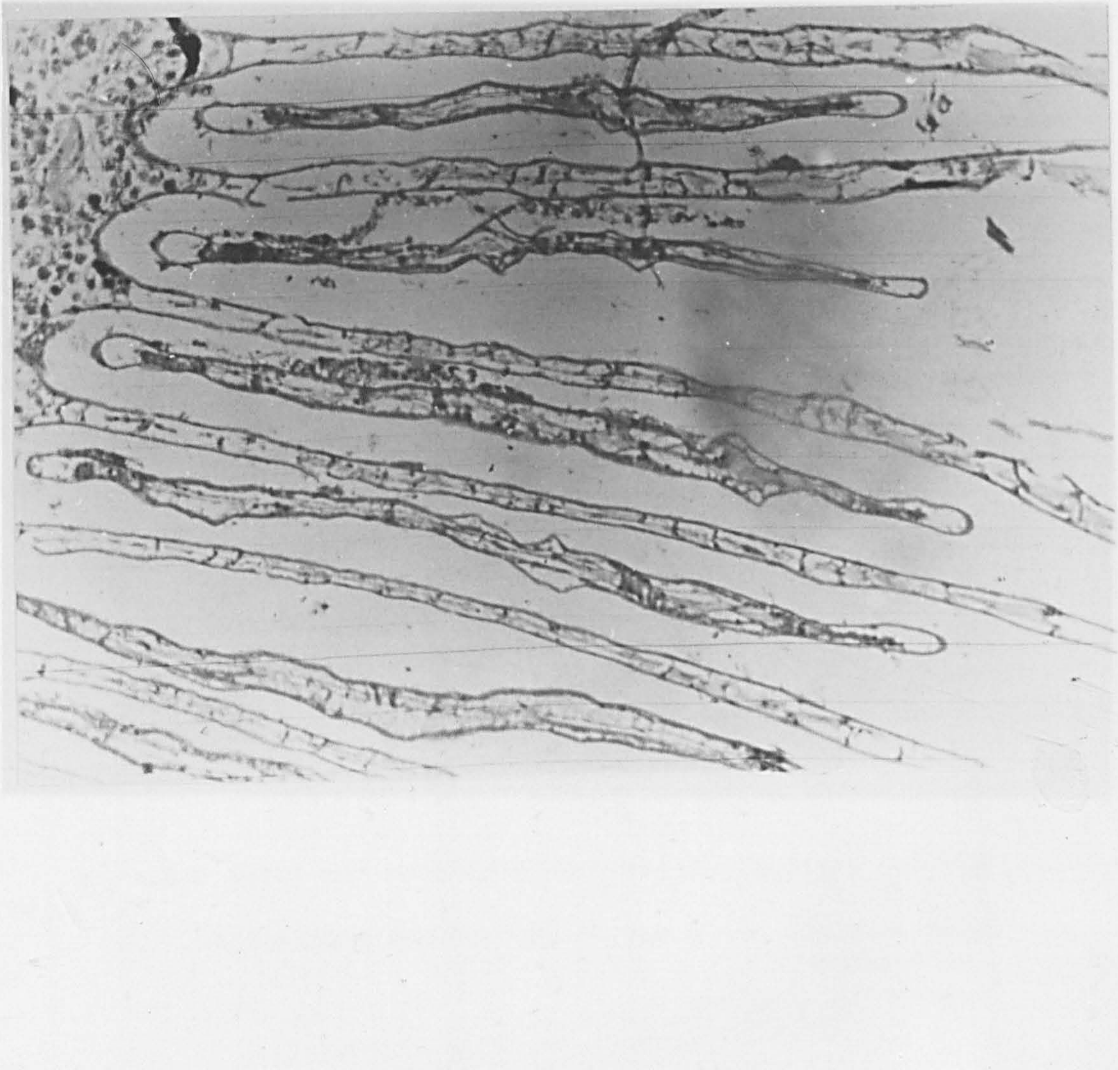
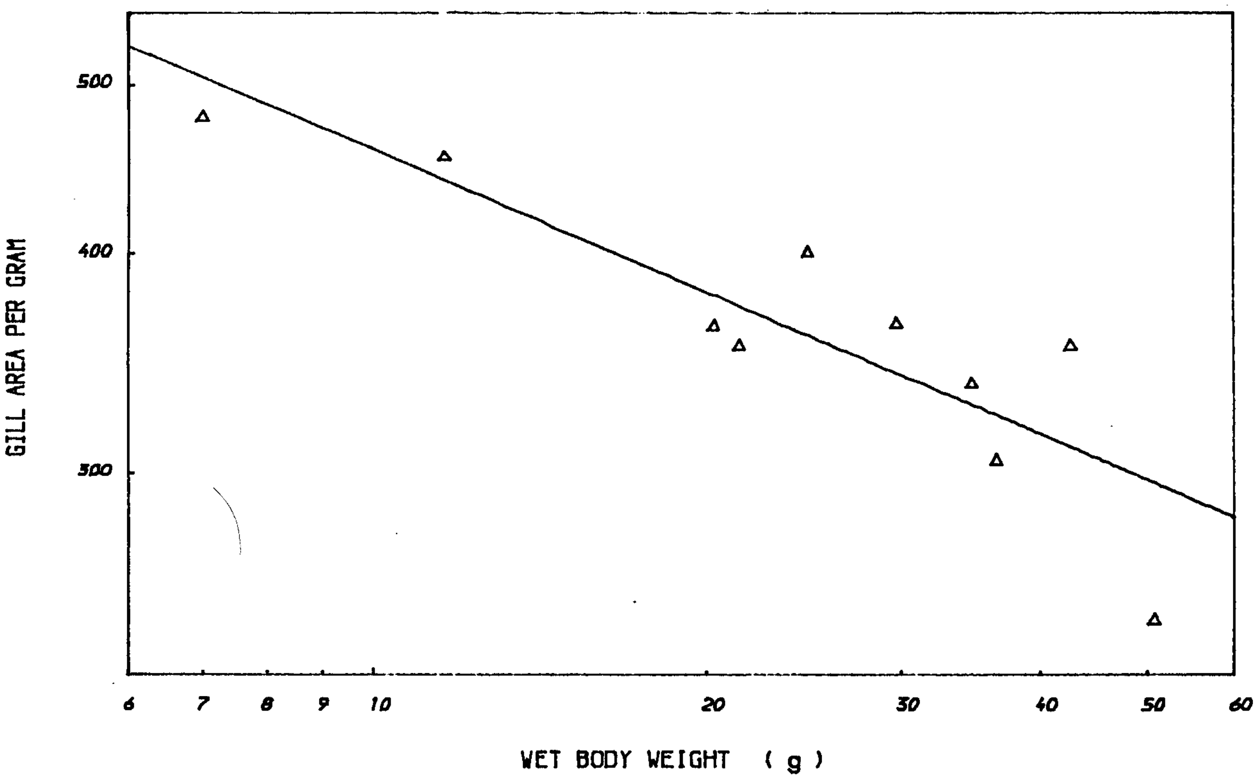


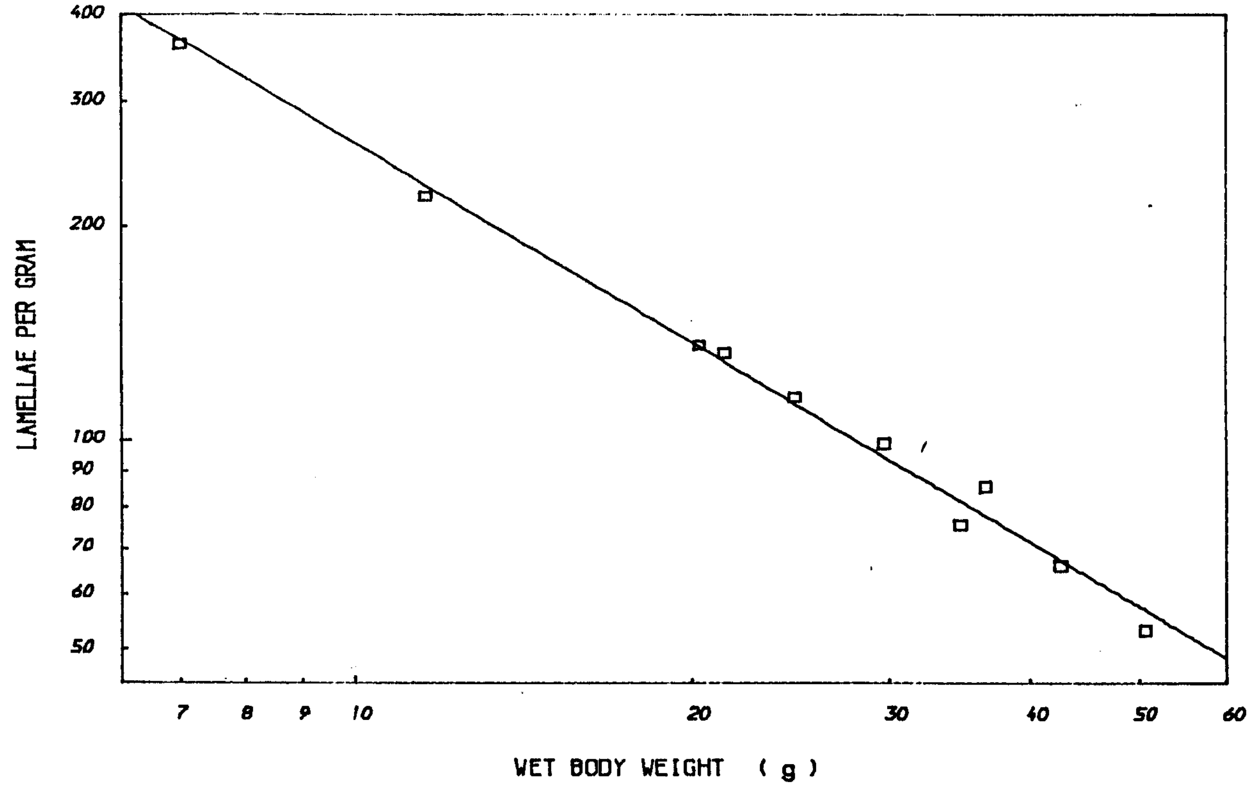
Fig. 6.3. Ocypode saratan: relationship between total gill area ($mm^2.g^{-1}$) and wet body weight. The regression equation is

log (gill area.g^{-1}) = 2.931 - 0.270 log (wet weight), r = -0.869, n = 10.

Fig. 6.2. Ocypode saratan: relationship between the total number of gill lamellae per g wet weight and wet body weight. The regression equation is

log (lamellae.g^{-1}) = 3.362 - 0.942 log (wet weight), r = -0.996, n = 10.


GILL AREA PER GRAM
500
400
300
6
7
8
9
10
20
30
40
50
60
WET BODY WEIGHT (g)


LAMELLAE PER GRAM
400
300
200
100
90
80
70
60
50
7
8
9
10
20
30
40
50
60
WET BODY WEIGHT (g)

6.3.3. Gill area

From the results given in Figs 6.3 and 6.4 it is clear that smaller crabs have a comparatively larger gill area $.g^{-1}$ body weight and a larger number of gill lamellae $.g^{-1}$ body weight than larger crabs. For example, a crab of 2.3cm carapace width and 7g weight had a gill area of $479.7mm^2.g^{-1}$ and 363.0 individual lamellae $.g^{-1}$ whereas a crab of 4.4cm carapace width and 50.7g weight had a gill area of $247.6mm^2.g^{-1}$ and 53.3 individual lamellae $.g^{-1}$.

Fig. 6.4 shows surface area of an average lamella for each gill in a range of crab sizes. When regression lines were fitted to the data and these were compared by covariance analysis the slopes were not significantly different ($P > 0.05$) but the intercepts (a) showed pronounced significant differences ($P < 0.001$).

The regression equations for each gill are given in the legend.

6.3.4. Branchial volume

Figs 6.5 and 6.6 present data on branchial volume using two methods of assessment, one using water to fill the branchial spaces and the other using paraffin wax. It should be remembered that the crabs used for the wax method lacked pereiopods but these were present in the case of the crabs used for the water method. Firstly, the wax method compares directly with the data of Diaz and Rodriguez (1977) for O. quadrata and the O. saratan results are very similar. Secondly, the branchial volume to weight relationships appear very similar when the wax and water methods used have been compared, despite the lack of limbs in the former case. This is almost certainly because the water penetrates all the branchial spaces including interlamellar spaces whereas the wax does not penetrate so well.

Fig. 6.4. Surface area of 'average lamella' (see text) of each gill of _O. saratan_. Curves were computer fitted following normal back-transformation of the regressions. The regression equations are:-

Gill 1. $\log y = -1.174 + 0.774 \log x$, $r = 0.892$, $n = 10$

Gill 2. $\log y = -1.187 + 0.677 \log x$, $r = 0.663$, $n = 10$

Gill 3. $\log y = -1.039 + 0.868 \log x$, $r = 0.913$, $n = 10$

Gill 4. $\log y = -0.485 + 0.633 \log x$, $r = 0.944$, $n = 10$

Gill 5. $\log y = -0.169 + 0.657 \log x$, $r = 0.935$, $n = 10$

Gill 6. $\log y = -0.159 + 0.602 \log x$, $r = 0.966$, $n = 10$

Gill 7. $\log y = -0.770 + 0.667 \log x$, $r = 0.931$, $n = 10$

Where y = surface area of lamella and x = wet body weight.

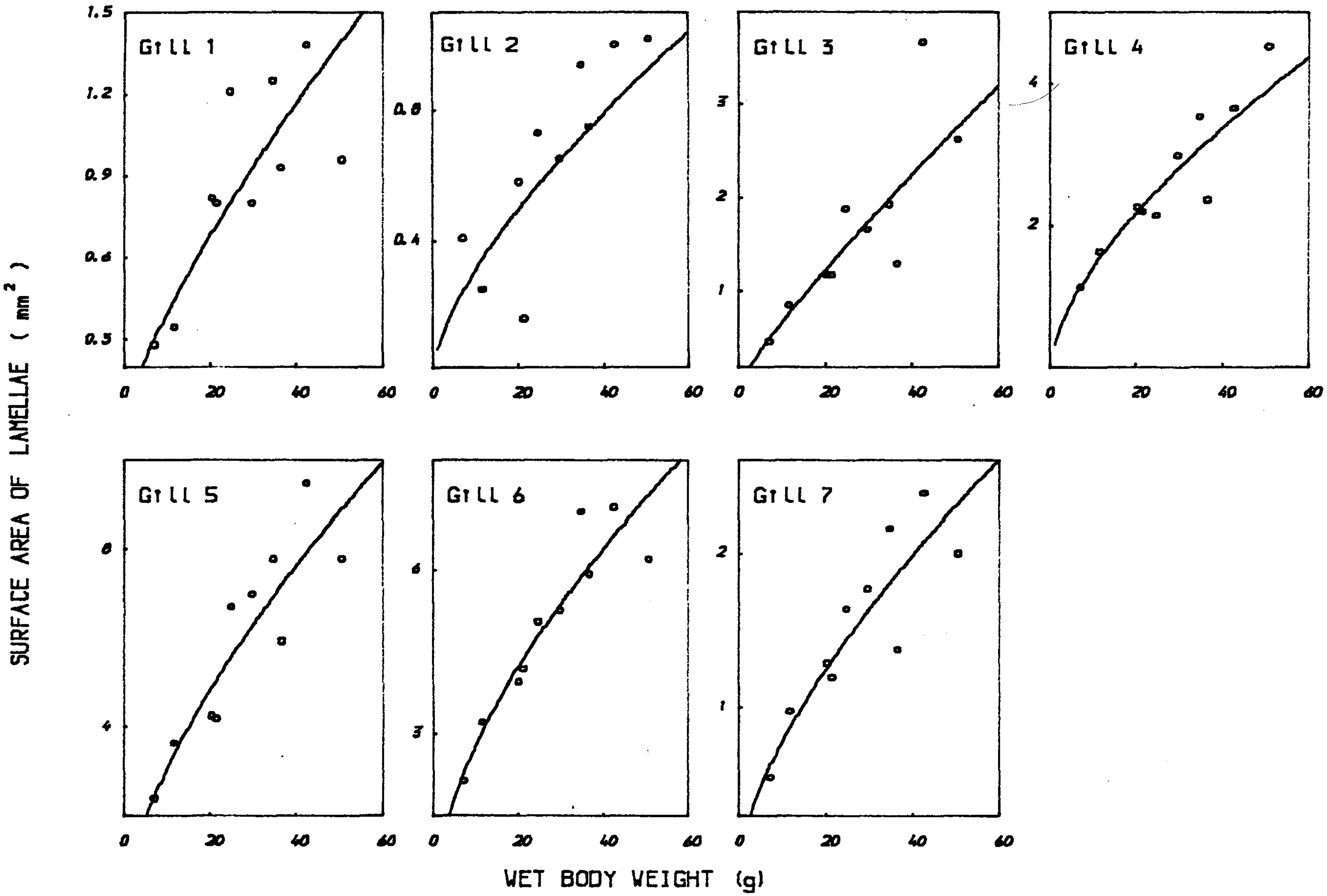

Gill 1
1.5
1.2
0.9
0.6
0.3
Gill 2
0.8
0.4
Gill 3
3
2
1
Gill 4
4
2
Gill 5
8
4
Gill 6
6
3
Gill 7
2
1
0
20
40
60
SURFACE AREA OF LAMELLAE (mm^2)
WET BODY WEIGHT (g)

Fig. 6.5. *Ocypode saratan*: relationship between mean branchial chamber volume and body weight (complete crabs) using the water method (see text). The regression equation is

log (mean branchial volume) = $-0.969 + 0.999$ log (wet weight), $r = 0.999$, $n = 44$.

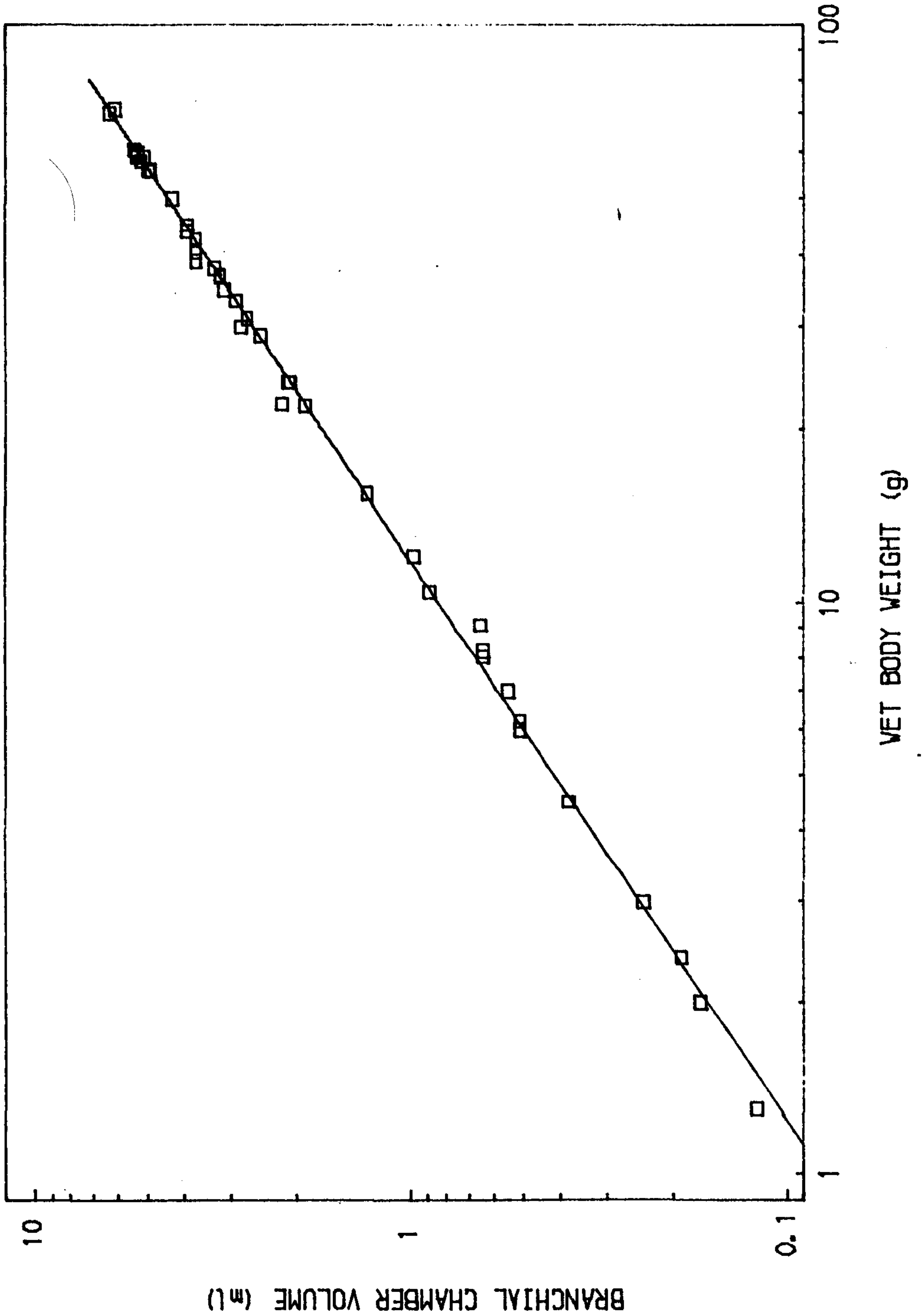
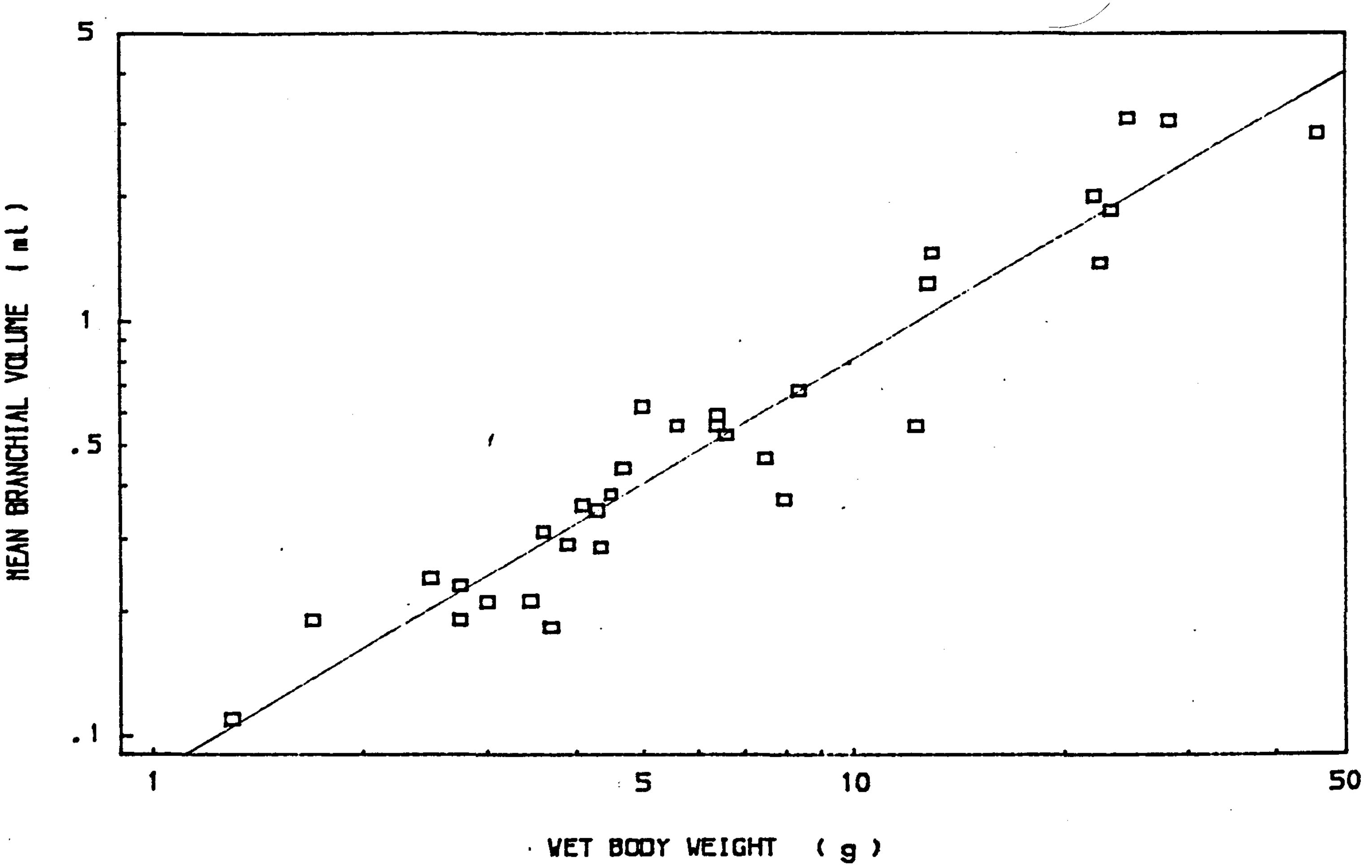

BRANCHIAL CHAMBER VOLUME (ml)
10
1
0.1
WET BODY WEIGHT (g)
1
10
100

Fig. 6.6. Ocypode saratan: relationship between mean branchial chamber volume and body weight (without legs) using the paraffin wax method (see text). The regression equation is

log (mean branchial volume) = - 1.094 + 0.999 log (wet weight), $r = 0.957$, $n = 32$.


5
1
.5
.1
1
5
10
50
MEAN BRANCHIAL VOLUME (ml)
WET BODY WEIGHT (g)

Therefore the wax gives a good indication of the volume of the epibranchial lung but total branchial volume is best assessed by the water method.

6.3.5. Interspecific comparison

Both the ocypodid Dotilla sulcata and the grapsid Metopograpsus messor had sclerotised gills but neither had 'lungs' or folded branchial walls. Both had commensal Epistylis sp(p) in their gill chambers. The water.uptake setae of D. sulcata are illustrated in Plate 6.12 and also the grooves on the carapace along which water is circulated from the anterior exhalent apertures of the branchial chambers for reoxygenation (and for thermoregulation) before re-entering the branchial chambers via the inhalent apertures at the bases of the 4th and 5th pereiopods (Fishelson, 1983). During uptake, water apparently passes into the space between the abdomen and sternum through openings formed by the shape of the 5th abdominal segment and runs along the edges of the abdomen to enter each branchial chamber via a channel beneath the first abdominal segment (Hartnoll, 1973). This mechanism is very different from that of O. saratan (see Chapter 7).

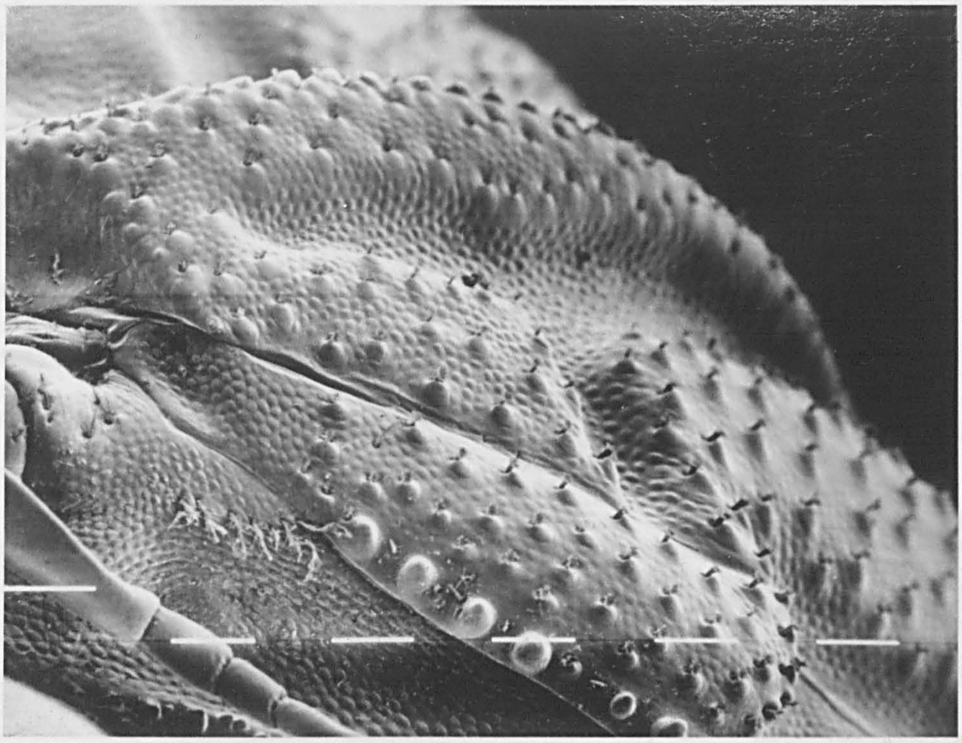
The disposition of setae on the anteroventral branchiostegite surfaces and grooves around the mouth suggest that M. messor may also recirculate branchial water by an analogous though slightly different mechanism to Dotilla as described for other grapsids (Alexander and Ewer, 1969; Hawkins and Jones, 1982).

6.4. Discussion

The branchial region of O. saratan is divided into an epibranchial 'lung' above each branchial chamber containing the gills. On each side, there are seven in number with gills 5 and 6 having their adjacent

Plate 6.12. a) Water circulation grooves in the carapace of *Dotilla sulcata* (S.E.M.). Scale bars = 1μm.

b) Abdominal water uptake setae of *D. sulcata*. (S.E.M.) Scale bars = 1μm.



a

b

lamellae interfoliated giving the appearance of a single structure. The gills are partly separated from the epibranchial 'lung' by the branchiostegal shelf. The orientation of the gills is such that the branchiostegal shelf lies immediately above the dorsal surfaces of gills 3, 4 and 5 and could potentially rest on their lamellae. It could be that the robust protuberances on the gill axis of each of these gills serves to prevent the branchiostegal shelf from collapsing their lamellae. The lamellae are in any case strengthened around their margins and have small nodular protuberances that serve to keep the lamellae apart. Similar nodules have been noted in *O. cordimana* by Greenaway and Farrelly (1984), in *Gecarcinus lateralis* by Taylor and Davies (1981) and in some other species (von Raben, 1934). Many authors have remarked on the strengthening of the gill lamellae of semiterrestrial and terrestrial crabs (see Introduction).

The orientation of the branchiostegal shelf is such that the gills are not completely covered by it but are in contact with the epibranchial space along a long slit-like aperture. Possibly the shelf and a similar but smaller extention on the inner side of each branchial chamber prevent spillage of water from the gills into the lungs when the crab is in the steep sections of its burrow. Certainly it distinctly separates the upper and lower branchial regions and increases the surface area for gaseous exchange (it contains branches of the afferent and efferent lung vasculature, Greenaway and Farrelly, 1984).

The structure of the epibranchial chamber suggests that the thoracic fold does more than increase area for gaseous exchange as suggested by Greenaway and Farrelly (1984) for *O. cordimana*. Its orientation is such that circulating air will be deflected backwards into the epibranchial chamber rather than short-circuit it by moving directly between the prebranchial apertures and the Milne-Edwards openings.

The scaphognathite is responsible for the circulation of air within the epibranchial lung and for drawing water into the branchial chamber around the gills (see Chapter 7). Its fine setae will form an efficient seal in the prebranchial chamber and the setae around the branchiostegite margin have been suggested by Wolcott (1984) to act as a gasket when wet thus sealing the branchial spaces. This enables the scaphognathite to generate considerable negative pressures when drawing water into its branchial chamber from the hydrophilic setal tufts between pereiopods 3 and 4. The structure of these tufts and the setation of the branchiostegite margin was very similar to that described by Wolcott (1984) for O. quadrata. According to Wolcott (1984) the scaphognathite overcomes the capillary attraction of the setal tufts and draws water into the branchial chamber. More of this is discussed in Chapter 7.

The walls of the epibranchial lung are heavily vascularised. and the surface blood vessels can clearly be seen corrugating the walls of the chamber. These corrugations are produced into a series of ridges which serve to increase surface area. Carli (1969) noted these ridges and they presumably correspond to the respiratory tufts of Pearse (1929b). Greenaway and Farrelly (1984) indicate that the ridges are formed by the major afferent and efferent blood vessels and lacunar beds of fine branches of the afferent and efferent vessels lie between them. Details of the circulatory system of O. cordimana are given in their paper.

The orientation of the crab in its life position is such that the branchiostegal shelf will be horizontal. Water will not drain from the branchial chamber unless the leg valve between pereiopods 3 and 4 is opened.

The epibranchial chamber of several crabs were infested with nematodes. The capillary lining was in these cases considerably disrupted and respiratory function was obviously impaired.

In contrast to these parasites, Epistylis sp. (generic identification confirmed by Prof. K. Vickerman) that were seen on the gill lamellae appear to be ectocommensals (Sprague and Couch, 1971). These ciliates are reported from the gills of crayfish and shrimps and Pearse (1932) found them on the gills of the terrestrial Coenobita clypeatus and two species of littoral grapsids. I have also seen them on the gill lamellae of the crabs Dotilla sulcata, Metopograpsus messor and Uca inversa. The microclimatic requirements of these cilates would form an interesting subject for investigation.

Gill area data are available for two other Ocypode species as is seen in the following table.

Table 6.3. Gill areas of Ocypode spp.

species	live weight (g)	gill area (mm²)	gill area (mm².g^{-1})	Authority
O. quadrata	min. 11.2		max. 446	
	mean 45.8	14,890*	mean 325	Gray (1957)
	max. 77.3		min. 197	*Hughes (1983)
O. platytarsis	0.5	150	300	
	1.0	300	300	
	2.0	600	300	Veerannan (1974)
	3.0	900	300	
	5.0	1,400	280	
	10.0	2,200	220	
O. saratan	11.6	5,277	454	present work
	42.6	15,123	355	

Both these sources of information require some explanation. Gray (1957) from 31 animals presented maximum, mean and minimum values for gill areas.g^{-1}. Since smaller crabs have a higher gill area.g^{-1} then I have arranged the data as above but the minimum and maximum values may not directly cross compare since Gray did not give a full table of data.

Veerannan (1974) presents tabulated data which only coincide with 2 of the 5 points on his graph and so are probably estimates based on his graphical trends. From his graph it appears that the crabs he actually looked at were approximately 0.5, 1.4, 4.6, 7.2 and 10g wet weight. This would account for the rounding of the figures in the above table.

I have included two examples of O. saratan at sizes which compare with Gray's information. My data are in agreement with those of Gray but differ from those of Veerannan who used a less accurate technique (only measured central lamellae of each gill). Even so, Veerannan's data give very low area values for crabs of equivalent size, twice the value would seem to be more appropriate though unlike O. quadrata the species does not have a similar size range to O. saratan. Hughes (1983), reworking Gray's original data, gives for an O. quadrata of 41.35g, a total gill area of 12,219mm^2 which agrees reasonably well with the data for O. saratan.

The number of lamellae in O. saratan also agrees closely with the data of Gray (1957) and as reworked by Hughes (1983). Gray indicated a mean number of 62 lamellae.g^{-1} (corrected from his platelet data), his mean body weight for O. quadrata was 45.8g. My data for a crab of 42.6g gives a mean lamella number of 66 lamellae.g^{-1}. The total lamella number for this crab was 2,800, comparing with Gray's mean value of 2,840. Hughes (1983), from Gray's original data gives for a crab of 41.35g a total lamella number of 2,324.

Hawkins and Jones (1982) compared information on the gill areas of 21 species of brachyuran crabs, drawing on information in the literature (mostly Gray, 1957) together with their own work on the grapsid Helice crassa and the ocypodid Macrophthalmus hirtipes. Their table clearly shows that the gill area is greatest in fully aquatic crabs, is less in intertidal species and is smallest in the semiterrestrial O. quadrata and O. platytarsis. These authors also examined the surface area of an average lamella for each gill of H. crassa and M. hirtipes in the same manner as I have done for O. saratan. There are, however, no similar data for any other Ocypode species with which the O. saratan data can be compared.

Experiments on branchial volume initially followed the technique of Diaz and Rodriguez (1977) so that mean branchial volume was plotted against wet body weight of a crab without legs. Diaz and Rodriguez (1977) adopted this technique since some of their crabs lacked some limbs and they required standardization. I followed their technique so I could exactly compare O. saratan with their O. quadrata.

Diaz and Rodriguez present a regression equation in the form of $y = ax^b$, where y = mean branchial chamber volume and x = body weight (g). Their equation is $y = 0.1062\ x^{0.862}$

My equation for O. saratan is $y = 0.081\ x^{0.999}$

This does not represent a very great difference in either the intercept or the slope and for a crab of around 10g the values would be the same.

The wax method compared above fills the epibranchial chambers but does not penetrate much beyond them. The water method that I also used penetrates all the branchial spaces and therefore gives total branchial volume. In this case whole crabs were used but the data were plotted for mean branchial volume as previously.

When the data for volume based on wax injection are compared with the data obtained by water injection of the branchial spaces, then the regression relationships are almost identical. Using the same form as previously $y = 0.0798\ x^{1.026}$ for the water method. The explanation for this is as follows. If body weight were to be computed for crabs with legs using the wax method for branchial volume, then the slope (b) would be less steep than for a crab without legs. A crab of a given branchial volume would have a greater weight. If the same weight crab had its branchial spaces filled with water, this would give a greater branchial volume than using the wax method because of the greater penetration of the water. If computed for all crabs the slope of the regression equation would increase. Therefore, the two effects cancel each other out. Had the legs of the crabs been removed in each case, then the slope of the regression line would have been steeper using water than using wax to fill the branchial spaces. In other words, the weight difference in crabs with legs is compensated for by the greater penetration of water.

From the scatter of data points about the regression lines it is clear that the water method is the most consistent to apply.

The linear regression relationship implies allometric growth of the branchial chamber. Diaz and Rodriguez (1977) found this to be true of all the species they examined. The species they looked at fell into three groups - 1) a group with large epibranchial chambers, eg. Gecarcinus lateralis, 2) a group with relatively small epibranchial chambers, eg. Eudaniella iturbei (freshwater/terrestrial crab) and 3) an intermediate category represented by O. quadrata. Group 1 had smooth branchial walls, group 2 had perforated branchial walls and O. quadrata had folded branchial walls. In all cases the walls were shown to be sites of oxygen uptake.

The structure of the epibranchial chamber wall of O. quadrata is described by Diaz and Rodriguez (1977). Towards the carapace was a thin layer of connective tissue containing chromatophores, then a layer of spongy tissue with numerous blood vessels and then a simple epithelial cell layer towards the lumen of the chamber. The vascularisation of the 'lung' was examined in O. ceratophthalmus and O. cordimana by von Raben (1934). Greenaway and Farrelly (1984) examined the venous system of O. cordimana in great detail and showed that the gills as well as the lungs were modified for aerial respiration. Storch and Welsch (1975) had described the gills of O. ceratophthalmus as being poorly adapted for aerial gas exchange but Greenaway and Farrelly (1984) disagreed with their interpretation. Storch and Welsch (1975) indicated that the gills were adapted for haemolymph filtration and osmoregulation and Flemister (1959) also indicated an osmoregulatory rôle in O. quadrata. It would appear from Greenaway and Farrelly (1984) that this is not at the expense of a respiratory function.

Finally, it is clear from the brief structural observations of Dotilla sulcata and Metopograpsus messor, that O. saratan shows more advanced adaptations to aerial conditions than these species which are restricted to the intertidal region but nevertheless also show morphological adaptations for aerial conditions.

CHAPTER 7. CARDIAC AND VENTILATORY ACTIVITY

7.1. Introduction

Scaphnognathite activity and branchial ventilation has been studied in a number of brachyuran crabs, particularly *Carcinus maenas* (Lim, 1918; Borradaile, 1922; Arudpragasam and Naylor, 1964a; Hughes *et al.*, 1969; Hume and Berlind, 1976; Taylor, 1976; Taylor and Butler, 1973, 1978; Taylor *et al.*, 1973, 1977; Cumberlidge and Uglow, 1977, 1978) and *Cancer* spp. (Pearson, 1908; Arudpragasam and Naylor, 1966; Coyer, 1977, 1979; McDonald *et al.*, 1977; McMahon and Wilkens, 1977; McMahon *et al.*, 1977; Burnett and Bridges, 1981) and there has been renewed interest in aquatic burying and burrowing species, eg. *Corystes cassivelaunus* (Arudpragasam and Naylor, 1966; Bridges, 1976, 1979), *Ebalia tuberosa* (Schembri, 1979, 1980, 1981a) and *Atelecyclus rotundatus* (Taylor, 1984) (cf. Garstang, 1896, 1897a, b, c; Bohn, 1902) whose ventilatory flows are modified to prevent gill clogging and to aid burrowing.

There is less information on other decapods than on brachyurans. Significant studies on ventilation in macrurous forms include those on the lobster *Homarus americanus* (Wilkes and McMahon, 1972; McMahon and Wilkens, 1975) and on crayfish (Dejours and Beekenhamp, 1977; Taylor and Wheatly, 1980). Work on shrimps includes that of Dyer and Uglow (1978a, b) and Uglow (1980) on *Crangon crangon*, Hagerman and Uglow (1979) on *Paleamon adspersus* and Morris (1983) on *Palaemon elegans*.

There is therefore a large amount of literature on branchial ventilation in decapod crustaceans with the earliest studies dating from the 19th century (Milne-Edwards, 1839; Garstang, 1896; Bohn, 1897, 1902). Information on scaphagnathite activity and associated heart activity has been most recently reviewed by McMahon and Wilkens (1983), updating the review of Wolvekamp and Waterman (1960). Wolvekamp and Waterman (1960), however, looked at respiration throughout the Crustacea but in recent years McMahon and Wilkens (1983) point out that investigations have concentrated on the larger decapods for which there has been considerable expansion of knowledge. Most information is, however, restricted to fully aquatic or intertidal species and there is relatively little information on the scaphognathite and cardiac activities of semiterrestrial and terrestrial decapods. This is also true for oxygen consumption and blood chemistry (see Chapter 8).

The scaphognathite is responsible for generating the respiratory current. During its undulatory movements, water (or air) is moved above and below the scaphognathite with both upward and downward strokes generating force (McMahon and Wilkens, 1983). The ventilatory current may be pumped forwards or backwards by the scaphognathite. In some terrestrial species (<u>Coenobita</u> spp., <u>Birgus</u> <u>latro</u>, both anomurans) branchiostegite movements may function as an accessory ventilatory pump (Borradaile, 1903; Harms, 1932; Wolvekamp and Waterman, 1960; McMahon and Burggren, 1972; McMahon and Wilkens, 1983) and in freshwater/land crabs of the genus <u>Holthuisana</u> (Sundathelphusidae) the scaphognathites are inactive in air and 'lung' ventilation is achieved by lateral oscillations of the thoracic walls inside the branchial chambers (Greenaway and Taylor, 1976; Taylor and Greenaway, 1979; Greenaway <u>et al.</u>, 1983b; Greenaway, 1984).

For aquatic crabs the rôle of the scaphognathite in branchial irrigation was investigated by the early workers (Milne-Edwards, 1839; Garstang, 1896; Bohn, 1897, 1902; Pearson, 1908). It was found that water normally passed forwards across the scaphognathite, being expelled anteriorally, but periodic reversals occurred forcing water posteriorly. In some species, eg. the sand burrowing crab *Corystes cassivelaunus*, water flow was normally in the reverse direction and this is also true of another sand burrowing species, *Atelecyclus rotundatus* (Taylor, 1984). The detailed analysis of Borradaile (1922) showed that in the shore crab *Carcinus maenas*, the scaphognathite normally pumped water forwards with water entering through the Milne-Edwards openings anterior to the base of the chelipeds and to a lesser extent through smaller apertures between the walking legs. Periodically the respiratory current was reversed. Subsequent work on this and other species indicates that *Carcinus maenas* is typical of most aquatic crab species (see McMahon and Wilkens, 1983). Haemolymph in the gill lamellae moves in the opposite direction to the forward respiratory current as it passes through the lamellae, aiding gaseous exchange (Hughes *et al.*, 1969). The control of reversals is complex (Young, 1975) and their function is unclear despite much research. Their primary function appears to be connected with cleaning apertures and interlammellar spaces (Hughes *et al.*, 1969). Borradaile (1922) considered current reversals had no other function than cleaning the gill chamber and disagreed with Bohn (1902) who thought they served to rest the scaphognathite muscles. Arudpragasam and Naylor (1964b), impressed by the regularity of reversals in *C. maenas* in clean water, suggested reversals irrigated the dorsal surface of the posterior gills but Hughes *et al.* (1969) could not substantiate this. McDonald *et al.* (1977) indicate that reversed pumping disrupts the counter current water flow across the gills thus lowering the effectiveness of gas exchange. The debate still continues (see McMahon and Wilkens, 1983) and a physiological rôle for reversals may still be found in such species.

In much of the recent work, studies on scaphognathite activity are combined with investigations of heart activity (gas exchange at the gills depends on cardiac and circulatory efficiency). Indeed, the activities of the two have been shown to be closely coordinated with evidence of common neuronal control and with the additional possibility of hormonal coordination (McMahon and Wilkens, 1983). Bradycardia or total cardiac arrest and apnoea (scaphognathite arrest) commonly occur in synchrony and tachycardia is often synchronised with increased scaphognathite frequency. J.L. Larimer, whose thorough approach helped develop the study of decapod crustacean respiratory physiology, noted synchronous cardiac and scaphognathite activity in the crayfish *Procambarus simulans* (Larimer, 1964). Such synchrony has now been reported in other crayfish, eg. *Orconectes virilis* (McMahon *et al.*, 1974); lobsters (eg. *Homarus americanus* (McMahon and Wilkens, 1972, 1975; Young and Coyer, 1979), *H. gammarus* (Butler *et al.*, 1978), *Nephrops norvegicus* (Young, 1978)), crabs (eg. *Carcinus maenas* (Cumberlidge and Uglow, 1977, 1978), *Cancer pagurus* (Ansell, 1973; Burnett and Bridges, 1981; Bradford and Taylor, 1982), *C. magister* (McDonald *et al.*, 1977), *C. productus* (McMahon and Wilkens, 1977), *C. borealis*, *C. irroratus* (Coyer, 1979), *Corystes cassivelaunus* (Bridges, 1979), *Ebalia tuberosa* (Schembri, 1979), *Atelecyclus rotundatus* (Taylor, 1984)) and shrimps (eg. *Crangon crangon* (Dyer and Uglow, 1978), *Palaemon elegans* (Morris, 1983)).

Pausing behaviour enables decapods to save metabolic energy since they do not then have to pump water and blood; oxygen consumption is dramatically reduced (McDonald *et al.*, 1977; McMahon and Wilkens, 1977; Burnett and Bridges, 1981; Bradford and Taylor, 1982; Taylor, 1984).

There is considerably less information on the respiratory physiology of terrestrial and semiterrestrial decapods than there is on aquatic species. Some aquatic species that have adopted an intertidal existence may be exposed to air and show structural modification of their gills (increased sclerotization) eg. *Carcinus maenas* (Taylor and Butler, 1978). When in air *C. maenas* shows a modified pattern of scaphognathite activity by engaging in sustained reverse pumping (Arudpragasam and Naylor, 1964a; Taylor *et al.*, 1973).

True semiterrestrial and terrestrial crabs have sclerotized gills and accessory respiratory structures to facilitate aerial respiration (see Chapter 7). According to Greenaway (1984) there are three main strategies of aerial gas exchange.

1. Use of gills and lungs for aerial respiration. Air is circulated through the gills and lungs by the scaphognathite, entering at the limb bases and leaving via the prebranchial apertures. The gills have strengthened lamellae which drain rapidly and usually have a small surface area. Examples are *Gecarcinus lateralis*, *Ocypode* spp. and *Gecarcoidea lalandii*.
2. Retention of water in branchial chambers and gills augmented by lungs. The scaphognathites recirculate water through the branchial chambers, and out of the prebranchial chambers where reoxygenation takes place before the water is recollected through Milne-Edwards openings. Examples are *Sesarma* spp., *Cyclograpsus punctatus* and *Helice crassa*.
3. Tidal ventilation of branchial chambers by means of lateral oscillations of thoracic body walls and not by scaphognathite action, eg. *Holthuisana* spp. In *H. transversa* air enters via the prebranchial apertures and does not flow over the gill lamellae. In *H. valentula* and *H. agassizi* air also enters via the Milne-Edwards openings and may

flow over the gills.

As shall be seen in this section of the thesis, Greenaway's above analysis does not hold wholly true for O. saratan.

McMahon and Wilkens (1983) state that 'in both anomuran and brachyuran air breathers the scaphognathite pump seems to function as well in aerial and aquatic ventilation.' They attribute this partly to the fringing hairs of the scaphognathite margin trapping water by capillary action and thus forming a good seal. In Chapter 6, it was indicated that in O. saratan the scaphognathite is bordered by very short plumed setae that undoubtedly form an efficient seal allowing it to generate considerable negative pressures in the branchial chamber (see this Chapter and Wolcott, 1976, 1984).

7.2. Material and Methods

Most of the crabs used for these experiments were obtained from Aum-Ali Island immediately southwest of Jeddah Islamic Harbour so as not to deplete the small crab population at Sharm Obhor. These crabs were placed in simulated natural conditions in an outdoor aquarium at the Marine Station of the Faculty of Marine Science, King Abdul-Aziz University, Jeddah (see Chapter 4). This holding facility could accommodate up to 30 crabs at any one time and some heart and scaphognathite records were taken from crabs living 'normally' in this simulated environment. In addition, a number of crabs were transferred to an indoor aquarium tank of length 1m, width 50cm and depth 1m. 8cm of gravel was placed in the bottom of the aquarium, covered with a fine mesh (2mm) plastic screen and then covered with a further 2cm of gravel. Plastic tubes enabled water to be added to and drained from the gravel bed and aeration stones were also placed in the gravel bed with air supplied from two standard aquarium air pumps. A small water pump enabled the water to be exchanged daily. 50cm of sand were placed over the saturated gravel bed. Crabs were held in the outdoor aquarium from one to three weeks before experiments, during which time they were fed on chopped fish. Crabs were held at the acclimation temperature indoors and maintained in a 12:12 LD regime for 7 days before experimentation except in the case of the 15°C and 35°C experiment where acclimation was for 24h since there was a risk of mortality. Heart rates at each acclimation temperature were measured over a 4 day period.

A closed circuit television system (see Chapter 4) was used to monitor crab activity during some oscillographic recordings.

Heart rate and scaphognathite rate experiments were conducted at a range of temperatures: 10°C, 20°C, 25°C, 30°C, 35°C and 40°C. The two extremes were not pursued since the crabs were obviously heavily stressed and records unreliable.

Heart rate and scaphognathite rate records were obtained using the impedance pneumograph technique (Hoggarth and Trueman, 1967; Trueman, 1967). For heart rate records, a small hole was drilled through the carapace on each side of the heart and a fine silver wire electrode was introduced through each hole and cemented in place using cyanoacrylate glue. For scaphognathite beat records two small holes were drilled in the ventral carapace lateral to the 3rd maxilliped, one hole near each end of the scaphognathite and a fine silver wire electrode was implanted in each hole and cemented in place with cyanoacrylate glue. Heart electrode implantation was relatively straightforward but for good records the length and position of scaphognathite electrodes was critical. Electrode wires were connected to impedance pneumograph couplers (Strathkelvin Instruments) and impedance changes were amplified and recorded using Washington MD2 or MD4 oscillographs (Searle Bioscience).

Air pressure changes in the epibranchial chamber were measured using a PT400 blood pressure transducer connected via an FC137 coupler to a Washington MD2 or MD4 oscillograph (all Searle Bioscience). A catheter constructed from the nozzle of a disposable syringe was cemented into the roof of the epibranchial chamber and polythene catheter tubing (c. 2mm internal diameter) was attached. The tubing was filled with seawater but none was introduced into the branchial chamber. Alternatively, narrower (1mm internal diameter) water filled catheter tubing was inserted into the epibranchial chamber and cemented in place. The catheter tubing connected with the PT 400 transducer in each case. The wider tubing was found to be the more successful in transmitting the air pressure changes in the epibranchial chamber of emersed crabs.

The direction of the respiratory current was revealed by this pressure method and was also traced using ink in immersed crabs, soap bubbles in emersed or paddling crabs and smoke in totally emersed crabs. Respiratory current direction was further investigated in crabs transported live to Glasgow University. A respiratory mask constructed from a balloon was sealed around the mouth region of the crab using cyanoacrylate glue. This was connected by polypropylene tubing to a burette. The burette was further connected to a reservoir of liquid soap such that a soap bubble could be introduced into the burette. The direction of movement of the bubble indicated the direction of respiratory pumping in crabs held in air and also enabled ventilation volume to be measured. This equipment was used with crabs held at 25°C ± 2°C.

The number of heart beats per minute was plotted as a function of body size (wet weight) on a double logarithmic system. Such a plot over an adequate size range gives a straight line with a negative slope. The regression of heart beats per minute against body size assumes the form

$$y = ax^{b}$$

or $\log y = a + b \log x$

where y = the heart rate in beats.min^{-1}

a = a constant denoting the intercept of the regression line on the y axis and x is the crab weight

b = slope of the regression line

Covariance analysis was applied to test whether differences in slopes and intercepts of the regression lines were statistically significant.

7.3. Results

7.3.1. Heart Rate

7.3.1.1. Effects of temperature and body size

All heart rate recordings were made in normoxic conditions. Fig. 7.1 presents the results of a wide size range of crabs in which heart rate was recorded at 15°C, 20°C, 25°C, 30°C and 35°C plus four data points at 40°C. The equations for the regression lines are given in the legend. Covariance analysis was applied to test whether the differences in the slope were significantly different. The data for 15°C and 20°C were significantly different from each other and from the data for 25°C, 30°C and 35°C which were not significantly different from each other. The intercepts of the regression lines

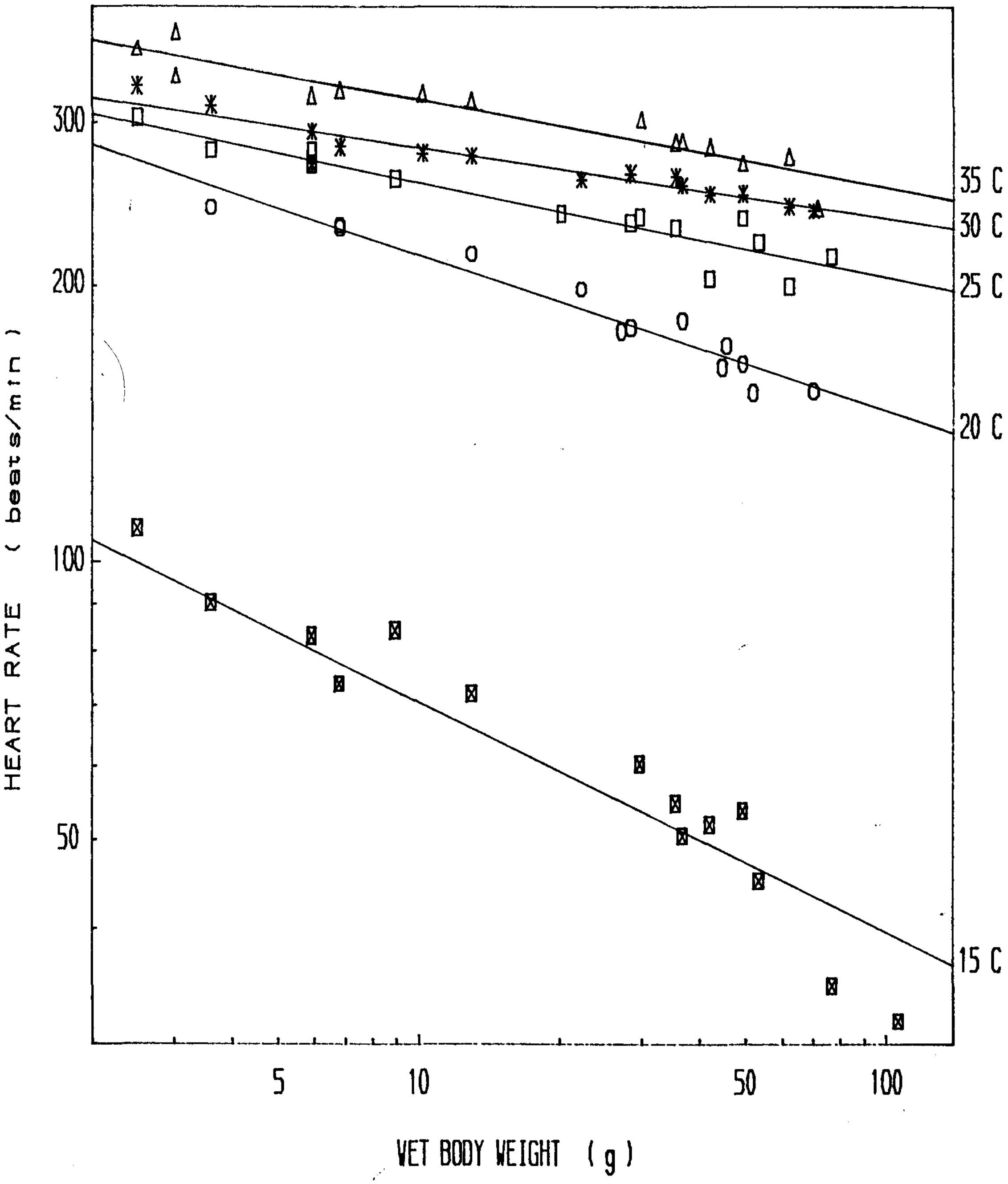
Fig. 7.1. Relationship between heart rate and body weight of *O. saratan* at different temperatures.

The regression equations are

	n	r
15°C $\log y = 2.097 - 0.249 \log x$	15	-0.944
20°C $\log y = 2.503 - 0.169 \log x$	13	-0.972
25°C $\log y = 2.516 - 0.103 \log x$	14	-0.939
30°C $\log y = 2.524 - 0.756 \log x$	15	-0.946
35°C $\log y = 2.593 - 0.920 \log x$	14	-0.897

where y = heart rate (beats.min^{-1}) and x = wet body weight.

To permit all data to be compared on the same figure, one data point has been omitted for 15°C but it is accounted for in the regression line. This crab was 0.79g and the heart rate was 84.3 beats.min^{-1}.


HEART RATE (beats/min)
300
200
100
50
5
10
50
100
VET BODY VEIGHT (g)
35 C
30 C
25 C
20 C
15 C

were significantly different from each other when each temperature was compared, particularly so in the case of the data for 15°C.

Fig. 7.2 shows an example of a rested crab at 20°C compared with a stressed crab at 40°C. Fig. 7.3 illustrates the effect of temperature on the heart rate of a crab of 28.4g wet weight (arbitrary choice of size). The Q_{10} relationships for a range of crab sizes are given below.

Table 7.1. Q_{10} values for heart rate of *O. saratan*

a) Crabs of known weight

wet weight (g)	carapace width (cm)	Q_{10} over 5°C intervals				Q_{10} over 10°C intervals		
		15-20°C	20-25°C	25-30°C	30-35°C	15-25°C	20-30°C	25-35°C
3.6	1.9	7.3	1.7	1.2	0.6	3.1	1.3	1.1
6.8	2.3	9.6	1.4	1.0	1.2	3.8	1.2	1.2
22.3	3.3	10.2	1.4	0.8	1.2	3.9	1.3	1.2
36.7	3.9	12.9	1.7	1.2	1.2	4.0	1.4	1.2
61.9	4.5	11.6	1.7	1.4	1.2	4.1	1.3	1.1

b) Estimates from regression lines

wet weight (g)	Q_{10} over 5°C intervals				Q_{10} over 10°C intervals		
	15-20°C	20-25°C	25-30°C	30-35°C	15-25°C	20-30°C	25-35°C
5	8.4	1.2	1.2	1.4	3.4	1.3	1.2
10	8.4	1.7	1.2	1.2	3.2	1.4	1.2
15	10.9	1.7	1.2	1.2	4.2	1.4	1.2
20	9.6	1.7	1.2	1.2	4.0	1.4	1.2
30	10.2	1.7	1.2	1.2	4.2	1.4	1.2
40	10.9	1.7	1.2	1.2	3.9	1.4	1.2

Fig. 7.2. Heart and scaphognathite recordings from O. saratan.

a) Rested crab at 20°C. H = heart, S = scaphognathite

b) Stressed crab at 40°C. H = heart, S = scaphognathite

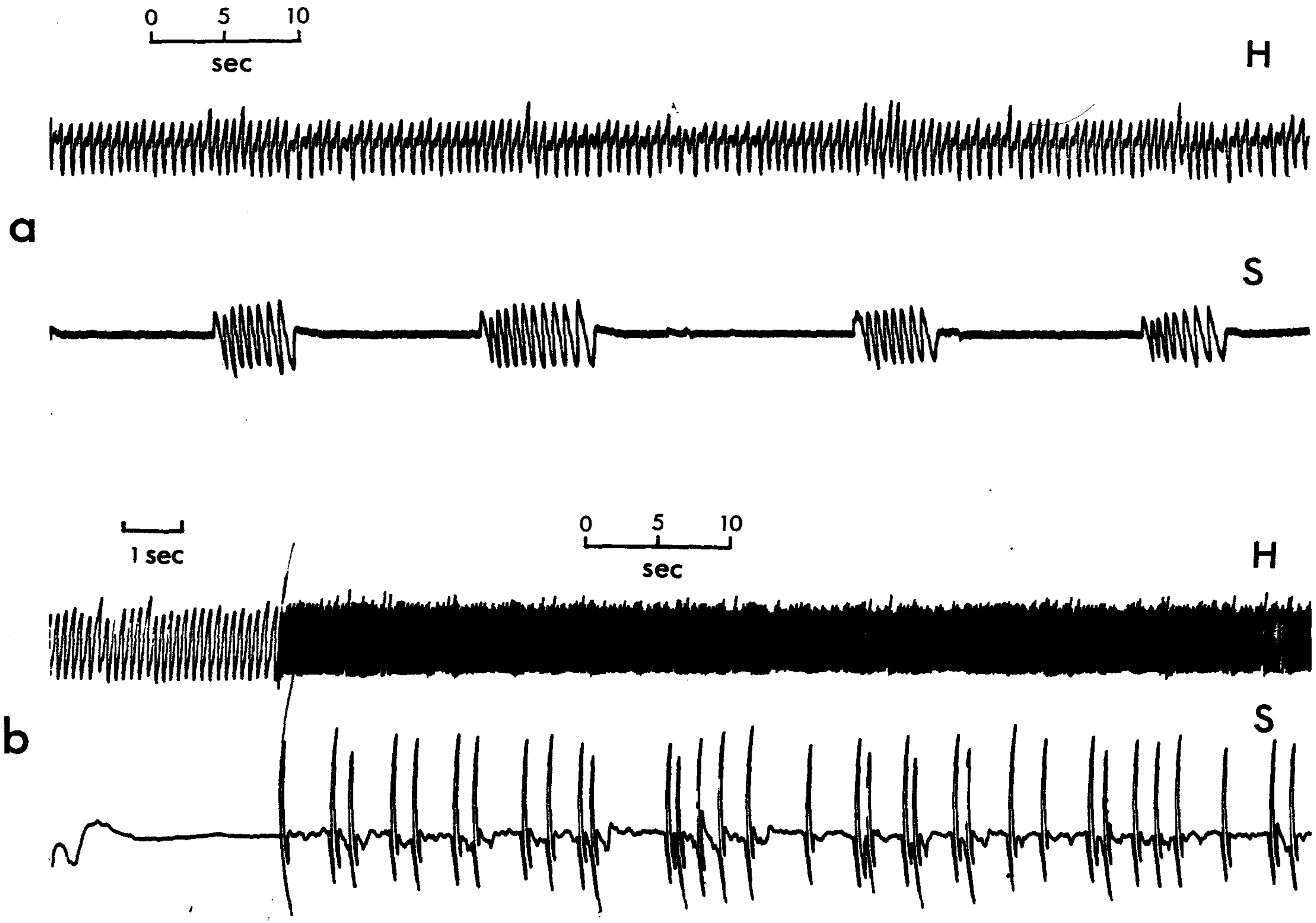
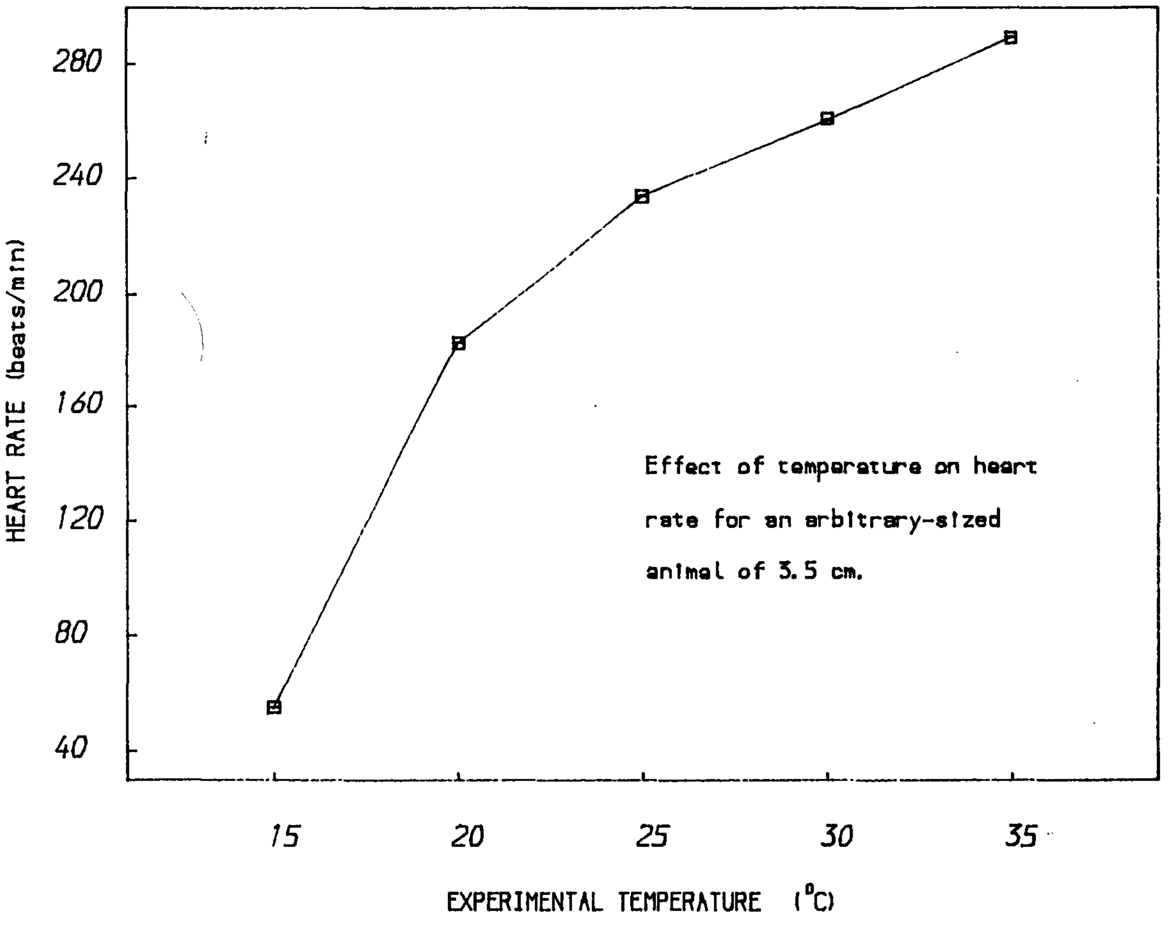

a
0
5
10
sec
H
S
b
1 sec
0
5
10
sec
H
S

Fig. 7.3. Effect of temperature on heart rate for an O. saratan of 3.5cm carapace width and 22.8g (arbitary choice of size).



Effect of temperature on heart rate for an arbitrary-sized animal of 3.5 cm.

The Q_{10}'s are very consistent over a wide temperature range but are higher between 15°C and 20°C. The crab does not normally experience temperatures below 20°C but is regularly exposed to high temperatures.

A few records of heart rate were obtained from crabs at 40°C. For example, a crab of 4.67g had a heart rate of 310 $beats.min^{-1}$ while a crab of 3.75g had a heart rate of 430 $beats.min^{-1}$. Crabs did not survive such exposure for long and insufficient data were obtained for statistical comparisons.

7.3.2. Scaphognathite activity

Scaphognathite activity is responsible for the circulation of air within the epibranchial 'lungs' and also for irrigating the gills. It was discovered that a number of different strategies of scaphognathite pumping were involved in achieving this.

Individual crabs showed great variability in scaphognathite activity and it was clear that a number of different pumping strategies were being employed. Without an understanding of these patterns, a consideration of scaphognathite rates was judged to have little meaning. In the following section the different patterns of scaphognathite activity are investigated rather than the rates.

7.3.2.1. Crab immersed

Crabs immersed in seawater pumped water forwards through the branchial chamber. The third and fourth pereiopods were held such that the setose valve-like aperture between them (posterior aperture) was held open. Milne-Edwards openings were periodically opened. It was observed that when first immersed Milne-Edwards opening was normally kept closed (by movement of the epipod base of the 3rd

Fig. 7.4. Scaphognathite and branchial pressure recordings from an immersed *O. saratan*.

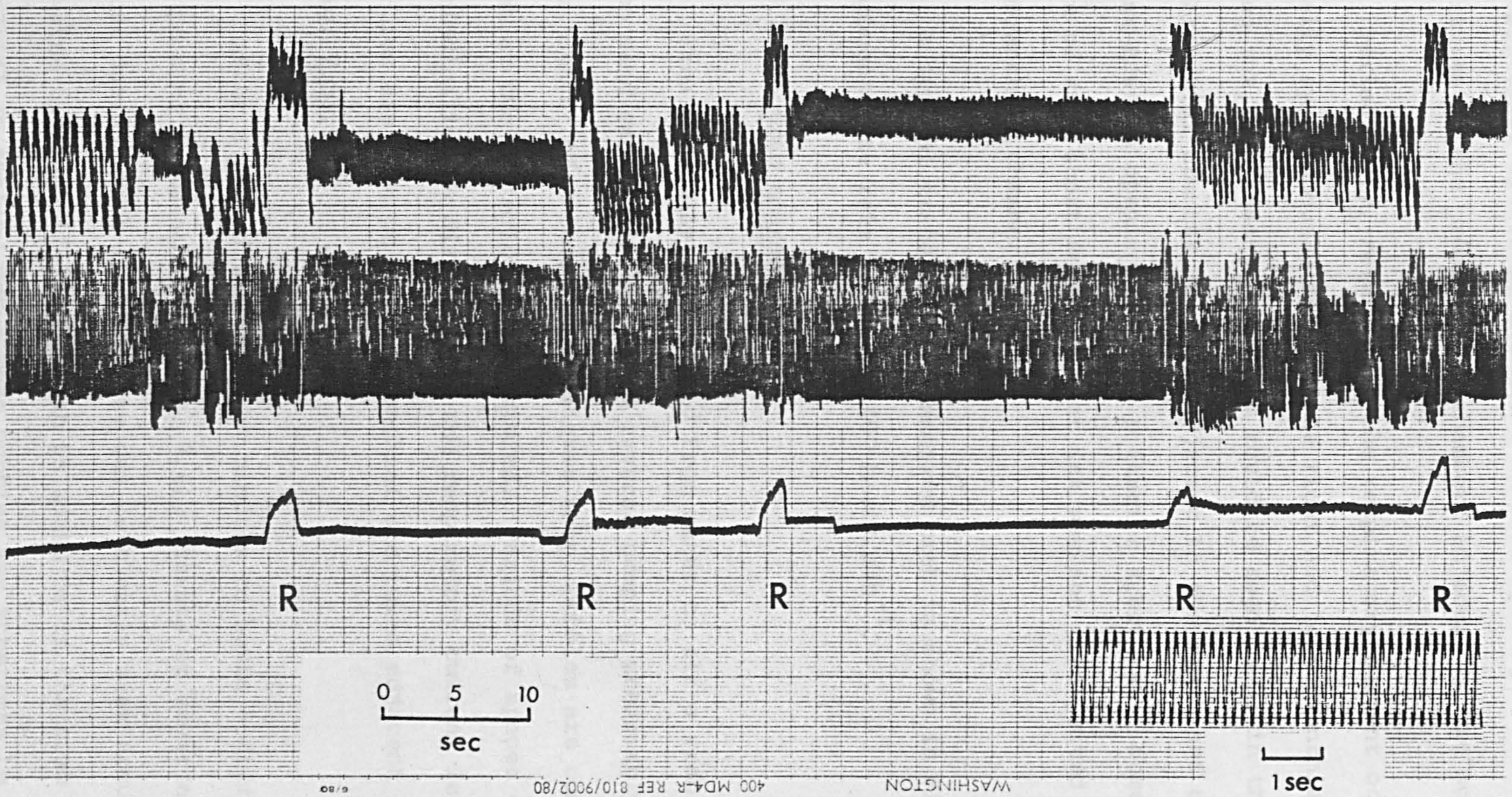
Upper trace - right branchial chamber pressure

Middle trace - right scaphognathite activity

Lower trace - left branchial chamber pressure

Inset (bottom right) - right scaphognathite activity at faster chart speed to show individual beats.

R = reversals of respiratory current, otherwise pumping forwards.


R
R
R
R
R
0 5 10
sec
1 sec
WASHINGTON
400 MD4-R REF 810/9002/80

maxilliped) but after several hours immersion it was normally open. Using ink, the passage of water could easily be traced: in through the posterior apertures and Milne-Edwards openings and out via the apertures of the prebranchial chambers adjacent to the mouth.

Periodically, reversal of the respiratory current occurred, usually synchronously between the right and left branchial chambers. Using ink, the passage of water could be seen to be in through the prebranchial chamber openings adjacent to the mouth and out through Milne-Edwards openings and the posterior apertures. Some reversals were of such short duration that ink was not transported beyond the prebranchial chamber.

A typical trace from an immersed crab is shown in Fig. 7.4. The scaphognathite rate is around 400 beats.min^{-1}.

7.3.2.2. Crab emersed

When initially transferred from water to air a crab placed on damp sand engages in sustained reverse pumping presumably to empty its 'lungs' of water. Using liquid soap, bubbles are continuously seen at the posterior leg apertures. Periods of apnoea occur and periodically the direction of the respiratory current is changed and bubbles are seen at the prebranchial apertures adjacent to the mouth (Fig. 7.5).

After a period varying from minutes to hours a different pattern of pumping is established (Fig. 7.6). Bursts of reversed pumping occur during which time bubbles can be clearly seen around the Milne-Edwards openings if liquid soap is added or if the crab is allowed to 'sit' in shallow water when bubbles may sometimes be seen around the posterior apertures. Between these bursts of reverse pumping

Fig. 7.5. Scaphognathite and branchial pressure recordings from an O. saratan recorded in air immediately following immersion.

Upper trace - branchial pressure

Lower trace - scaphognathite activity

Both records are from the same side of the crab. The pattern is one of almost continous reverse pumping. The pressure record is not very clear but bubbles were continuously seen at Milne-Edwards opening and the posterior branchial aperture except during the ventilatory pauses.

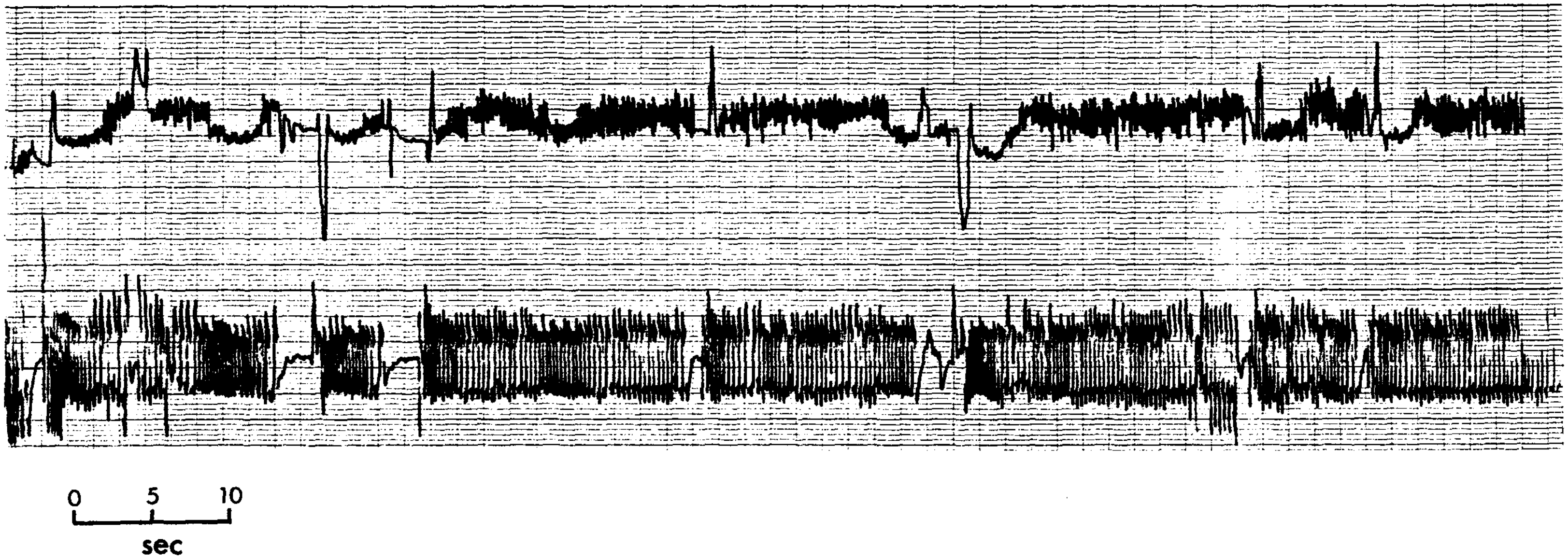
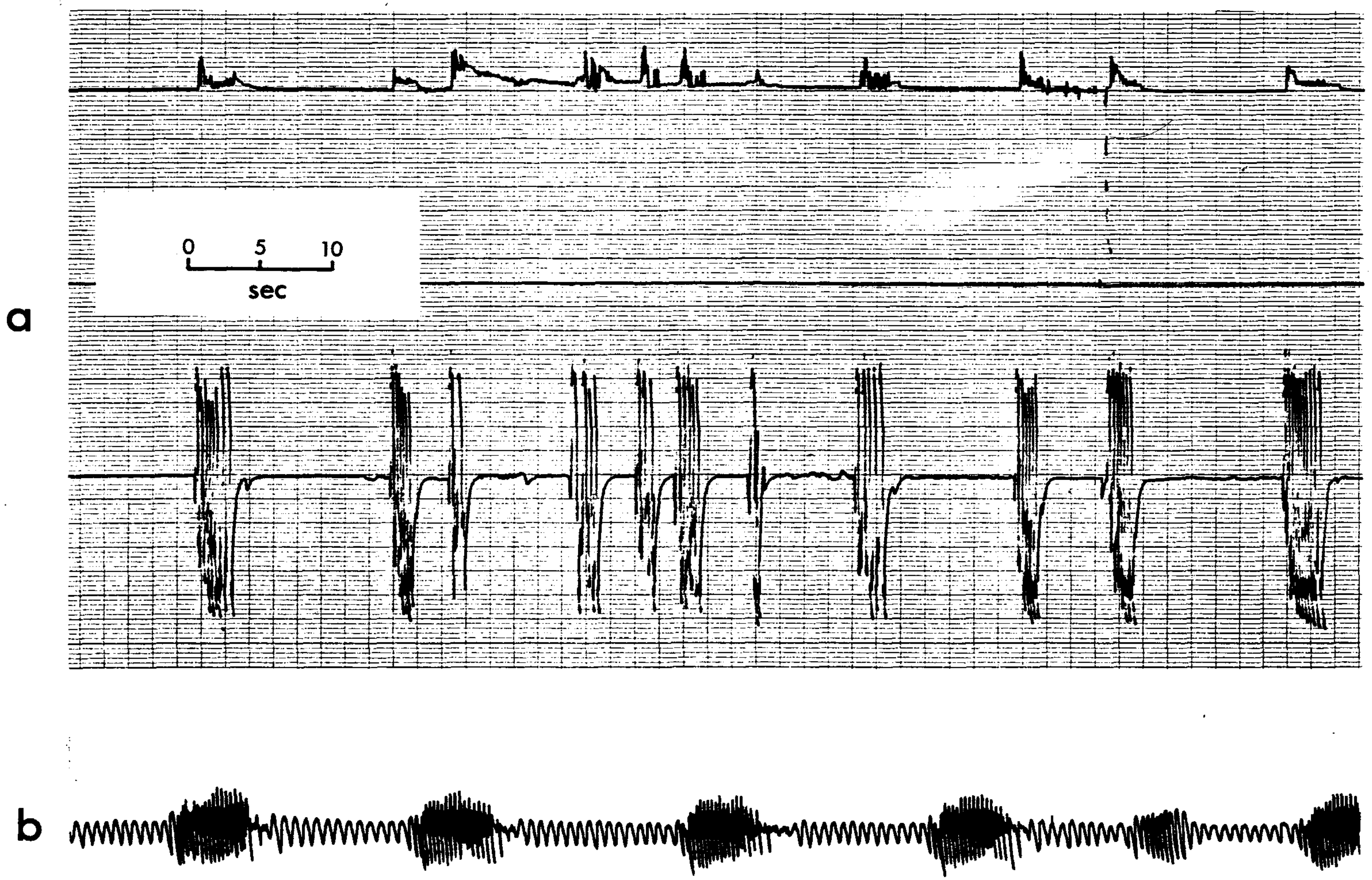

0
5
10
sec

Fig. 7.6. a) Scaphognathite activity of an unstressed O. saratan

Upper trace - branchial pressure

Lower trace - scaphognathite activity

b) Scaphognathite activity in a more active crab. This crab had earlier been stressed by immersion and showed the illustrated pattern of pumping in air before returning to the pattern seen in (a). Speed as in (a).


a
0
5
10
sec
b

the scaphognathite may be inactive or beat slowly probably in a forward direction (pressure traces difficult to interpret). Periodic bursts of more intense forward pumping may occur. This pattern of bursts of reverse pumping is maintained when the crab raises its body from the substratum but it was noticed that on several occasions when the crab was orientated obliquely such that one branchial chamber was raised from the substratum and the other was in contact with it via the leg tufts then the pattern of pumping was asynchronous between the chambers with more periods of forward pumping in the lower chamber.

Rested crabs, maintained on dry sand in air showed a consistent pattern of bursts of reverse pumping separated by periods of apnoea. Air current direction was confirmed using smoke and by branchial pressure recordings. The same pattern occurred when the body was in contact with dry sand or raised from it. The posterior apertures were maintained closed during this pattern of pumping. Air was expelled only through the Milne-Edwards openings.

7.3.2.3. Branchial flushing

A distinctive pattern of scaphognathite activity was seen in crabs that had been in dry sand for several hours and were then placed on damp sand or in very shallow water (Fig. 7.7).

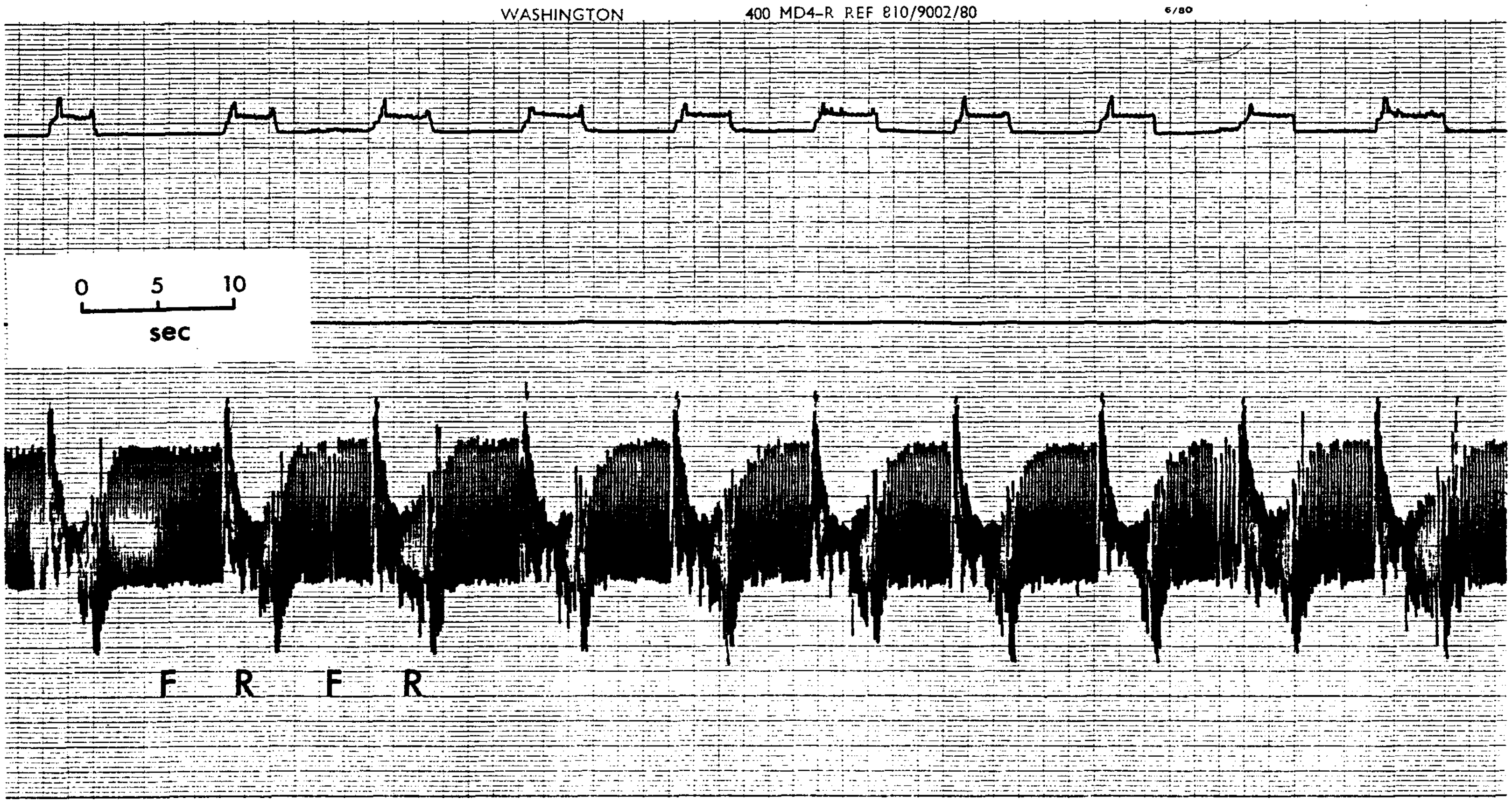
First of all the scaphagnathite pumps forwards, Milne-Edwards opening is closed and the apposed setal tufts of the posterior branchial aperture are applied to the damp substratum or immersed. Reversed pumping then commences and Milne-Edwards opening is opened by movement of the epipod base of the third maxilliped. Immediately before it opens there is a spike on the branchial pressure trace. The posterior aperture is then opened and water is expelled from the

Fig. 7.7. Scaphognathite and branchial pressure recordings from an <u>O. saratan</u> engaged in the branchial flushing pattern described in the text.

Upper trace - branchial pressure

Lower trace - scaphognathite activity

F = forward pumping, R = reverse pumping


WASHINGTON
400 MD4-R REF 810/9002/80
6/80
0
5
10
sec
F
R
F
R

branchial chamber until forward pumping is recommenced with associated closure of the inhalent apertures.

It should be noted here that although the posterior aperture is 'closed', ie. the setal fringes of the bases of the third and fourth pereiopods are apposed, this does not mean that water uptake does not take place. The hydrophilic setae retain moisture and the negative pressure generated by forward pumping draws this into the branchial chamber. It was noticed, however, that the setal fringes of the posterior aperture were not always closely apposed when they were immersed in shallow water in contrast to being applied to damp sand.

The pattern of alternating forward and reversed pumping described above results in flushing of the branchial chamber and probably has a cleaning function in addition to exchanging the water around the gills. To what extent the 'lung' walls were flushed could not be determined but water was seen to bubble from the appropriate prebranchial chamber aperture beside the mouth during forward pumping.

7.3.2.4. Water uptake

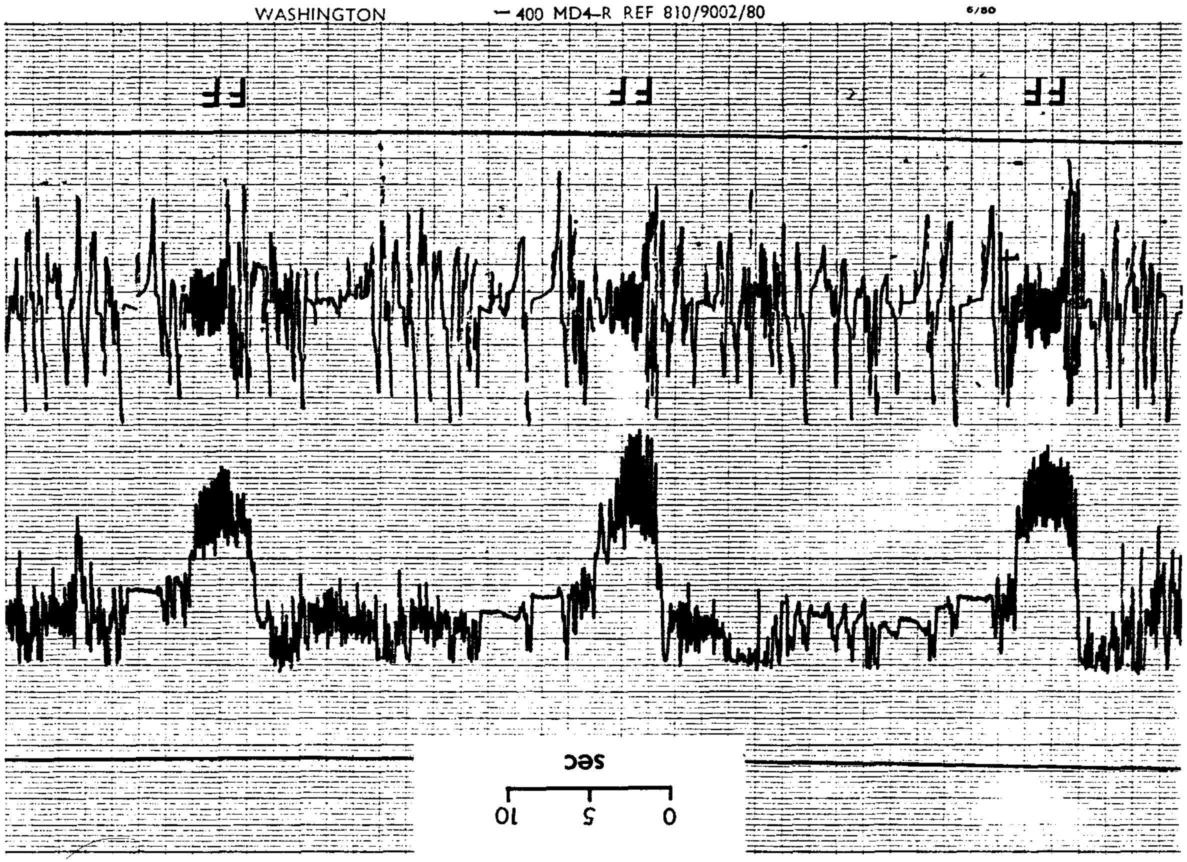
Often following a period of branchial flushing but at other times occurring without it, crabs would display a characteristic pattern of scaphognathite beat which resulted in the bulk uptake of water into the branchial chamber. The Milne-Edwards opening was closed and forward pumping was established. The crab then increased the rate of scaphognathite beat and engaged in a burst of rapid forward pumping during which the pressure in the branchial chamber dropped markedly. Throughout, the setal tufts of the posterior branchial aperture were held in contact with the damp substratum. This response was consistently seen in crabs that had been kept for several hours in dry

Fig. 7.8. Scaphognathite and branchial pressure recordings from <u>O. saratan</u> engaged in water uptake from damp sand.

Upper trace - branchial pressure

Lower trace - scaphognathite activity

FF = fast forward pumping


WASHINGTON
— 400 MD4-R REF 810/9002/80
6/80
FF
FF
FF
0
5
10
sec

conditions.

A characteristic result is shown in Fig. 7.8. The scaphognathite rate may reach 300 beats.min^{-1}.

7.3.2.5. Unilateral and bilateral pumping

Normally, the two scaphognathites behaved synchronously in that the direction of pumping was the same in each branchial chamber and changes in the direction of pumping occurred synchronously. This was true at least for immersed crabs and emersed rested crabs.

On a number of occasions one scaphognathite was observed to cease beating while the other continued and alternation of this activity was also observed.

Synchronous recordings of the branchial flushing pattern were attempted and suggested partial asynchrony between the branchial chambers in some cases and complete asynchrony in others. On one occasion both branchial chambers were recorded during the fast forward filling pattern. On this latter occasion only one branchial chamber was involved at a time but the record was not extensive.

7.3.2.6. Ventilation volume

Fig. 7.9 presents data on the volume of air ventilated by rested crabs. In this case scaphagnothite pumping occurred in bursts and was in the reverse direction, ie. in through the anterior prebranchial apertures such that the soap bubble moved down the burette. As might be expected larger crabs ventilated more air but when considered as ventilation volume per g of wet weight, all crabs were similar (NB. b = 0.998).

It was noticed that when disturbed, a pattern of alternating

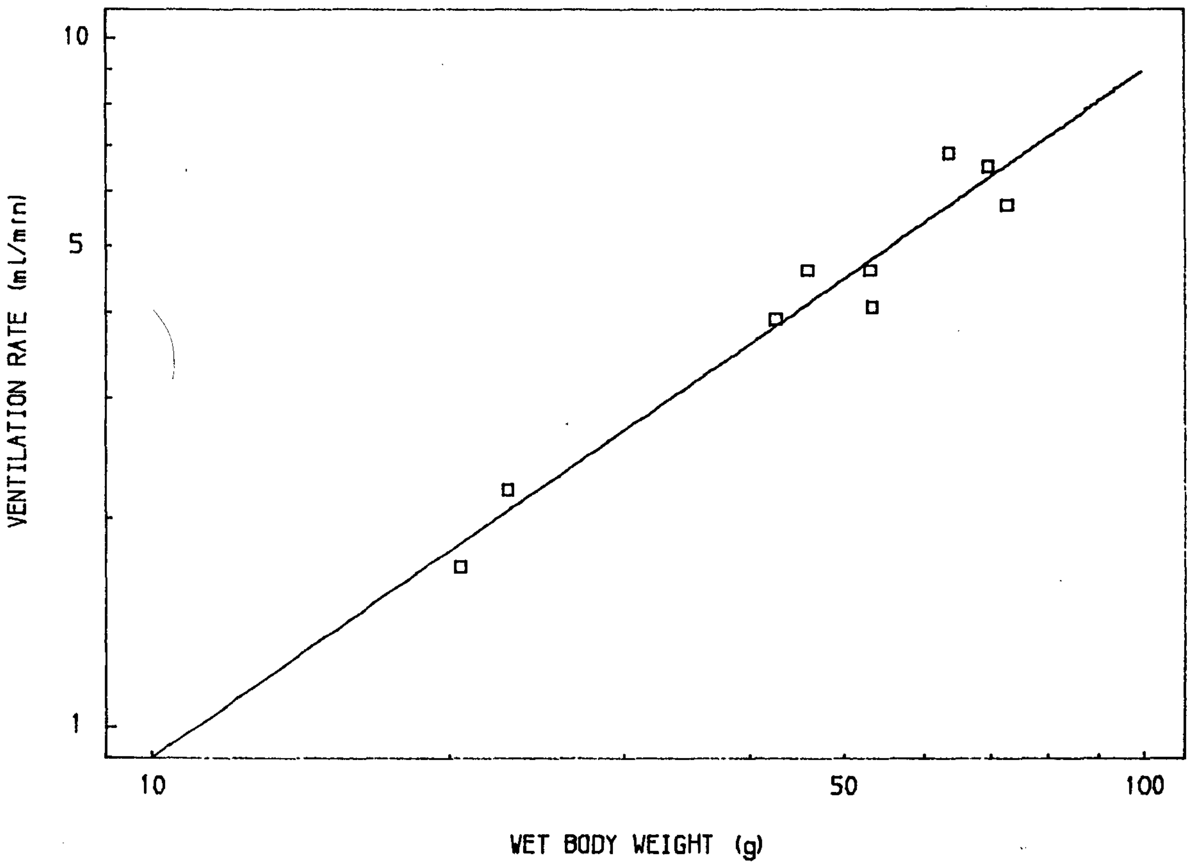
Fig. 7.9. Ventilation volume in O. saratan of differing size. The regression equation is

$$\log y = -2.403 + 0.998 \log x$$

where y = ventilation volume in ml.min^{-1} and

x = wet body weight

$n = 10$, $r = 0.970$


10
5
1
VENTILATION RATE (ml/min)
10
50
100
WET BODY WEIGHT (g)

forward and reverse pumping often occurred but such crabs were not included in the above analysis.

7.3.3. In situ recordings

Crabs wired for heart and usually also scaphognathite records were free to move normally in the outside crab tank at Obhor. Observations and TV records showed that the patterns obtained in the laboratory were also seen under these more natural conditions. The normal pattern of ventilation in quiescent crabs was one in which bursts of reverse pumping were separated by periods of apnoea. The frequency of bursts of pumping was greatly variable even within individual crabs and no consistent explanation could be determined. Heart rate was lowest in the case of inactive crabs within their burrows and increased with activity. NB. Plate 7.1.

In one day a crab of 4.2cm carapace width had a heart rate of 220 beats.min^{-1} in the afternoon when the environmental temperature was 39^{o}C. The crab was within its burrow where the temperature would have been lower (not measured) but the burrow did not provide the protection of deep field burrows. This crab and all the others left their burrows and entered the water. In the evening the temperature dropped to 29^{o}C and the heart rate fell to 190 beats.min^{-1}. During the night the temperature dropped to 24^{o}C and the heart rate dropped to 180 beats.min^{-1}. The scaphognathites were relatively inactive at high temperature with long periods of apnoea but the regular burst pattern was re-established during the evening and night. When crabs were active and running, bursts of reverse pumping became irregular and scaphognathite activity was sometimes continuous though still irregular. It was difficult to interpret such traces. Burrowing caused electrode interference obscuring the trace.

Plate 7.1. The crab occupying this burrow has been wired for oscillographic recordings of heart rate.

Patterns of scaphognathite burst activity (reversals) varied from 10 bursts.min^{-1} to one burst every 6 minutes in this series of observations. It was difficult to determine whether scaphognathite beats that occurred at low frequency between some reversals were pumping in a forward or reverse direction.

7.3.4. Synchronous cardiac and ventilatory activities

Periods of apnoea often coincide with periods of cardiac arrest in aquatic crabs. Such behaviour was not seen in O. saratan. Fully rested crabs maintained the pattern seen in Fig. 7.2a. Periods of apnoea occurred regularly but were not associated with cardiac arrest or ventilatory bursts.

In some cases there was a suggestion of slight bradycardia following ventilatory bursts. Both scaphognathite rate and heart rate were higher in active animals than rested ones but because of the complications imposed by the different patterns of scaphognathite activity this was not analysed.

7.4. Discussion

The heart rate of O. saratan was consistently higher in small crabs than large crabs over the whole range of experimental temperatures investigated. The data presented show that O. saratan is well adapted to survive in the wide range of environmental temperatures it experiences. The Q_{10} data were very consistent between 20°C and 35°C, particularly so between 25°C and 35°C. As has been seen in Chapters 3 and 4, O. saratan avoids potentially lethal extremes of temperature by behavioural means but is clearly physiologically adapted to survive in its high temperature environment. Q_{10} relationships were also derived from oxygen consumption measurements and these are compared with the present heart rate data in Chapter 8.

The size and temperature relationships shown here appear to be typical for Brachyura. For example, Ahsanullah and Newell (1971) showed similar relationships for the shore crab Carcinus maenas, and Taylor and Davies (1981) showed a similar relationship in the terrestrial crab Gecarcinus lateralis. The Q_{10} data presented for C. maenas by Ahsanullah and Newell (1971) contrast with the O. saratan data in that they show little stabilization across the range of environmental temperature.

The information obtained on ventilation is particularly interesting since it demonstrates a number of different pumping strategies and clear adaptations to the semiterrestrial mode of life of O. saratan. O. saratan in water behaves like an aquatic crab. Its pattern of pumping is forwards (ie. water enters through Milne-Edwards openings and the posterior inhalent apertures and is expelled from the prebranchial chambers alongside the mouth) and periodic reversals of the respiratory current occur. When in air, however, O. saratan displays a distinctive pattern of pumping when quiescent, which consists of bursts of reverse pumping separated by periods of apnoea and has distinctive patterns of scaphognathite activity for flushing out (alternating forward and reverse pumping) and filling the gill chamber (burst of fast-forward pumping). The situation in active crabs is still unclear.

Greenaway (1984) considered that Ocypode spp. had gills which drained rapidly and the implication was that water was not retained in the branchial chamber. Bliss (1968), however, stated that Ocypode and Uca regularly carry a small amount of water in their branchial chambers in contrast to Gecarcinus lateralis and Cardisoma guanhumi. My observations also confirm that some water is retained in the branchial chambers in contrast to the air filled epibranchial chambers. The structure of the branchial chamber and epibranchial chamber may provide an explanation for the pumping patterns seen. If O. saratan engaged in normal forward pumping in air it might lose the water retained in its branchial chambers if the posterior apertures between pereiopods 3 and 4 were opened. The orientation of the crab is such that this argument would not be true if the air came in only through the Milne-Edwards openings since these are near the top of the gill region of the branchial chambers. In aquatic crabs, however, during forward pumping water enters via all inhalent leg apertures. Particularly during reverse pumping, it seems that the circulation of air in the epibranchial chamber will be aided by the thoracic fold which seems to direct inhalent air back into the epibranchial chamber before it leaves via Milne-Edwards opening. It may be that air circulation is less efficient during forward pumping with the suction pressure of the scaphognathite restricting circulation in the upper part of the epibranchial chamber. Reverse pumping with its positive pressure increase in the epibranchial chamber would overcome this. There is also the possibility that the thoracic fold would be pushed against the thoracic wall in sustained forward pumping, reducing the amount of respiratory surface available for gas exchange.

The posterior inhalent apertures are probably not involved in admitting air in contrast to the suggestions of Little (1983). Stebbing (1893) described the posterior aperture (denouncing Milne-Edwards and supporting Müller who thought the setal leg tufts were olfactory) and noted that water could stream into the branchial chamber through it. He made no comments about air circulation.

Little (1983), apparently drawing on Stebbing's account supposed air would enter the branchial cavity through this opening as well as Milne-Edwards opening and that the structure of the opening would prevent drainage. While the ridges around the opening within the branchial chamber may prevent some drainage, in my observations aerial circulation was almost entirely between the prebranchial apertures and Milne-Edwards openings, normally in a reverse direction. The advantage of bubbling air through the water surrounding the gills as suggested by Little (1983) may seem obvious but if it occurred in my observations it was by deflection (by maxilliped epipods?) of the stream entering through Milne-Edwards openings during forward pumping episodes. Since the maxilliped epipods can 'stir' the water around the gills and air in the epibranchial 'lung' will pass over the branchial water then it may not be necessary to bubble air through the water surrounding the gills. Indeed, the extent to which the branchial water is permitted to drain under aerial conditions is not clear. The structure of the gills suggests aerial respiratory adaptation and Greenaway and Farrelly (1984) consider this to be the case in O. cordimana. Therefore, it may not be necessary for the gills to be immersed at all as long as they are moist. Nevertheless, present observations agree with the statements of Bliss (1968) and Little (1983) that some water is retained in the branchial chambers. This aspect and the circulation of water or air amongst the gills requires investigation, particularly in active crabs in which the scaphognathite pattern was difficult to interpret. The normal pattern of scaphognathite activity was by bursts of reverse pumping and these were sustained for many hours without alteration at least in quiescent crabs.

This differs from the pattern of branchial circulation in

Gecarcinus lateralis which behaves similarly to an aquatic crab but drawing air in only through Milne-Edwards openings with it then flowing through the anterior gills (there is no standing water in the branchial chambers and the posterior gills are specialised for osmoregulation) before leaving via the prebranchial chamber (Taylor and Davies, 1981). G. lateralis pumps air forwards at a high rate with periodic reversals but the extraction of oxygen is very low (typical of air breathers) and this may be due to poor air circulation (Taylor and Davies, 1981). G. lateralis has large globular epibranchial chambers without folded walls in contrast to the pyramidal epibranchial chambers of Ocypode spp. with their folded surfaces.

A closer situation to that in O. saratan is seen in the land hermit crab Coenobita clypeatus which under normoxic conditions shows pulses of scaphognathite activity (forward pumping) separated by periods of apnoea (McMahon and Burggren, 1979). What is particularly interesting is that periodically (particularly when the ventilatory requirement is high) there are pulses of branchiostegal pumping which the authors considered homologous to reverse pumping in aquatic macrurans. McMahon and Burggren (1979) interpreted this as an adaptation for better branchial ventilation and for renewing conditions within the mollusc shell occupied by the crab.

In contrast to Coenobita spp., another coenobitid, Birgus latro only has rudimentary gills and has well developed branchial 'lungs' with well vascularised folded walls (Semper, 1878; Harms, 1932). It does not occupy a mollusc shell when adult. Cameron and Mecklenberg (1973) have shown that it has a variety of patterns of scaphognathite activity including intermittent irregularly occurring bursts when at rest. Air movement is forwards, emerging through the prebranchial apertures either side of the mouth. Branchiostegal movements occurred in inactive animals but were not thought to be important in ventilation. Cameron and Mecklenberg (1973) also showed that the gecarcinid, Gecarcoidea lalandii, showed irregularly spaced pulses of scaphognathite activity when at rest (probably forward pumping judging from their hypoxia data).

O. saratan contrasts with the traces presented for these species in that its pulsing activity is far more regular and is achieved by reverse pumping.

The freshwater derived landcrabs of the genus Holthuisana do not use their scaphognathites in air but ventilate by thoracic wall movements (Greenaway et al., 1983). Rested large H. transversa showed a pattern in which respiratory movements occurred in fairly regular short pulses. Air movement was tidal, entering and leaving through the prebranchial apertures with one branchial chamber in alternate phase with the other.

Therefore, although the mechanisms differ between species, there is a tendency for ventilatory activity to occur in bursts in rested terrestrial and semiterrestrial crabs.

The posterior aperture to the branchial chamber has a specialised function in relation to water uptake. This is partly examined in Chapter 6 and has been investigated by Wolcott (1984). He demonstrated considerable branchial suction pressure (the pressure gradient reached 76mm Hg ≡ 1 metre of water). My studies show that the pressure is at least 10% of this but calibration problems prevented precise measurements. The present studies indicate that the scaphognathite generates this negative pressure by engaging in intense bursts of forward pumping during which the setal tufts at the bases of the legs are applied to the damp sand. Water is taken up into the setal tufts by capillary attraction and the capillarity of the sand and the tufts is overcome by the scaphognathite's generation of negative pressure such that this water is transported into the branchial chamber. From here water is passed to the mouth and taken in to make good desiccation losses. Wolcott (1984) and Wolcott and Wolcott (1985) clearly imply that water uptake by this means occurs within burrows but that it has developed from the flotation feeding technique seen in ocypodids. The Wolcotts did not see this form of deposit feeding in *O. quadrata* (in contrast to Robertson and Pfeiffer, 1982) but it is common in *O. saratan* and may account for the frequent application of the setal tufts to the substratum at the tide edge seen in the present studies.

The branchial flushing pattern seen here for *O. saratan* was not detected in *O. quadrata* by Wolcott (1984) but he did not record the activity of the scaphognathite directly though its movements were apparent in his pressure traces.

CHAPTER 8. OXYGEN CONSUMPTION

8.1. Introduction

A substantial amount of literature exists on various aspects of the respiratory physiology of decapod crustaceans and there has been considerable progress in recent years (cf. reviews of Wolvekamp and Waterman (1960) with McMahon and Wilkens (1983) and Mangum (1983)). The combined approach of Larimer (1961) who examined the relationship between oxygen consumption and ventilation in the crayfish *Procambarus simulans* has been followed by numerous subsequent workers. Larimer also investigated haemocyanin equilibrium in crayfish under respiratory stress (Larimer and Gold, 1961). Additionally, he investigated cardiac responses during hypoxia (Larimer, 1962) and examined tactile, flow, temperature and chemical stimuli which could induce short term fluctuations in ventilation and circulation (Larimer, 1964).

There are now numerous studies of oxygen consumption in decapod crustaceans, often combined with studies of ventilatory and cardiac activity and haemocyanin function. Most studies are of subtidal and intertidal species but the list of species is not extensive and most work has concentrated on several species of reptantian decapods with little work on natantian decapods. The reptantia that have received the most attention are various crayfish species (Larimer, 1961; Wiens and Armitage, 1961; Flindt and Karman, 1972; Dejours and Beckenkamp, 1977; Angersbach and Decker, 1978: Rutledge, 1981; Wilkes and McMahon, 1982), the lobsters *Homarus americanus* (McLeese, 1964; McLeese and Watson, 1968; McMahon and Wilkens, 1975; Penkoff and Thurberg, 1982) and *H. gammarus* (Thomas, 1954; Spoek, 1974; Butler *et al.*, 1978; McMahon *et al.*, 1978), crabs of the genus *Cancer*, *C.pagurus* (Aldrich, 1975a, b, c; Ansell, 1973; Bradford and Taylor, 1981), *C. magister* (Johansen *et al.*, 1970; McMahon *et al.*, 1977; McMahon *et al.*, 1979; McDonald *et al.*, 1980), *C. productus* (McMahon and Wilkens, 1977; deFur and McMahon, 1978), the swimming crab *Callinectes sapidus* (Mangum and Weiland, 1975; Laird and Haefner, 1976; Batterton and Cameron, 1978; Booth *et al.*, 1982) and the shore crab *Carcinus maenas* (Arudpragasam and Naylor, 1964b; Newell *et al.*, 1972; Wallace, 1972, 1973; Marsden *et al.*, 1973; Breteler and Klein, 1975; Truchot, 1975; Al-Wassia *et al.*, 1976; Taylor, 1976; Taylor, 1977; Al-Wassia, 1978; Taylor and Butler, 1978; Aldrich, 1979; Taylor and Wheatly, 1979; Truchot, 1979). There is also less extensive information on other aquatic species. This includes work on *Nephrops norvegicus* (Bridges and Brand, 1980), rock lobsters (*Panulirus* spp.) (Nimura and Inoue, 1969; Winget, 1969), hermit crabs (Davenport *et al.*, 1980; Bridges and Brand, 1980; Wernick and Penteado, 1983; the anomuran *Galathea strigosa* (Bridges, 1976; Bridges and Brand, 1980), the thalassinids *Callianassa californiensis* and *Upogebia pugettenis* (Thompson and Pritchard, 1969) and various crabs - *Corystes cassivelaunus* (Bridges, 1976; Bridges and Brand, 1980), *Libinia emarginata* (Aldrich, 1975c; Burnett, 1979), *Maia squinado* (Aldrich, 1975a, b), *Chionectes opilio*, (McLeese and Watson, 1968), *Ovalipes ocellatus* (Birchand *et al.*, 1982), *Pugettia producta* (Weymouth *et al.*, 1944), *Menippe mercenaria* and *Panopeus herbstii* (Leffler, 1973), all subtidal, and the intertidal *Macrophthalmus hirtipes* (Hawkins *et al.*, 1982), *Helica crassa* (Shumway and Jones, 1981; Hawkins *et al.*, 1982), *Pachygrapsus crassipes* (Roberts, 1957a, b), *Hemigrapsus* spp. (Dehnel, 1958, 1960) and *Uca* spp. (Brown *et al.*, 1954; Tashian, 1956; Vernberg and Vernberg, 1966).

The only fully comprehensive respiratory study on a natantian is that of Morris (1983) for the rock pool shrimp Palaemon elegans. Other natantian studies include those of McFarland and Pickens (1975) on Palaemonetes vulgaris and Nelson et al. (1977) on Macrobrachium rosenbergii.

There is, however, information on the haemocyanin of an extensive list of aquatic decapod crustacean species (see Mangum, 1982, 1983).

Compared with aquatic decapods, there have been fewer studies on O_2 consumption of terrestrial and semiterrestrial species and little has been done on the oxygen carrying characteristics of their haemolymph. Ayers (1938) compared the oxygen consumption of seven species of crabs in relation to habitat. Three species were entirely aquatic, three were intertidal and the other was the land crab Ocypode quadrata which had the highest rate of oxygen consumption. Flemister and Flemister (1951) showed that the respiration rate was elevated in submerged O. quadrata and that this increase was least when the crab was in an environment in which the chloride ion concentration equalled that of the blood. Increased oxygen consumption in hypotonic and hypertonic environments was due to increased ion regulating activities at the antennal glands and gills.

Vernberg (1956) compared the oxygen consumption of excised gill tissue and mid-gut gland in nine crabs, three subtidal, four intertidal and two supratidal including O. quadrata whose gill tissue had the highest rate of oxygen consumption. The rate of oxygen uptake of gill tissue decreased progressively through the crab species as the habitat became increasingly marine. High rates of oxygen consumption of gill and mid-gut gland tissue correlated with high activity - the very active O. quadrata was very similar to the swimming crab Callinectes sapidus in this respect. Mid-gut gland oxygen consumption did not correlate with habitat differences. Veerannan (1974) compared the respiratory metabolism of a subtidal, an intertidal and a supratidal crab, the last being O. platytarsis. He claimed that all three species were metabolically equally efficient with loss of respiratory surface being compensated for by increased respiratory efficiency. In O. platytarsis, aerial respiration was increasingly important with increasing size.

Burnett (1979) investigated the effects of environmental oxygen levels on the respiratory function of haemocyanin in O. quadrata exposed to normoxic and hypoxic conditions. O. quadrata blood had a high concentration of haemocyanin which was 96% oxygen saturated at the gills making a high rate of blood circulation unnecessary. Cardiac output decreased during progressive hypoxia in contrast to the situation in the aquatic spider crab Libinia emarginata.

Work on oxygen consumption in terrestrial and semiterrestrial crabs is, however, not restricted to Ocypode species. The anomuran coconut crab Birgus latro has received attention (Harms, 1932; Cameron and Mecklenberg, 1973; McMahon and Burggren, 1979b) as have land hermit crabs Coenobita spp. (Burggren, 1975; McMahon and Burggren, 1979a; Burggren and McMahon, 1981). The land crab, Cardisoma carnifex was investigated by Wood and Randall (1981), and C. guanhumi by Cameron (1975), O.'Mahoney (1977) and Herreid et al. (1979). Other land crabs whose oxygen consumptions have been studied are Gecarcoidea lalandii (Cameron and Mecklenberg, 1973) and Gecarcinus lateralis (von Raben, 1934; Richmond, 1968; Taylor and Davies, 1981, 1982). Many of these papers also contain information on the properties of the blood. Haemocyanin characteristics of terrestrial and semiterrestrial decapods are reviewed by Mangum (1983) (see also Young, 1972a, b; Mangum, 1982).

The above species are marine land crabs. Aerial and aquatic respiration in the freshwater land crab Holthuisana transversa has also received detailed study (Greenaway and Taylor, 1976; Taylor and Greenaway, 1979; Greenaway et al., 1983a, b; Greenaway, 1984).

All of the above crabs have structural adaptations for respiration in air including epibranchial 'lungs' (see Chapter 7). Intertidal reptantian decapods, however, may undergo aerial respiration, eg. Carcinus maenas (Newell et al., 1972; Taylor and Butler, 1978), Callinectes sapidus (O'Mahoney, 1977), Macrophthalmus hirtipes (Hawkins et al., 1982), and Helica crassa (upper shore to semiterrestrial) (Hawkins et al., 1982).

Against this background the oxygen consumption of O. saratan was investigated under aerial conditions at a range of temperatures and under aquatic conditions at a single temperature. Some information was also obtained on the oxygen affinity of the haemocyanin and other blood characteristics.

8.2. Material and Methods

For determination of the rate of oxygen consumption in air, the aerial respirometer employed was that described by Davies (1966). This constant pressure respirometer consists of an acrylic respiration chamber (various sizes depending on crab size) which is screwed into a baseplate and is in connection with a similar compensation chamber through a series of connecting tubes and a manometer capillary (containing kerosene) drilled into an acrylic manometer block mounted above the baseplate. A metric micrometer head (Moore and Wright) mounted in the manometer block and in connection with the respiration chamber, enables volumetric measurements to be made. As the crab consumes oxygen in the respiration chamber and as the CO_2 produced is absorbed by KOH on filter paper, a decrease in pressure results. The micrometer head is then adjusted to equalise pressure (level the kerosene manometer) and the volume advanced by the micrometer spindle is equivalent to the oxygen consumed.

Six constant pressure respirometers were employed simultaneously. They were mounted in a water bath maintained at the required temperature and shielded with opaque plastic sheeting so as to minimise disturbance caused by observer movement or movement from adjacent crabs.

Experimentation indicated that the disturbance caused by handling the crabs and placing them in the respirometers resulted in elevated $\dot{V}O_2$ that normally took 4 to 6 hours to decline to a constant rate characteristic of unstressed, inactive crabs. At $40^{\circ}C$, however, the $\dot{V}O_2$ was continuously high and mortalities occurred during the acclimation period: only large crabs survived experimentation. To avoid similar mortalities it was decided to reduce the settling in period at $35^{\circ}C$ to 3 hours.

The temperatures employed were 15, 20, 25, 30, 35 and $40^{\circ}C$. $10^{\circ}C$ was also attempted but crab mortality was 100%.

Aquatic respiration was investigated using the continuous flow respirometer of Al-Wassia (1978) at $25^{\circ}C$. This respirometer consisted of a cylindrical acrylic respirometer chamber immersed in a reservoir tank of temperature controlled seawater ($25^{\circ}C$). Water was pumped from this tank up to a gas exchange column and then ran by gravity from a constant head into the respirometer and then back into the reservoir. The oxygen tension of water samples withdrawn from the inlet and outlet tubes of the respirometer were measured using a Radiometer E5046 0_2 electrode mounted in a thermostatted cell maintained at the same temperature ($25^{\circ}C$) as the respirometer. The oxygen electrode was connected to a Strathkelvin 781b oxygen meter. The apparatus also incorporated a flow meter and a bubble trap.

The rate of oxygen consumption at different temperatures was plotted as a function of body weight on a double logarithmic scale giving a straight line with a negative slope.

For the regression of weight specific oxygen consumption against body weight

$$y = ax^{b}$$

where y is the volume of oxygen consumed per unit time, x is body weight and a and b are constants.

$$\frac{y}{x} = ax^{b-1}$$

since b is usually less than 1, b-1 will have a negative value

$$\log y = \log a\text{-}b \log x$$

where y = oxygen consumption of the crab in $\mu \ell O_2.g^{-1}.h^{-1}$

w = body weight (g)

a = intercept

b = slope of the regression line

Covariance analysis was employed to test whether the differences in slope (b) or elevation (a) in $\dot{V}O_2$ determinations at different temperatures were significantly different.

Q_{10} determinations were also made using the general formula

$$Q_{10} = \left(\frac{R_2}{R_1}\right)^{\frac{10}{T_2-T_1}}$$

where R_1 = rate of oxygen consumption at temperature 1 (T_1)

and R_2 = rate of oxygen consumption at temperature 2 (T_2)

For blood characteristics I am indebted to Dr C.R. Bridges and Dr C.R. Morris (University of Düsseldorf) who agreed to examine some blood samples from my O. saratan for the in vitro determinations of haemocyanin oxygen affinity at a range of temperatures (20°C - 35°C).

Oxygen binding curves were constructed using spectrophotometric methods in a diffusion chamber. Several curves were constructed at each temperature using blood equilibriated with different CO_2 tensions, this serving to vary blood pH. The same blood was used in the tonometers of a Radiometer BSM2 which received the same gas mixtures as the diffusion chamber. By this means pH was determined using the micro pH electrode in the BMS2, near to the half saturation point (P50). For the full methodology see Morris and Bridges (1985). I have included some of the information that resulted from this original exercise. Later Drs Bridges and Morris obtained a further series of blood samples and characterised the blood more fully (Morris and Bridges, 1985).

I was able to conduct some in vivo investigations on O. saratan blood at Glasgow using the same techniques as used by Taylor and Davies (1981) for Gecarcinus lateralis and Taylor (1984) for Atelecyclus rotundatus. O. saratan were maintained at 25°C and acclimated for at least 7 days. Pre-branchial blood samples were withdrawn using a hypodermic syringe inserted through the arthrodial membrane at the base of one of the pereiopods. Post-branchial blood was withdrawn by hypodermic needle through a 1mm thick rubber membrane glued with cyanoacrylate adhesive over a small hole previously drilled through the carapace above the pericardium. Care was taken to ensure that the crabs were undisturbed prior to sampling in order to obtain values representative of quiescent crabs.

The blood samples were used for PO_2 and pH determinations. The PO_2 of the blood samples was determined by injecting the samples into a thermostatted cell (at 25°C) containing a Radiometer oxygen electrode connected to an oxygen meter (Strathkelvin Instruments). Blood pH measurements were made at the same temperature (25°C) using a Radiometer capillary pH electrode contained in a Radiometer BMS2 and calibrated using precision pH buffers.

Oxygen content of the blood was also determined at Glasgow using the method of Morris and Bridges (1985).

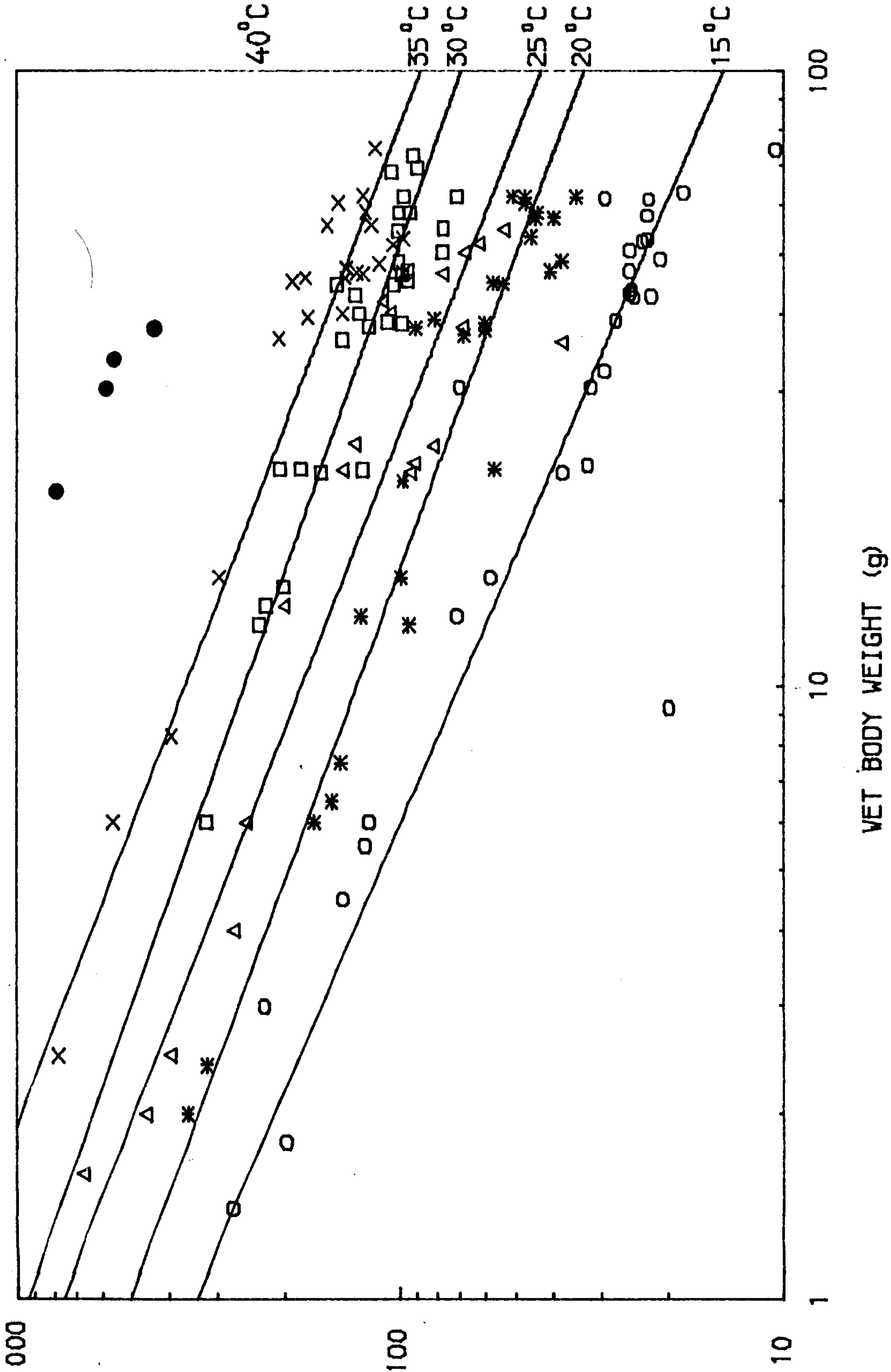
8.3. Results

8.3.1. Aerial weight specific oxygen consumption

8.3.1.1. Effect of temperature

The changes in $\dot{V}O_2$ exhibited by crabs acclimated to 25°C and then exposed to different temperatures within the normal environmental range (15°C to 35°C) are shown in Fig. 8.1. The regression lines of logarithmically transformed data of weight specific oxygen consumption at different temperatures against body weight have similar slopes indicating that the effect of temperature was constant over the crab size range. Covariance analysis of these data showed there was no significant difference in the slopes of the regression lines but the differences in the elevations of the lines were significant.

Fig. 8.1. Relationship between aerial weight specific oxygen consumption and body weight of _O. saratan_ at different temperatures.


OXYGEN CONSUMPTION (uL. O₂/g/h)
1000
100
10
WET BODY WEIGHT (g)
1
10
100
40°C
35°C
30°C
25°C
20°C
15°C

Most crabs did not survive exposure to 40°C but several data points obtained for larger crabs are shown in Fig. 8.1 though insufficient data were obtained for statistical comparison. There was 90% experimental mortality at 40°C: only the largest crabs survived. At 10°C there was 100% mortality during acclimation or experimentation and consequently no useful data were obtained.

Table 8.1. Regression equations for $\dot{V}O_2$ against fresh weight (g).

Aerial respiration

Temperature °C	Regression equation $\log y = \log a - b \log x$	r	n	P
15	$y = 2.532-0.688x$	-0.921	29	s
20	$y = 2.700-0.592x$	-0.959	27	s
25	$y = 2.879-0.625x$	-0.940	19	s
30	$y = 2.968-0.566x$	-0.918	30	s
35	$y = 3.172-0.615x$	-0.950	24	s

Aquatic respiration

Temperature °C	Regression equation $\log y = \log a \pm b \log x$	r	n	
25	$y = 2.431-0.445x$	-0.899	13	s

The regression line is in each case a highly significant fit, $P < 0.001$.
$y = \dot{V}O_2$, x = fresh weight, for air mean $b = 0.617$

A comparison of the $\dot{V}O_2$ data from 15, 20, 25, 30 and 35°C shows that as the temperature increases, oxygen consumption ($\mu l.g^{-1}.h^{-1}$) increases throughout the range of crab weights (Fig. 8.1).

The covariance comparisons are summarized in the following table where a is the intercept and b the slope of the regression lines tabulated above.

Table 8.2. Covariance comparisons of $\dot{V}O_2$

Compared groups	a	b
15-20°C	S ($P < 0.005$)	NS
20-25°C	S ($P < 0.025$)	NS
25-30°C	S ($P < 0.01$)	NS
30-35°C	S ($P < 0.05$)	NS
all combined	S ($P < 0.005$)	NS
aerial-aquatic		
25°C - 25°C	S ($P < 0.001$)	NS ($0.1 > P > 0.05$)

Table 8.3. Q_{10} relationships for O_2 consumption of *O. saratan*

weight (g)	15-20°C	20-25°C	25-30°C	30-35°C
2	2.0	1.7	1.7	2.0
5	2.6	1.7	1.7	2.0
10	3.6	2.0	2.0	2.0
15	3.6	2.0	2.3	2.0
20	4.0	2.0	2.3	2.0
30	4.4	2.0	2.3	2.0
40	4.8	2.0	2.0	2.0

weight (g)	15-25°C	20-30°C	25-35°C
2	1.8	1.8	1.8
5	2.2	1.8	1.9
10	2.5	1.9	1.9
15	2.3	1.9	1.8
20	2.7	2.0	1.9
30	2.7	2.0	2.0
40	3.3	2.2	1.9

The Q_{10} values derived from the $\dot{V}O_2$ data were not entirely constant over the range of temperatures employed. The main differences are seen when the $\dot{V}O_2$ data from 15°C and 20°C are compared. Here Q_{10} values range from 2.0 for a 2g crab to 4.8 for a 40g crab. Otherwise

Fig. 8.2. Relationship between aquatic weight specific oxygen consumption and body weight in <u>O. saratan</u> at 25°C.

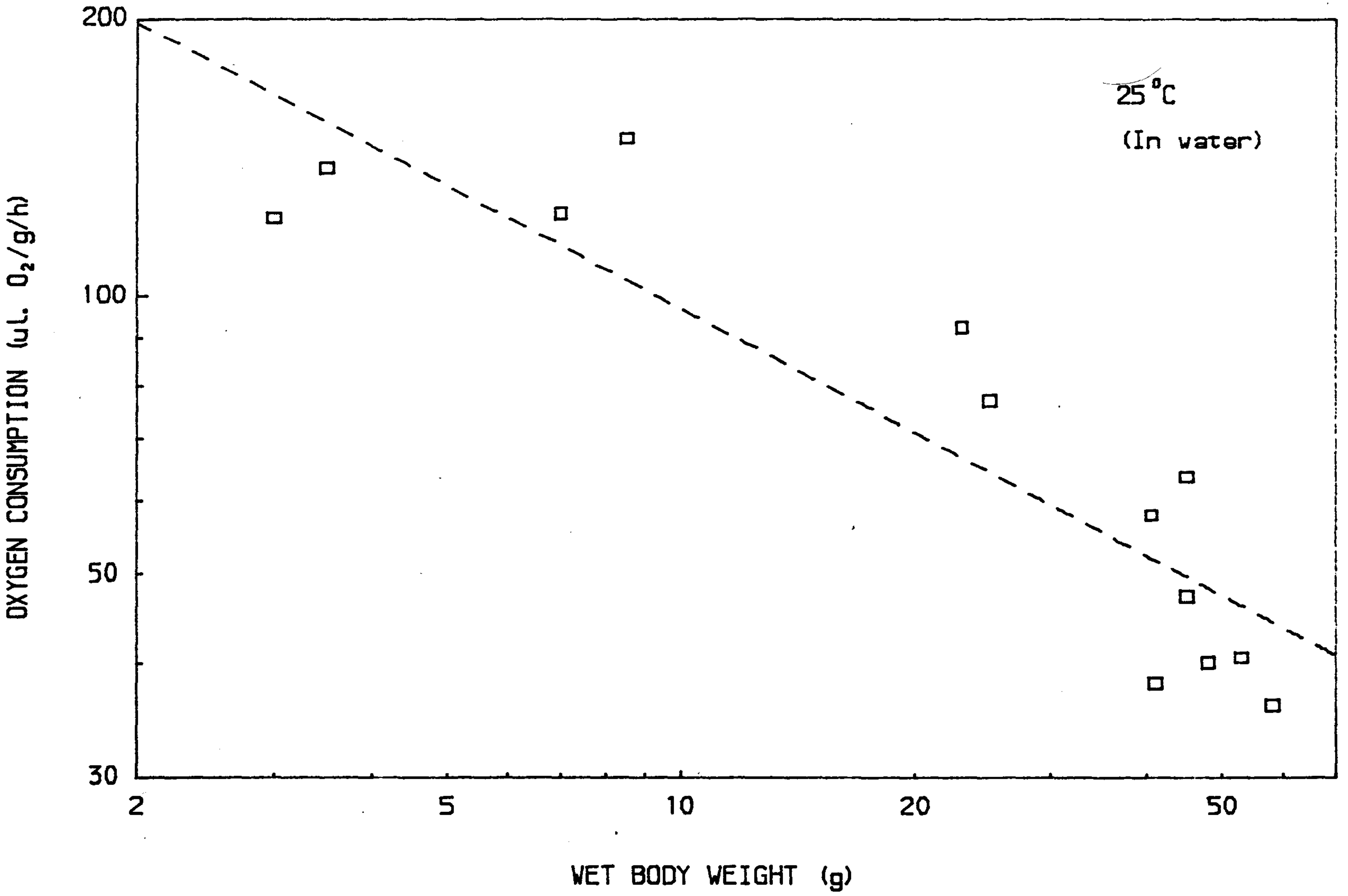
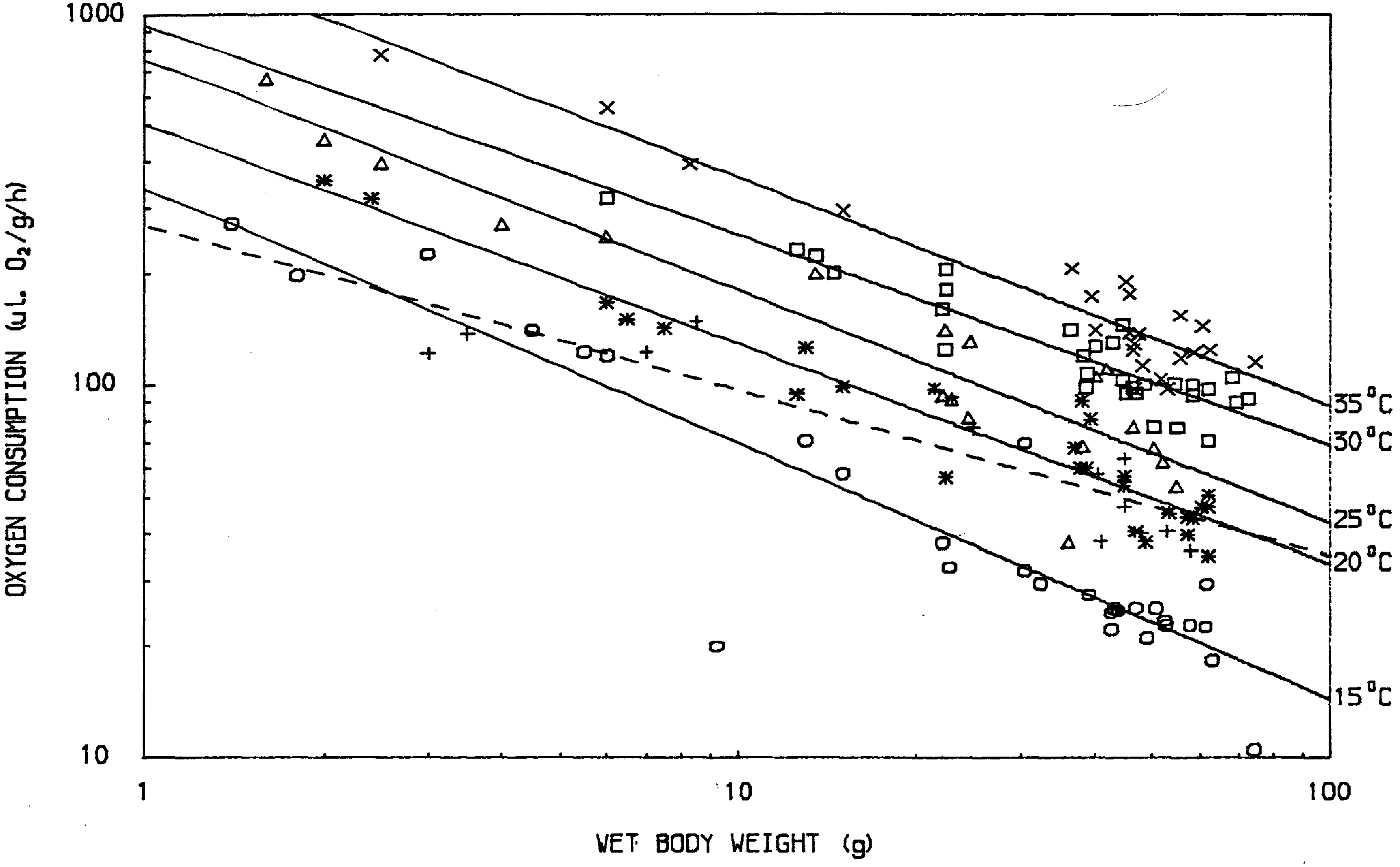

25 °C
(In water)
200
100
50
30
2
5
10
20
50
OXYGEN CONSUMPTION (uL. O_2/g/h)
WET BODY WEIGHT (g)

Fig. 8.3. Data of Figs 8.1. and 8.2. combined to compare aerial and aquatic weight specific oxygen comsumption of O. saratan.


OXYGEN CONSUMPTION (uL. O_2/g/h)
1000
100
10
1
10
100
WET BODY WEIGHT (g)
35°C
30°C
25°C
20°C
15°C

values are between 1.7 and 2.0 and are lowest in the smaller crabs at higher temperatures.

8.3.2. Aquatic weight specific oxygen consumption

Aquatic oxygen consumption was only investigated at one temperature, 25°C, which was close to environmental sea temperature (see Chapter 2). During immersion crabs appeared to be stressed and this is also evident from the data presented in Chapter 7. The data obtained for weight specific O_2 consumption are shown in Fig. 8.2 and the aerial and aquatic data are combined in Fig. 8.3. Statistical comparisons were tabulated in section 8.2.1. Although the slope of the regression line for aquatic respiration at 25°C appears rather different from that obtained for aerial respiration at the same temperature, covariance analysis showed it was not significantly different at the 5% level but the value was only just less than the significance value (F_s with 1 and 29 d.f. = 3.916 cf. 5% significance level of 4.17).

8.3.3. Blood characteristics

Fig. 8.4 presents oxygen dissociation curves for *O. saratan* haemocyanin, constructed at 30°C. This illustrates the general pattern seen at each temperature tested. The results indicate a significant Bohr effect. Hill plots of the data at each temperature were used to precisely define the $P_{50's}$ of the curves measured at a range of pH values.

Fig. 8.5 illustrates the pH dependence of log P_{50} for the haemolymph at a range of temperatures. The regression equations for the lines are given in the legend. At the *in vivo* pH of 7.8 (see Table 8.4) the P_{50} will have a value of 13.2 Torr at 25°C and 13.8

Fig. 8.4. Oxygen dissociation curves for <u>O. saratan</u> haemocyanin constructed at 30°C using PCO_2 to vary pH. The value 1 of S, the Hill coefficient may be regarded as 100% saturation.

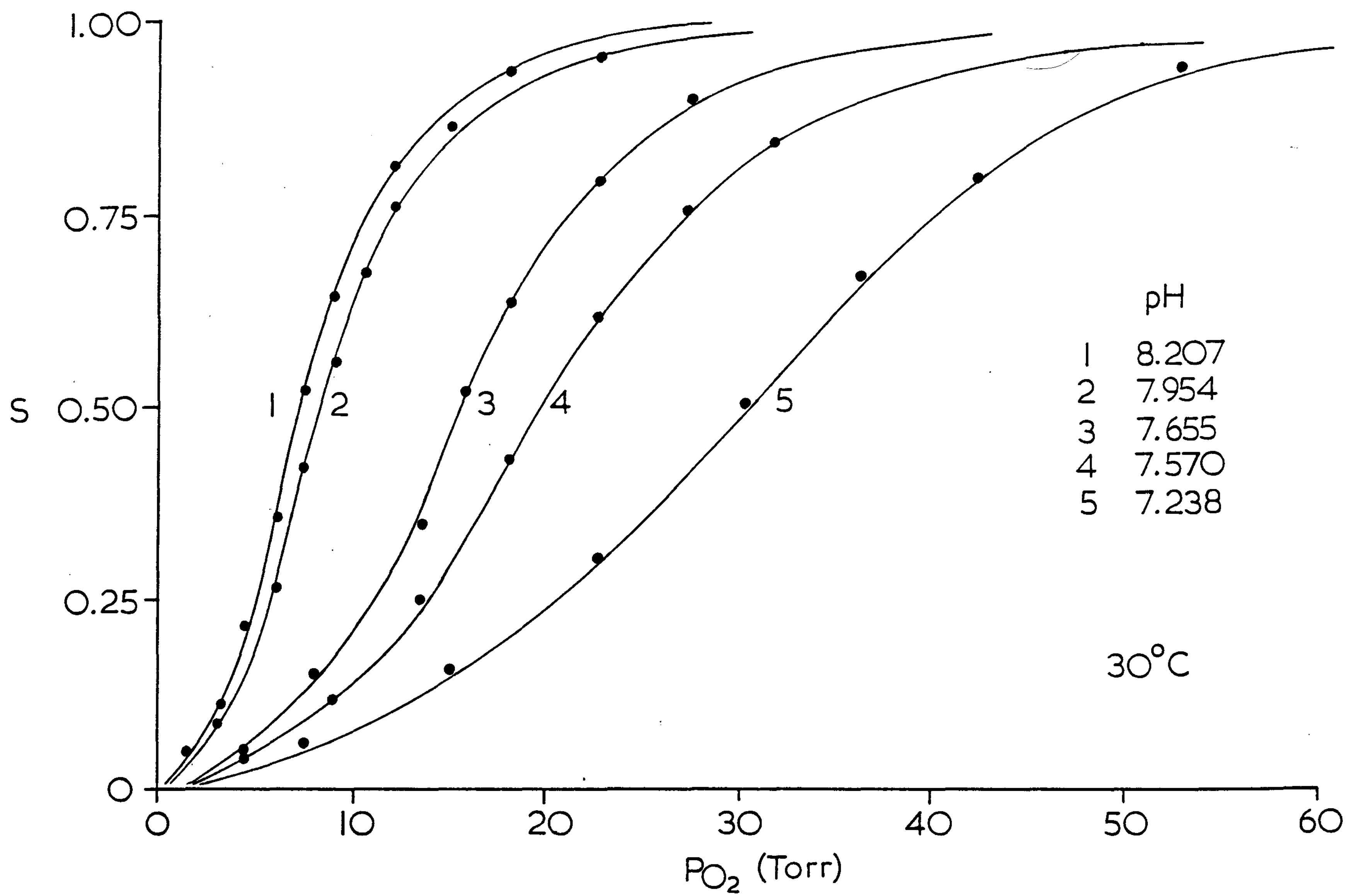

S
1.00
0.75
0.50
0.25
0
0
10
20
30
40
50
60
P_{O_2} (Torr)
1
2
3
4
5
pH
1 8.207
2 7.954
3 7.655
4 7.570
5 7.238
30°C

Fig. 8.5. The pH dependence of log P_{50} for the haemolymph of _O. saratan_ at 20, 25, 30 and 35°C. The regression equations are

20°C $y = 6.121 - 0.656x$, $r = -0.996$

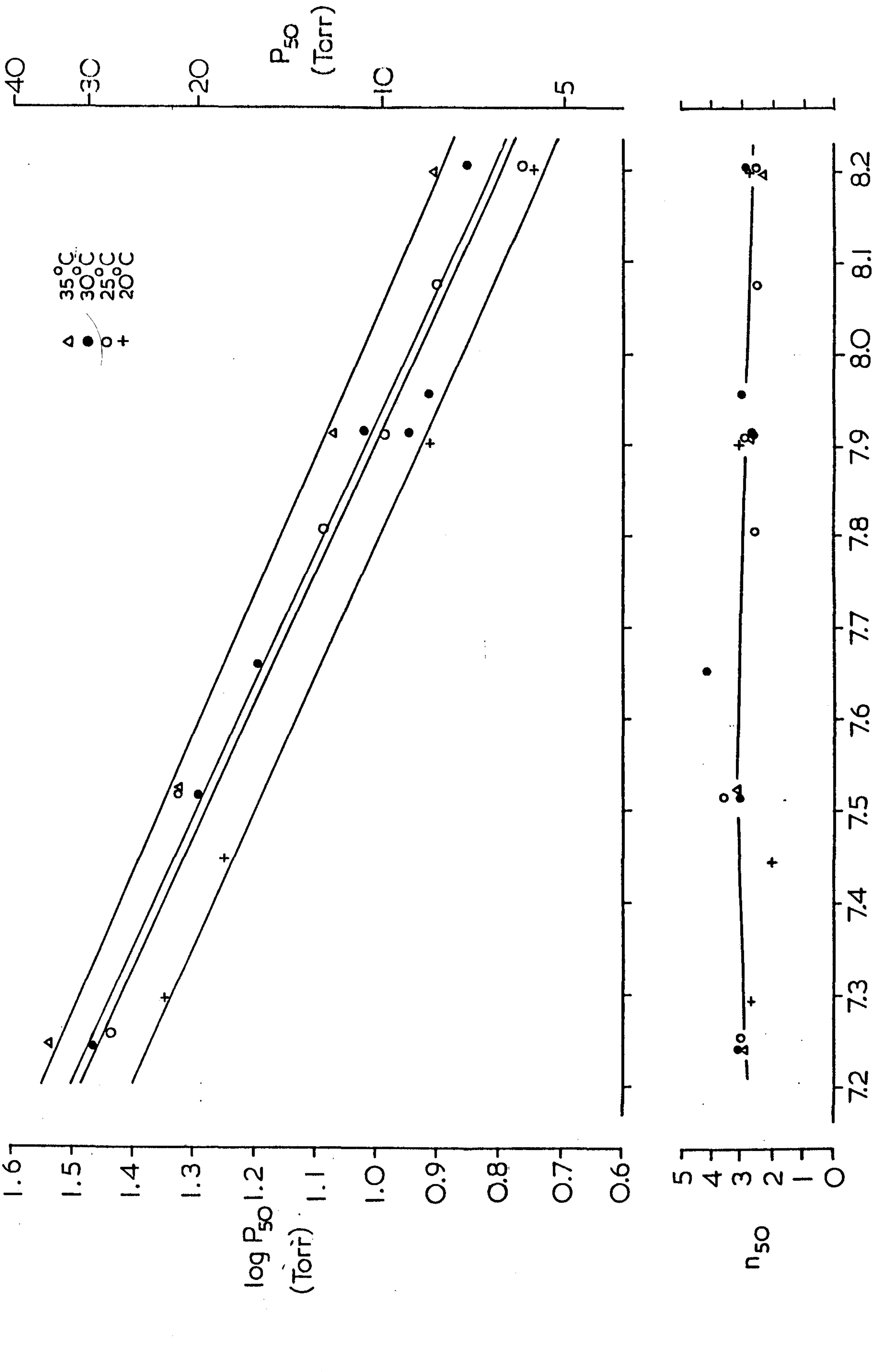
25°C $y = 6.562 - 0.703x$, $r = -0.992$

30°C $y = 6.346 - 0.674x$, $r = -0.982$

35°C $y = 6.212 - 0.648x$, $r = -0.998$

where $y = \log P_{50}$ and $x = \text{pH}$

The pH dependence of cooperativity measured at P_{50} is given in the lower part of the figure.


△ 35°C
● 30°C
○ 25°C
+ 20°C
log P_{50} (Torr)
1.6
1.5
1.4
1.3
1.2
1.1
1.0
0.9
0.8
0.7
0.6
P_{50} (Torr)
40
30
20
10
5
n_{50}
5
4
3
2
1
0
pH
7.2
7.3
7.4
7.5
7.6
7.7
7.8
7.9
8.0
8.1
8.2

at 30°C. The haemocyanin of O. saratan exhibits a normal positive Bohr effect. The Bohr factor ($\Delta \log P_{50} / \Delta pH$) lies between -0.648 and -0.703 ($\bar{x} = -0.670$) at temperatures in the range of 20°C to 35°C. The slopes of these calculated regression lines are not significantly different and it would appear that the Bohr factor is insensitive to temperature at least over this temperature range.

The cooperativity of the oxygen binding to the haemocyanin (n_{50}) is independent of pH within the physiological pH range. It lies within the range found in other decapods (Mangum, 1983). At the same time there is no apparent effect of temperature on cooperativity and this is also normal (Morris et al., 1985).

The in vivo data show that the pH of the blood is quite high and this is consistent with the information available for O. quadrata (Burnett, 1979), Table 8.4 gives the in vivo data for O. saratan. This pH range is within the normal range for decapod crustaceans (Mangum, 1983).

The values for the oxygen tension in the post-branchial haemolymph (P_aO_2) are quite high as has been found in many other decapods (Mangum, 1983). At these in vivo oxygen tensions the haemocyanin will be fully saturated on leaving the gills/lungs.

The oxygen carrying capacity of the haemocyanin was equivalent to 1.64ml/100ml.

Table 8.4. The oxygen tension of pre- and post-branchial blood of O. saratan at 25°C.

	Pre-branchial blood		Post-branchial blood	
	PvO_2 (Torr)	pHv	PaO_2 (Torr)	pHa
$\bar{x}$	19.86	7.778	72.15	7.837
S.D.	±2.82	±0.033	±12.39	±0.103
n	7	7	6	6

8.4. Discussion

Generally speaking, the standard levels of oxygen consumption in terrestrial and semiterrestrial crustaceans are greater than in aquatic species (McMahon and Wilkens, 1983). Oxygen extraction efficiency is generally much lower than in aquatic crabs and the ventilation rate is consequently high (Taylor and Davies, 1981; McMahon and Wilkens, 1983). O quadrata increases ventilation in response to hypoxic or hypercapnic conditions (Burnett, 1979), in common with other species, eg. Birgus latro (Cameron and Mecklenberg, 1973) and Coenobita clypeatus (McMahon and Burggren, 1979a). Ventilation increases are also associated with increased activity in Cardisoma guanhumi (Herreid et al., 1979) and Coenobita clypeatus (McMahon and Burggren, 1979a). The ventilation rate of O. saratan was not high except in immersed crabs.

The rôle of the haemocyanin in blood oxygen transport has been investigated in only a few species of semiterrestrial crabs. From the data currently available, however, it appears that the blood of the majority of semiterrestrial species is characterized by having a higher haemocyanin oxygen carrying capacity and a somewhat higher oxygen affinity than that of most marine crabs. The haemocyanin oxygen carrying capacity in Ocypode saratan was 1.64 ml/100ml and is slightly lower than that of O. quadrata (2.55ml/100ml) (Burnett, 1979).

Morris and Bridges (1985) stated the oxygen carrying capacity of *O. saratan* haemocyanin was 1.59-1.62ml/100ml which agrees with the present data. Even higher oxygen carrying capacities have been recorded, however, in other semiterrestrial species, eg. 2.9ml/100ml in *Cardisoma carnifex* (Burggren and McMahon, 1981), 2.83ml/100ml in *C. guanhumi* (Redmond, 1962), 2.0ml/100ml in *Birgus latro* (Burggren and McMahon, 1981) and 3.5ml/100ml in *Coenobita clypeatus* (McMahon and Burggren, 1979a).

The haemocyanin of *O. saratan* also exhibited a moderately high oxygen affinity (P_{50} = 13.2 Torr at 25°C and ph = 7.8). The oxygen affinity of *O. saratan* is slightly higher than that of *O. quadrata* (P_{50} = 27.5 Torr at 25°C; Burnett, 1979). The oxygen affinity of these two species, however, is not particularly high when compared with that of some other terrestrial and semiterrestrial crabs, eg. 3.9 Torr (pH = 8.18) in *Cardisoma guanhumi* (Young, 1972a) and 4.5 Torr (pH = 7.53) in the same species (Redmond, 1962), 6.6 Torr (pH = 7.62) in *Coenobita clypeatus* (McMahon and Burggren, 1979a) although somewhat lower oxygen affinities have been reported in other species, eg. 20 Torr (pH = 7.3) in *Gecarcinus lateralis* (Taylor and Davies, 1981), 13 Torr (pH = 7.46) and 25 Torr (pH = 7.46) in *Cardisoma carnifex* and *Birgus latro* respectively (Burggren and McMahon, 1981). It has been suggested that many semiterrestrial species have high affinity pigments since it will enable the oxygen in the branchial chambers to be virtually exhausted between periods of ventilatory activity and this may represent an adaptation for conserving water (McMahon and Burggren, 1979a; McMahon and Wilkens, 1983).

7

Semiterrestrial species also show variation in the magnitude of the Bohr effect. Values for the Bohr factor (Δ log P_{50} /Δ log pH) range from -0.39 (Redmond, 1968) and -0.43 (Taylor and Davies, 1981) in Gecarcinus lateralis to -0.84 in Coenobita clypeatus (McMahon and Burggren, 1979a) and -1.19 in Cardisoma guanhumi (Redmond, 1962). The value of -0.67 obtained during the present study for O. saratan is slightly lower than the value recorded by Burnett (1979) in O. quadrata (-0.76).

If meaningful comparisons of the rôle of the haemocyanin in blood oxygen transport are to be made, it is essential that the oxygen tensions of the pre- and post-branchial blood are known. The values of PaO_2 and PvO_2 in O. saratan reported here are quite high but are similar to those found for many other crabs. There does, however, appear to be some variation between species, some of which ? may be attributable to differences in experimental techniques between different workers. The high values for PaO_2 and PvO_2 in O. saratan are in contrast to the much lower values (PaO_2 = 20 Torr; PvO_2 = 9 Torr) in O. quadrata (Burnett, 1979). Assuming that the animals used by Burnett (1979) were not stressed and that the values reported by him were also for quiescent animals, it is difficult to provide an explanation of the differences in the PO_2 of the blood in these two species. Since the oxygen affinity of the haemocyanin of O. saratan was higher than that of O. quadrata, it might have been expected that the values of PaO_2 and PvO_2 in the former species would have been lower than in the latter whereas the reverse is the case. A satisfactory explanation of this anomaly must await further studies.

Since the oxygen affinity of the blood of O. saratan is moderately high (P_{50} = 13.2 Torr at 25°C and pH = 7.8), even at the in vivo pre-branchial oxygen tension of 20 Torr the haemocyanin will be reasonably saturated (c. 75%). This appears to indicate that, as in some other crabs, the haemocyanin does not play a major rôle in oxygen transport to the tissues in quiescent crabs. Most of the oxygen taken up by the tissues in resting animals is transported in solution in the blood. The oxygen bound to the pigment may therefore be used as an oxygen store during times of stress or high activity as has been shown in some other aquatic crabs (McMahon and Wilkens, 1975; Taylor 1976).

There is an extensive literature on the relationship between the rate of oxygen consumption and body size in marine invertebrates (Newell, 1979; Branch and Newell, 1980) and Bridges and Brand (1980) present comparative information on the relationship between $\dot{V}O_2$ (weight specific O_2 consumption) and body weight (w) in the decapod crustaceans and indicate that the value of b (slope) in the equation $\dot{V}O_2 = aw^{b-1}$ (see Material and Methods) may be extremely variable - between 0.286 and 0.877 in the data presented. Zeuthen (1953) suggested that metazoan metabolism varied with the 0.67 power of body weight (ie. b = 0.67) since it was related to total cell-surface area but additional factors affect metabolism giving a variation in b values (see Hemmingson, 1950, 1960; Bridges and Brand, 1980). Bridges and Brand (1980) specifically compared two burrowing species with two non-burrowing species and demonstrated that the former had significantly higher b values which they interpreted as being correlated with their more sedentary mode of life. O. saratan, although a burrowing species, is extremely active. Its b values were in fact low, the mean value from the aerial respirometry was 0.381 and from the water respirometry 0.555. Taylor and Davies (1981) showed a b value of 0.47 for Gecarcinus. There is more and more evidence of wide variability in such values and Schmidt-Neilson (1984) urges caution in the interpretation of metabolic rate and body size information for invertebrates. The picture for warm blooded vertebrates seems much more consistent. Wolcott (1978) gives a b value of 0.69 for O. quadrata which differs from the data presented here for O. saratan. It must be stressed, however, that the differences in this value between decapod species is unclear and may reflect differences in experimental techniques and in the size ranges of animals used.

The rate of weight specific oxygen consumption in water was consistently lower in water compared with the rate in air. Exactly the same relationship was found in Gecarcinus lateralis by Taylor and Davies (1982). Flemister and Flemister (1951), however, indicated an oxygen consumption for O. quadrata of $139\mu l.g^{-1}.h^{-1}$ (size range not given) which is in the same range as that reported here for O. saratan. They state that oxygen consumption was greater in submerged crabs but they present no actual data on which to evaluate this statement. Although not significantly different at the 5% level the difference in slope of the aquatic regression line for O. saratan compared with that fitted to the aerial data suggests that the O_2 consumption of smaller animals is reduced by a proportionately larger amount than in the larger animals investigated.

The reduction in O_2 consumption of G. lateralis in water compared with its rate in air was interpreted as being due to the respiratory system failing to deliver sufficient oxygen to meet the demands of the tissues (Taylor and Davies, 1981). In both G. lateralis and O. saratan the scaphognathite rate in water is dramatically increased when compared with the rates in air. Despite this respiratory response to submersion and the accompanying changes in blood gas transport (see Taylor and Davies, 1982), the crabs are unable to maintain a sufficient supply of oxygen to meet the demands of the tissues. An increase in scaphognathite rate and decrease in heart rate associated with submergence in G. lateralis (Taylor and Davies, 1982) was also observed in O. saratan under similar conditions. This response is similar to that seen during hypoxia in marine decapods since for terrestrial and semiterrestrial crabs water is essentially a hypoxic medium. Observations on O. saratan suggested they were stressed during submergence. Crabs did not survive prolonged submergence but the period of survival varied from days to weeks. Pearse, 1929b showed that O. quadrata died following prolonged submersion. The same was true of G. lateralis (Dr A.C. Taylor pers. comm. and Gross, 1964) which will only withstand short periods of immersion.

Hawkins et al. (1982) have examined aerial and aquatic respiration in two littoral crabs and Newell et al. (1972) have looked at this in the shore crab Carcinus maenas. Since these species are basically aquatic species it is not surprising that these species showed higher weight specific oxygen consumption rates in water than in air. Veerannan (1974) examined aerial and aquatic respiration in O. platytarsis. His technique for comparing aquatic versus aerial respiration rates is highly questionable but his actual oxygen consumption rates compare well with those of O. saratan. At 27^{o}C, his rate for aquatic respiration in an 8g crab was 120μl.g^{-1}.h^{-1} and the rate for a 5g crab was 138μl.g^{-1}.h^{-1}. These values are comparable with O. saratan and show a similar inverse relationship with body weight.

In aerial conditions a 5g O. platytarsis had a weight specific O_2 consumption of 160μl.g^{-1}.h^{-1} and for an 8g crab the value was c. 125μl.g^{-1}.h^{-1}. Again, these values are comparable with those of

O. saratan.

Differences in the Q_{10} relationships when heart rate and oxygen consumption are compared suggest that either there are compensatory changes in the blood oxygen delivery or that there are changes in the stroke volume of the heart. At present this cannot be decided and it invites further investigation.

There is a bigger drop in $\dot{V}O_2$ at lower temperatures for larger animals than for smaller animals and the same trend is seen in heart rates. Thus heart rate is maintained at a higher rate in large animals than might be predicted if it was a simple 1:1 relationship. Oxygen affinity of the blood is only slightly temperature dependent between 20 and 35°C (Morris and Bridges, 1985) but was not investigated at lower temperatures either here or by Morris and Bridges (1985) but it is unlikely that the respiratory properties of the blood would vary with crab size. Therefore, the explanation for the differences above may lie in relative changes in heart stroke volume with crab size at different temperatures.

SUBDIVISION B. WATER RELATIONS

CHAPTER 9. DEHYDRATION

9.1. Introduction

Water uptake has been partly considered in Chapter 7 in so far as the irrigation of the branchial chamber of O. saratan has been investigated. Wolcott (1984) indicated that some of this water was seen to pass to the mouth and be ingested in O. quadrata. Water is also taken in as a component of food (see Edney, 1960). In addition there is an extensive literature on water uptake prior to moulting (reviewed by Skinner, 1985) and the rôle of the water absorbing pericardial sacs has been investigated in land crabs including Ocypode spp. by Bliss (1963, 1968, 1979); Bliss and Mantel (1967, 1968) and Rao (1966, 1968a).

In contrast to water uptake, there is water loss. This poses potentially lethal problems for terrestrial and semiterrestrial decapods. Edney (1960) lists the sources of water loss as by transpiration, during the moult and by excretion. Herreid (1969a, b) lists five potential losses; by discharging water from the gill chamber, by faecal losses, by urination, by evaporation from the gills and gill chamber during respiratory ventilation and by other integumentary losses, ie. evaporation from the general body surface.

Water gains and losses create potential osmotic problems. According to Edney (1960) since there is no external aqueous medium, in the generally accepted sense of the term no osmotic problem exists for animals in air but there is a tendency to lose water to the environment and dangerously concentrate body fluids. Osmotic problems in Crustacea are most recently reviewed by Mantel and Farmer

(1983). They indicate that the Gecarcinidae (*Gecarcinus*, *Cardisoma*) are hyperosmotic to concentrations less than seawater and hypoosmotic above 1000mOsm (100% seawater). They tolerate desiccation yet do not produce hyperosmotic urine. Many species of the families Grapsidae and Ocypodidae are subjected to desiccation and varying salinities and in general they are strongly hyperosmotic in dilute media and hypoosmotic at salinities greater than that of seawater where they maintain a very constant internal salt concentration.

For *Ocypode* spp., osmotic information exists for *O. ceratophthalmus* (Gross, 1964), *O. cursor* (Borut and Neumann, 1966), *O. quadrata* (Gifford, 1962) and the species which is the subject of this thesis, *O. saratan* (Spaargaren, 1977). Their data are tabulated by Mantel and Farmer (1983) and are given in slightly modified form below:

	O. ceratophthalmus			*O. cursor*			
Medium	495	985	1655	100	500	1000	1500
Haemolymph	785	860	920	750	750	750	750
Urine	785	860	920	-	-	-	-

	O. quadrata				*O. saratan*			
Medium	250	600	1100	1250	290	580	870	1160
Haemolymph	735	890	920	1105	890	890	1020	1210
Urine	830	1040	1040	1200	-	-	-	-

values are in mOsm.kg^{-1}

Thus in *O. ceratophthalmus* the urine is isosmotic to the haemolymph but in *O. quadrata* the urine is slightly hyperosmotic to the haemolymph. Despite this, according to Wolcott (pers. comm. and Wolcott and Wolcott, 1985) *O. quadrata* may procure water from dilute sources and then needs to conserve salt which it does by retaining urine and extrarenally reducing its salt concentration. O. saratan, however, has no contact with dilute media. Spaargaren (1977) states that O. saratan osmoconforms above 25^{o}/oo salinity but can osmoregulate at lower salinities, this being interpreted along evolutionary lines. Clearly, a re-examination of the ionic concentrations would be worthwhile in O. saratan but this Chapter addresses itself only to water loss.

In relation to water loss there is not much information. Herreid (1969a) states 'the paucity of data on water loss .... is evident' and the recent reviews (Little, 1983; Powers and Bliss, 1983) suggest that this is still true. Recent work has, however, provided fascinating adaptive information on the freshwater derived land crabs of the genus Holthuisana (Parathelphusoidea, Sundathelphusidae) that occur in arid regions of Australia. H. transversa loses water by evaporation at a low rate and can tolerate a 45% loss of its body water. It is capable of absorbing condensation within its burrow enabling it to survive drought and it has well developed osmoregulatory abilities (Greenaway and MacMillen, 1978; MacMillen and Greenaway, 1978; Greenaway, 1980, 1981).

The anomuran Birgus latro (Coenobitidae) can tolerate a 22% loss of body water and the brachyurans Gecarcoidea lalandii and Cardisoma carnifex (Gecarcinidae) can tolerate a 15-18% loss of body water (Harris and Kormanik, 1981). Herreid (1969a) reports lethal percentage weight losses for Cardisoma guanhumi, Gecarcinus lateralis and the ocypodid Uca minax of 16%, 22% and 18% respectively. Herreid (1969a) also reported that the rate of water loss was less in crabs from drier habitats than in those from aquatic habitats. Aquatic crabs, eg. Callinectes sapidus, Aranaeus cribarius, Menippe mercenaria, lost water two to five times more rapidly than semiterrestrial species and at a higher rate than the intertidal mud crabs Panopeus herbstii, Sesarma reticulata and S. cinereum. These lost about twice as much water as the semiterrestrial crabs. The semiterrestrial crabs were Cardisoma guanhumi, Ocypode quadrata, Uca minax, U. pugilator and Gecarcinus lateralis which lost less water than the rest. Consistently, small crabs lost more water.$g^{-1}.h^{-1}$ than large ones and evaporative loss increased at higher temperature. The main route of water loss was the integument exclusive of the gill chamber (Herreid, 1969a, b). Evaporative cooling has been shown to be important in semiterrestrial and terrestrial Crustacea (Edney, 1952, 1960; Smith and Miller, 1973; Powers and Bliss, 1983).

It is also evident that rates of water loss vary with relative humidity (Edney, 1951a, b, 1960, 1961; Williamson, 1951) as does the efficiency of evaporative cooling.

It has been shown that the distribution of many terrestrial and semiterrestrial crustaceans can be partly explained in terms of their rates of water loss and temperature/humidity requirements, eg. Edney has demonstrated this for both isopods (1951a) and crabs (Uca spp.) (1961). There are, however, many other factors which may govern distribution (as Edney (1951a) himself cautioned), for example, in the intertidal mud crabs Helice crassa and Macrophthalmus hirtipes, Jones and Simons (1982) demonstrated that differential desiccation tolerances did not determine distribution but rather feeding and burrowing adaptations related to substrata characteristics.

The natural variation in temperature and relative humidity to which O. saratan is subjected in the field is detailed in Chapters 2 and 3 and it is clear that the environmental conditions are often severe. The burrowing mode of life, however, provides protection from environmental extremes and the importance of this is clear from the results of this section.

9.2. Material and Methods

The crabs used in these experiments were collected from Sharm Obhor and Al-Quaid Island and held in a large outdoor aquarium in which natural conditions were simulated (see Chapter 4) and then transferred to an indoor aquarium at 25°C for 24h before experimentation. Undamaged specimens were then placed in desiccators of 4.2ℓ volume with a stainless steel mesh separating the crabs from the salt solutions employed to control relative humidity. Temperature was maintained at 25°C and oxygen was not limiting. The saturated salt solutions used are tabulated below. The reported values are taken from O'Brien (1948) and Winston and Bates (1960) but humidities were checked using a digital combined temperature humidity probe (Theis Clima, Model 462). The measured values differed slightly from the theoretical predictions.

	RH% value obtained	RH% value reported at 25°C	
silica gel	0		
LiCl	20 ± 5	13.0	12.0
$MgCl_2$	40 ± 3	33.0	32.5
$NaNO_2$	60 ± 5	(66.0) 20°C	64.0
$(NH_4)_2SO_4$	80 ± 2	81.1 - 83.0	80.0
water	90		
		O'Brien (1948)	Winston and Bates (1960)

The differences between observed and expected values at the lower relative humidities were probably due to the water retained in the crabs' branchial chamber elevating relative humidity.

The desiccators were placed within an environmental cabinet (Fisons Fi-Totron Model 600H) in which temperature and humidity were controlled to equal that in the desiccators at all but 0% and 20% RH. Cabinet temperature was 25°C ± 1°C and cabinet relative humidities were 40%, 60%, 80%, 90%. For 0% and 20% RH the cabinet just provided temperature control. The advantages of setting the desiccators within the environmental cabinet were firstly that it provided a controlled temperature environment and secondly the lids could be removed from the desiccators without greatly disturbing the conditions within them.

Before experimentation, excess water was wiped from each crab using tissue paper and each crab was numbered on the dorsal carapace. Maximum carapace width was measured using vernier callipers and weight was recorded to the nearest mg. Crabs were then placed individually in the desiccators (several animals together may modify the desiccating conditions, (Edney, 1951; Cloudsley-Thompson, 1977)) and removed after 24h and reweighed (D_sW). Finally, crabs were killed and dried to constant weight in an oven (Heraeus K1150/1). The difference between the initial wet weight (WW) and the final dry weight (DW) represented the water content of the crab. The percentage of water lost after 24h was then calculated for each crab.

The percentage of water lost (y) during the experiment was therefore calculated as

$$y = \frac{WW - D_sW}{WW - DW} \times 100$$

The relationship is expressed exponentially using the least squares method

$$\text{Weight loss } y = a.x^b$$

$$\log y = \log a + b \log x$$

If the weight loss (y) and the body size (x) are expressed logarithmically a straight line is obtained. The intercept (a) gives the level of the line and the constant (b) its slope. Covariance analysis was applied to test whether differences were significant.

This method does not take account of the relative proportions of carapace to tissue and some water loss occurs during handling, either from the branchial chamber apertures or as urine squirted from the antennal glands in a defense reaction as reported for O. saratan by Parenzan (1931). The branchial chamber water is, of course, free water and as such is a source of body weight error. A 53.2g crab lost 5mg of water at each urination. A large crab usually did this once or twice during handling but small crabs did it as many as 4 times.

Obviously, when animals were introduced into the desiccators their moisture caused an increase in the relative humidity and the system required several hours to re-equilibriate. The method is, therefore, crude but is sufficient to demonstrate some of the problems posed by water loss.

9.3. Results

9.3.1. Effect of size on water loss

The experiment was conducted at 25°C. From Fig. 9.1 it can be seen that the percentage of body water lost is greater in small crabs than in large ones at the relative humidities tested.

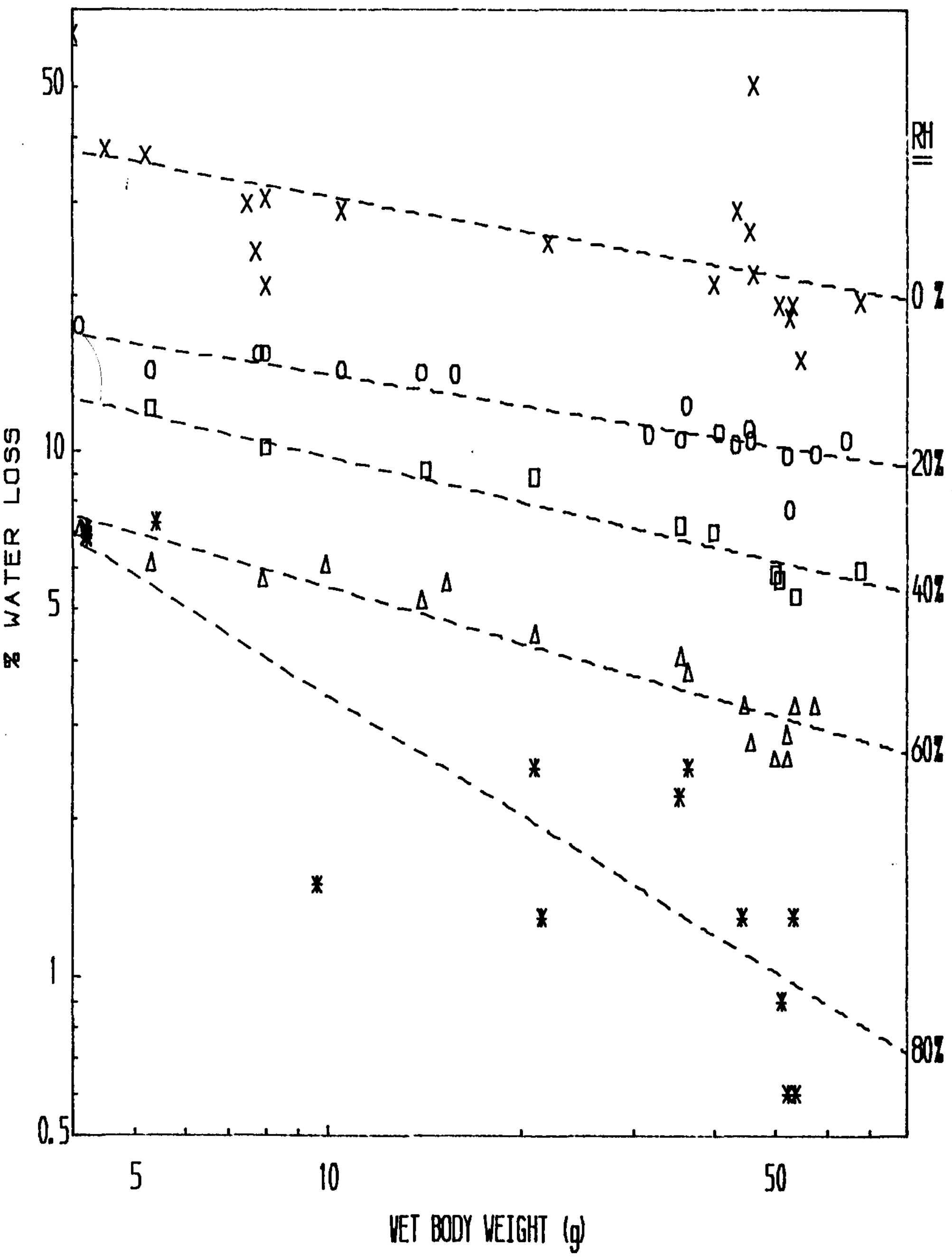
9.3.2. Effect of relative humidity on water loss

From Fig. 9.1 it is also apparent that the crabs lost most water at low relative humidities and that with increasing relative humidity the percentage weight losses decreased. The data for 90% RH have

Fig. 9.1. Percentage loss of body water in different sized *O. saratan* after 24h at 25°C at the relative humidities indicated. The regression equations are

		n	r
0%RH	$\log y = 1.707 - 0.219 \log x$	20	-0.640
20%RH	$\log y = 1.342 - 0.196 \log x$	19	-0.903
40%RH	$\log y = 1.275 = 0.287 \log x$	11	-0.965
60%RH	$\log y = 1.084 - 0.346 \log x$	18	-0.959
80%RH	$\log y = 1.286 - 0.752 \log x$	15	-0.898

where y = % water loss and x = wet body weight.



50
10
5
1
0.5
% WATER LOSS
5
10
50
VET BODY VEIGHT (g)
RH
0 %
20%
40%
60%
80%

been omitted from the figure since over the 24h experimental period no weight loss trend was apparent and the scatter of data points were not significantly correlated to the regression line, probably due to variable amounts of free water in the branchial chambers and on the body surfaces. The difference in the slope of the regression line at 80% RH when compared with the others may also reflect a loss of free water rather than tissue water.

Covariance analysis indicated that the elevations of the regression lines were significantly different in each case. Covariance analysis also indicated a significant difference in the slope of the line fitted to the 80% RH data when compared with 60% RH. The combined covariance analysis of the data for 0% to 60% RH gave a value for the comparison of the slopes which just exceeded the significance value at the 5% level. Further covariance comparisons within this group gave a significant difference (just exceeding the 5% value) only between the lines fitted to the data at 20% RH and 40% RH. Given the small significance value it would be unwise to comment on this without further information.

9.4. Discussion

The water loss results for O. saratan are similar to those reported for other semiterrestrial and terrestrial species (see Introduction). Smaller crabs lost more weight per gram than larger crabs under the same conditions of temperature and relative humidity. Herreid (1969a) noted that a similar pattern occurs in birds, mammals and reptiles and attributed it to scale functions, eg. an increase in surface area relative to body mass and, to a minor extent, an increase in respiratory water loss.$g^{-1}.h^{-1}$ in small crabs reflecting the exponential increase in metabolism related to body weight.

Herreid (1969b) showed clearly that the major route of water loss in crabs was via the integument and suggested that interspecific differences were related to differences in integument permeability. Comparing extremes, Herreid (1969b) stated that the shell of the aquatic Menippe mercenaria was fifteen times more permeable than that of the terrestrial Gecarcinus lateralis. Gross (1957) indicated that the crabs with the least permeable integuments withstood the greatest osmotic stress. Herried (1969b) discussed the evolutionary implications of this and concluded that 'whatever the initial selective force, a relatively impermeable integument has survival value on land: as such it is a parallel development that occurs in vertebrates and insects.'

Herreid (1969a) showed that in all the species he studied there was a progressive decrease in the rate of water loss throughout the experiment. The greatest change occurred during the first 90 minutes and was partly attributed to the loss of body surface water, after which the rate of water loss was fairly stable.

Although the experiments on O. saratan were not designed to follow changes in the rate of water loss with time, it is thought that increased ventilatory activity caused by handling must contribute to initial high losses. Measurements of ventilation volume showed that the stressed rate was several hundred percent higher than in unstressed animals (see Chapter 7). The stressed pattern of ventilation involved forward and reverse pumping which resulted in observable water loss at the branchial apertures. Small crabs have a higher metabolic rate than large crabs as evidenced by data on heart rate (Chapter 7) and oxygen consumption (Chapter 8) and in stressed crabs both of these are elevated.

Employing the assumption of Herreid (1969a), respiratory water loss in O. saratan can be estimated. For example, a 45.8g crab was seen to pump 276ml of air per hour at close to 22°C. If this is assumed to be dry on entry into the gill chambers and fully saturated with water vapour on leaving, since saturated air at 22°C contains 19mg water.ℓ^{-1}, then only 5.2mg water.ℓ^{-1}.h^{-1} (or 0.1mg.g^{-1}.h^{-1}) will be lost via the gill chamber. Since under natural conditions humid air enters the gill chamber this value will be even lower. Total water loss of a crab of this size at 0% RH would be 4.9mg.g^{-1}.h^{-1}. Therefore, respiratory water loss would be 2% of the total evaporation at this temperature.

Under normal circumstances, the burrowing mode of life of O. saratan enables it to avoid the dangers of desiccation. The temperature within the burrow is fairly constant, avoiding environmental extremes, and the relative humidity is high. Also, although most burrows do not extend to or below the water table, the lower sections are excavated in damp sand from which the hydrophilic setal tufts between the third and fourth pereiopods should be able to extract water, although this activity has not been observed within burrows (see Chapter 7). During dry winds crabs plug their burrows thus preserving their microclimate. Crabs do not emerge during the warmest part of the day (see Chapter 4) during most of the year and most activity is crepusular or nocturnal.

This insulating effect of the burrow is discussed in Chapter 3 and has been noted for other species (eg. Gecarcinus lateralis, (Bliss, 1968)).

The pale colouration of O. saratan will also be advantageous in reducing body temperature as has been described for Uca spp.

(Smith and Miller, 1973).

O. satatan, therefore, avoids environmental extremes by behavioural means and further work is necessary to examine whether its behavioural repertoire in this respect is as varied as that of Uca spp. which show a variety of orientational responses to sun and wind and can change colour and body wetness (Smith and Miller, 1973). O. saratan, however, can also withstand considerable loss of body water. It should be noted that all the data plotted are for crabs that survived the experiment. However, some crabs, particularly small ones did not survive in 0% RH and a few died at 20% RH.

CHAPTER 10. GENERAL DISCUSSION

Within the genus Ocypode there are species which are mainly eulittoral, eg. O. ceratophthalmus, O. gaudichaudii, some largely extralittoral species, eg. O. cordimana, O. africana, some species influenced by freshwater, eg. O. fabricii, O. mortoni and many supralittoral species including O. quadrata and O. saratan (Vannini, 1976a; George, 1982). There are also preferences for exposure and shelter, eg. O. occidentalis and O. gaudichaudii respectively (Crane, 1941). The precise ecological requirements of Ocypode spp. are little known and there is still less information of the physiological requirements.

In this thesis I have attempted to discover more of the ecology and behaviour of O. saratan, which occurs in the potentially severe environments of the coasts of the Red Sea, and discover how by behavioural and physiological means it adapts to or is adapted to its environment.

O. saratan lives in an environment which is bordered by desert and environmental air temperatures may exceed 40°C in summer and drop below 15°C during winter nights. Relative humidities are also greatly variable, from below 5% to 100%. Easterly winds off the desert are associated with the lowest relative humidities in the Jeddah region. Sand surface temperatures may exceed 50°C but within the crab burrows conditions are much more stable. It is clear that the burrows provide protection from extreme environmental conditions.

Vannini (1980a) discussed the adaptive value of burrows of Ocypode spp. and noted that amongst other things, they provided protection against climatic stress. Data in support of this view have been detailed in this thesis. Similar conclusions have been reached by workers on *Uca* spp. (eg. Smith and Miller, 1973) and recently some similar evidence has been given for the Red Sea terrestrial hermit crab *Coenobita scaveola* (Achitov and Ziskind, 1985) which will dig into the sand or occupy rock crevices to avoid conditions of high temperature and low relative humidity. Burrows, of course, have other functions, eg. protection from predation and conspecific aggression, and may be for reproduction (copulation, protection of ovigerous females, etc.) (Vannini, 1980a). Access to damp sand is also important (Warburg and Shuchman, 1979; Wolcott, 1984) and the present work agrees with that of Wolcott (1984) for *O. quadrata* in showing that *O. saratan* is able to generate negative pressures within its branchial chambers which enable sand moisture to be drawn into the gill chamber from setal tufts between its 3rd and 4th pereiopods. Neither species has been observed to do this within its burrow but it seems likely that this will occur.

Crabs were not active out of their burrows during the warmest hours of the day. Only in winter, when daytime temperatures were lower, were crabs seen to be active throughout the day. During most of the year the crabs emerged from their burrows in the late afternoon and were active throughout the night and during the early daylight hours of the morning. Their activities were either burrow orientated, ie. involved with burrow maintenance or, in the case of males in the breeding season, involved in pyramid construction and maintenance, or were involved with feeding and replenishment of branchial water. Several different types of feeding were seen and feeding activity was greatest at low tide even though the tidal range was very small. Many crabs brought bivalves dug from the water's edge back to their burrows for feeding but deposit feeding only occurred in the damp intertidal sand. Crabs also engaged in scavenging and general herbivorous foraging along the strand.

The burrowing and general behaviour of O. saratan enables it to avoid the dangers of its high temperature environment by behavioural means. Water loss is greatest at high temperatures and low relative humidities and under these conditions in the field crabs protected themselves by plugging their burrows with sand.

O. saratan, however, is also physiologically adapted both to semiterrestrial conditions and to its high temperature environment. The terrestrial adaptations of these crabs are similar to those described for other terrestrial species in that the branchial chamber is expanded to form an epibranchial lung and the gill lamellae are strengthened and reduced in number by comparison with aquatic crabs. Gill area is similarly reduced and aerial respiration is more efficient than aquatic respiration with submerged crabs responding as though water was a hypoxic medium. Patterns of ventilatory activity were quite different in air than in water.

Temperature adaptation was seen in the Q_{10} relationships for heart rate and weight specific oxygen consumption which indicated that crabs were physiologically stressed at low temperatures but Q_{10}'s were similar between 20°C and 35°C and had relatively low values. This can be interpreted as an adaptation to the environmental range of high temperatures (see Newell, 1979). Also the temperature insensitivity of the Bohr factor in relation to the blood characteristics supports this argument.

The zonation of crabs on the shore reflects reproductive differences but also the smallest crabs which have the highest metabolic rates at elevated temperatures and are the most susceptible to desiccation occur closest to the sea where temperatures appear to be more stable.

Patterns of zonation are quite varied in different *Ocypode* species and may also vary within the same species looked at in different places (Fellows, 1973; Vannini, 1980a). The same is true of burrow structure. The burrows of *O. saratan* appear to include the most complex burrows constructed by any *Ocypode* species and the zonation pattern described here for *O. saratan* was the same in all the areas that were visited. Juvenile burrows occurred closest to the sea and the burrows of mature male crabs occurred furthest up the beach. Female crabs burrowed in an intermediate position. In each case the burrow structure was distinctive. It is clear that there is much still to be learnt about the population biology of *Ocypode* species including *O. saratan*. All aspects of its biology invite further work including a quantitative assessment of human impact on crab populations in the same manner as carried out by Wolcott and Wolcott (1984) for *O. quadrata*.

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