

STUDIES ON THE TEREDINIDS OF COCHIN HARBOUR

By

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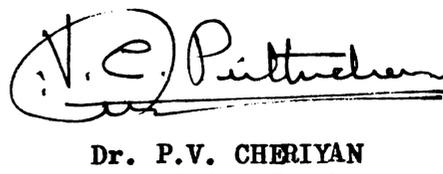
THESIS

**Submitted to the University of Cochin
in partial fulfilment of the requirements
for the degree of Doctor of Philosophy**

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CERTIFICATE

This is to certify that this thesis is an authentic record of the work carried out by Mr. M.V. Mohan, M.Sc., under my supervision in the University Department of Marine Sciences and that no part thereof has been presented before for any other degree in any University.

A handwritten signature in black ink, appearing to read 'P.V. Cheriyan', is written over a horizontal line. The signature is enclosed within a rectangular box that is open on the right side.

Dr. P.V. CHERIYAN
Supervising Teacher

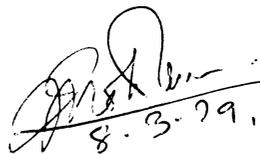
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8.3.79.

M.V. MOHAN

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CHAPTER I

GENERAL INTRODUCTION

Destruction of underwater timber structures such as jetty piles, fender piles, wooden hulls of boats and ships, sluice gates etc., are caused by marine wood borers belonging to the class Crustacea of Phylum Arthropoda and class Bivalvia of Phylum Mollusca. The crustacean wood borers are recruited from three families, Cheluridae of the order Amphipoda, Limnoriidae and Sphaeromidae of the order Isopoda. Of the crustacean borers, the most destructive are limnoriids and sphaeromids popularly known as 'gribbles' and 'pill bugs', respectively. The wood borers of Phylum Mollusca belong to the families Teredinidae (Shipworms) and Pholadidae (Piddocks), which are specially adapted for boring into the wood. Shipworms derive nourishment from the wood while pholads bore into wood for shelter only. The crustacean borers attack the surface of the wood rendering it spongy or honeycombed, while the molluscan borers, especially teredinids penetrate deep into the wood making it weak and fragile.

The wood destroying nature of shipworms was known even to very ancient people and is found mentioned by Pliny, Ovid, Aristophanes and Homer. Ancient mariners dreaded them since their ships, commentably all the ships of Columbus' fourth voyage, were wrecked by the menace of wood borers. A gruesome account of the destructiveness of shipworms can be found in the accounts of the voyages of Dampier, Cook and Drake. The wooden dykes of Holland were damaged seriously as a result of the ravages of shipworms thereby endangering the safety of that country of being flooded. The treatise of Sellius (1733) was the first most important pre-Linnean work on Teredinidae

and he proved that shipworms were molluscs. Linnaeus (1758) instituted the genus Teredo including in it two species: T. navalis and T. lapidaria and placed the genus in Vermes Intestina rather than in Vermes Mollusca (Turner, 1966). Among the earlier workers who have made important contributions since the work of Sellius and Linnaeus are Deshayes (1848), Quatrefages (1849), Hatschek (1880) and Sigerfoos (1908). The exhaustive book "Marine Borers, an Annotated Bibliography", by Clapp and Kenk (1963) provides abundant information about the various aspects of the family Teredinidae. Further, valuable and comprehensive information regarding the different aspects of shipworms, elsewhere from India, can be obtained from the report of the committee on marine piling investigations and industrial research of the National Research Council, Washington (1924, 1927) and from the works of Bartsch (1922), Blum (1922), Edmondson (1942), Clapp (1951), Nair (1962), Turner (1966), etc. Investigations on the teredinids along the coasts of India have been conducted by Erlanson (1936), Gravely (1941), Roonwal (1954, 1954a), Nair (1954, 1955, 1956a, 1965, 1966, 1968), Nair and Saraswathy (1971), Roch (1955), Palekar (1956), Palekar and Bal (1955, 1957), Palekar et al. (1964), Becker (1958), Nagabhushanam (1958, 1960, 1962a), Ganapati and Lakshmana Rao (1959), Ganapati and Nagabhushanam (1959), Rajagopalaiengar (1961, 1964), Cheriyan (1966), Saraswathy (1967), Santhakumary and Nair (1969, 1975), Kalyanasundaram and Ganti (1975), etc.

The shipworms are of great economic importance since they attack wood, living or dead, floating or fixed, found in the seas, brackish water or even freshwater. In 1921, shipworms invaded the San Francisco Bay destroying wooden pillars, piers, boat hulls, wharf pilings, etc., causing

damages worth millions of dollars. The U.S. Navy has estimated that every year over 50 million dollar damages were caused to boats, barges, bulkheads and other marine timber structures. Though shipworms have been reported from all the seas, they are particularly destructive in the tropical waters. India lying in the tropics ($8^{\circ} 4'$ to $37^{\circ} 6'$ North latitude and $68^{\circ} 7'$ to $97^{\circ} 25'$ East longitude), has a very extensive coast line of 5640 km. The underwater timber structures like piles, jetty and wharf fenders, boats, catamarans, stakes, Chinese net poles, etc., are severely attacked by wood borers causing loss of millions of rupees. It is estimated by Becker (1958) that in India alone the periodic cost of replacement of fishing crafts destroyed by wood boring organisms amounted to 2.5 million rupees. Recently, a survey conducted along the Kerala coast by the Forest Research Institute, Dehra Dun (unpublished) revealed that for maintenance and replacement of wooden structures used in fishing operations only, like mechanized and non-mechanized fishing boats, stake net poles, Chinese net poles, etc. the amount spent is about 1.5 million rupees per annum. Considering the money spent on maintenance of the underwater wooden structures in harbours and jetties, passenger boats and country crafts, sluice gates etc., which is not included in the above estimate, the expenditure will be much greater.

The family Teredinidae includes 66 species under 14 genera (Turner, 1966). Along the Indian coast 23 species of teredinids have so far been recorded. Of the 8 species recorded from the South West Coast of India, namely, Dicyathifer manni, Teredora princessae, Teredo furcifera, T. clappi, Lyrodus pedicellatus, Nausitora hedleyi, Bankia companellata and B. carinata, only two species, viz. Teredo furcifera and Nausitora hedleyi have been found to be most destructive in Cochin Harbour.

The genus Teredo which was instituted by Linnaeus (1758) includes 12 species, T. aegypos, T. bartschi, T. clappi, T. fulleri, T. furcifera, T. johnsoni, T. mindanensis, T. navalis, T. peculiarifer, T. portoricensis, T. somersi and T. triangularis. The genus is distributed throughout the world. They usually live in marine conditions though some are brackish-water forms. The genus is represented in India by 4 species, T. furcifera, T. clappi, T. triangularis and T. fulleri of which the former two are recorded from Cochin Harbour. The genus Nausitora, which was instituted by Wright (1864), is restricted to tropical and subtropical waters. It includes 5 species, N. dryas, N. dunlopei, N. excolpa, N. fusticula and N. hedleyi. N. dryas and N. excolpa are confined to tropical Eastern Pacific, N. dunlopei and N. hedleyi to tropical Indo-Pacific and N. fusticula to tropical Western Atlantic (Turner, 1966). The genus Nausitora is generally confined to brackishwater since they breed at low salinities and the larvae are intolerant to higher salinities. Two species of the genus occur in India, viz. N. dunlopei and N. hedleyi. N. dunlopei has been recorded from freshwater, 150 miles above the mouth of Ganges (Wright, 1864) and breeds when the salinity is below 10 ‰ (See Turner, 1966). N. hedleyi is a typical euryhaline species capable of tolerating wide ranges of salinity (0.65-33.68 ‰), and the breeding and larval development are restricted to low saline period (Saraswathy, 1967).

Research on shipworms of the Indian region has been initiated by Erlanson (1936). Hitherto work on teredinids of this region is mainly restricted to taxonomy, biology and bio-chemistry (Nair and Saraswathy, 1971; Purushotham and Rao 1971, 1971a) and studies on the eco-physiology of shipworms are rather found neglected. The Cochin Harbour region is generally subjected to great fluctuations in the hydrographic conditions and therefore the

organisms get exposed to a variety of stresses and strains and hence are compelled to make physiological compensations and adaptations. Bullock (1955), Prosser (1955), Kinne (1971) and Vernberg and Vernberg (1972) have stressed the importance of the study on the nature of physiological adaptations and its variations in different animal populations. In the Cochin Harbour region, a typical estuary, the most destructive shipworms are the euryhaline Nausitora hedleyi and the stenohaline Teredo furcifera (Nair, 1965). Hence, a study on the eco-physiology of teredinids of the Cochin Harbour region in general and N. hedleyi and T. furcifera in particular was carried out.

On the ecological part, the occurrence, abundance and seasonal variation of the different species of teredinids in relation to the hydrographic conditions such as temperature, salinity, dissolved oxygen, phosphate, silicate, nitrite and pH were studied by conducting field tests and field collections in the Cochin Harbour region. On the physiological part, investigations on the salinity tolerance and metabolism were conducted under laboratory conditions. On N. hedleyi investigations were carried out in the laboratory to determine the salinity tolerance limit and the extent to which it can tolerate sudden variations in salinity, and metabolic studies in relation to acclimation medium, size, salinity and dissolved oxygen. On T. furcifera, metabolic studies were carried out only in the acclimation medium in relation to body size and dissolved oxygen.

CHAPTER II

HABITAT

The shipworms inhabit diverse habitats like sea, estuaries, backwaters and some times even freshwater. They attack all types of cellulose materials, both living and dead, found in their respective habitats. Not even the buoys and floats are spared from the fury of t^eredinids, apart from other vulnerable objects like wooden stakes, poles, dikes, etc.

In the marine habitat, the distribution of shipworms extends from the shallow coastal regions to deep waters (Bartsch, 1927; Roch, 1940; Turner, 1966). Turner (1966) has reported the occurrence of Bankia carinata at a depth of 7488 m in the Banda Sea. Those inhabiting the brackish waters usually show considerable capacity to tolerate wide ranges of salinity. Wright (1864) has reported Nausitora dunlopei from the river Comer, a tributary of the Ganges, 150 miles above the mouth of the river. Thus, with exquisite adaptations, they infest submerged timber structures from sea to freshwater.

The occurrence and abundance of shipworms in a locality depend on the environmental factors like temperature, salinity, oxygen, turbidity, pollutants, intensity of fouling organisms, currents, illumination, intensity of other boring organisms, the effectiveness of local larval sources and the presence or absence of predators and parasites.

Temperature plays an important role in the activities of shipworms in the temperate regions. It acts as a limiting factor in growth, reproduction and distribution. The modifying effects of temperature can alter the salinity tolerance range of an organism (Kinne, 1963). Majority of shipworms are found to be active, and breed in warmer months of the year (Kindle, 1918; M'Gonigle, 1926; Mackenzie, 1927; Nelson, 1928; Cheney and Searles, 1935; Zvorykin, 1941;

Tarasov, 1943; Dons, 1945, 1949; Mawatari, 1950; Nagabhushanam, 1962a). An increase in the normal summer temperature in higher latitudes results in increased activity (Cheney and Searles, 1935; Clapp, 1935; Tarasov, 1943; Riabchikov, 1957), and long and severe winters lead to reduced activity (Anon, 1943a).

In temperate regions, a rise in the environmental temperature induced spawning activity in many shipworms (Grave, 1928; Nelson, 1929; Johnson and Miller, 1935; Imai et al., 1950; Scheltema and Truitt, 1954; Quayle, 1959 ; Loosanoff and Davis, 1963) and increasing temperature accelerates growth rate (Sigerfoos, 1908; Potts, 1921; Needler and Needler, 1940; Quayle, 1953; Nair, 1956 ; Nagabhushanam, 1961). Adults of most shipworms are tolerant to wide ranges of temperature (Anon, 1927; Cheney and Searles, 1935) which enables them to enjoy a wide distribution, though there are variations in the optimum activity temperature and temperature tolerance limit, depending on the geographical location of the species (Anon, 1927; Roch, 1932; Zvorykin, 1941; Mawatari, 1950; Imai et al., 1950).

The activity of shipworms varies with salinity and the salinity tolerance range changes with the geographic location of the species. Thus, the lower salinity tolerance limit of Bankia setacea was reported to vary from 7.5 ‰ to 20 ‰ in different latitudes (Barrows, 1917; Kofoid, 1921; Miller, 1926; White, 1929; Black and Elsey, 1948). For B. minima, the minimum salinity for normal activity was found to be 32 ‰ and still higher in the Adriatic species (Roch, 1940). B. hawaiiensis could tolerate fresh-water for 2 days (Edmondson, 1942). Teredo navalis was reported to tolerate wide ranges of salinity (Blum, 1922; M'Gonigle, 1926; Miller, 1926; Kofoid et al., 1927; Imai et al., 1950). Though some species of the genus Nausitora

can tolerate marine conditions, the genus in general is confined to brackishwater (Nair, 1954; Nagabhushanam, 1960). N. dunlopei has been collected from freshwater conditions from the river Comer (Wright, 1864). Cheriyan (1966) observed that N. hedleyi can survive in distilled water for 192 hours.

Light is an important factor influencing the settlement of shipworm larvae (Nagabhushanam, 1962b). The larvae of shipworms appear at night to concentrate in the surface waters and move to deeper waters in daytime. The settlement is expected to be maximum at an illumination of 160 foot candles which represents deep shade (Owen, 1953).

The rate of flow of water significantly influences the settlement of shipworm larvae. Nagabhushanam (1961a) while studying the settling rate of T. furcifera and B. companellata has stated that some velocity of the water current induces the settlement of the shipworm larvae and that the settlement is more rapid in flowing waters than in still waters.

The infestation of teredinids are reported to be influenced by the oxygen content, pH, turbidity, pollution, growth of foulers, nature of timber, competition with other borers, etc. T. navalis can remain active even when the oxygen content in the water falls to 0.98 mg/L (Roch, 1932). Roch (1931) has reported that T. navalis can remain tightly closed in its burrow for long periods, and survival may be due to energy release from anaerobic glycolysis (Lane, 1959). Shipworms are found to be sensitive to increased acidity (Allen and Carter, 1924; Mawatari, 1950). Turbidity is important especially in shallow coastal waters and estuaries. Shipworms are reported to be less active in places where the water is muddy or silty

(Denison, 1852; Devenish-Meares, 1904; MacKenzie, 1927; Nair, 1962).

Harbours, estuaries and coastal regions are subjected to pollution either through industrial or human sewage which directly or indirectly affects shipworms. Areas with high content of H_2S are comparatively free of teredinids (Hartley, 1840; Jarvis, 1855; Buren, 1875; Levy Salvador and Prudon, 1930; Kurien, 1958; Cheriyan, 1967b). Oil pollution too can keep untreated timbers from the attack of teredinids (Nicholson, 1925; Wedekind, 1950).

Marine foulers hinder the attachment of shipworm larvae by acting as a mechanical barrier or by utilizing them as food (Nagabhushanam, 1960a). Nair (1962) has stated that mat forming organisms act as an effective protector against shipworm attack. Barnacles play an important role in inhibiting the settlement of shipworm larvae (Redgrave 1920; Von Schrenk, 1935 and Anon, 1943).

The resistance of timber to shipworm attack varies from species to species. Wood with resinous materials, alkaloids, poisonous inclusions, tannin, gummy deposits, waxy materials or oily substances are comparatively resistant. A few species of wood with good resistance against shipworm attack are Jarrah (Eucalyptus marginata), turpentine (Syncarpia laurifolia), Greenheart (Nectandra rodioei) Iron wood (Eusideroxylon zwageri), Bitter Angelins (Andira vermifuga), Huon pine (Dacrydium franklinii) and teak (Tectona grandis) (Nair and Saraswathy, 1971).

Activity of fungi, coming under Deuteromycetes (Fungi imperfecti), leads to wood deterioration called 'soft rot', thereby rendering the wood more susceptible to subsequent attack by shipworms. In Cochin Harbour

five species of fungi recorded are Gnomonia longirostris, Halophaeria quadricornuata, Torpedospora radiata, Corollospora pulchella and Lulworthia Sp. (Nair, 1968).

Grave competition between crustacean and molluscan borers for their common and limited substrate is avoided by adjusting their mode of attack. While crustaceans attack the surface of the wood, shipworms penetrate deep into it, thereby enabling the borers to utilize the entire piece. M'Gonigle (1925) has reported that on the Atlantic coast of Canada, while high salinity and low temperature favour the attack of Limnoria, low salinity and higher temperature favour the attack of Teredo. Destruction of shipworms due to heavy crustacean attack may occur (Walsh, 1920; Miller, 1926; Roch, 1937) probably by exposing the bare ends of the calcareous tubes of teredinids to mechanical damage.

In the Cochin Harbour region, a heterogeneous assemblage of marine foulers is observed on the wooden test panels. The marine foulers include diatoms, algae, algal spores, protozoans, poriferans, coelenterates, annelids, arthropods, bryozoans, molluscs, tunicates and others. Diatoms are very prominent foulers and among them the most abundant are Rhizosolenia sp., Pleurosigma sp., Nitschia sp., Biddulphia sp. and Chaetoceros sp. Oscillatorea sp. is the important multicellular algal fouler. It is confined to the narrow belt of light penetrating zone. Important foulers among protozoans are stalked ciliates, Vorticella sp., Zoothamnium sp. and Folliculina sp., Sponges, though frequent, are usually solitary and occasionally seen in gregarious numbers. The hydroid settlement starts from October/November onwards when the salinity is moderately high and

reaches its peak during March/May. Bimeria franciscana is the most abundant hydroid in this harbour. Sporadic occurrence of seaanemones (Sagartia sp.) is noticed with heavy settlement during the post-monsoon months. The serpulids, Ficopomatus macrodon and Mercierella enigmatica, which occur during the post-monsoon months and Perinereis cavifrons, a free living polychaete, which occurs throughout the year with a peak in pre-monsoon are the prominent foulers among polychaetes. Barnacle is represented by Balanus amphitrite amphitrite which is present throughout the year with peak intensity during October to December and April to June. Corophium triaenonyx, Melita zeyalanica, Cirolana fluviatilis, C. willeyi, Rhynchoplax alcocki are the common crustacean foulers. The important foulers belonging to bryozoa are Schizoporella unicornis, Victorella pavida and Bowerbankia gracilus. Modiolus undulatus, M. striatulus, Perna viridis and Crassostrea madrasensis are the important foulers among bivalves. Apart from those mentioned above, other foulers like nematodes, planarians and harpacticoids are the most noteworthy.

The marine wood borers of Cochin Harbour belong to class Crustacea and class Bivalvia. The most important crustacean wood borers are Sphaeroma terebrans, S. annandalei and S. annandalei travancorensis, which are brackish-water forms and occur almost throughout the year. Of the bivalve wood borers, the pholads and the teredinids are the most harmful. Martesia striata, the pholad, is present during the high saline months. Of the 8 species of shipworms recorded from the Cochin Harbour region (Ref. Chapter I), only 4 are collected from the test panels. They are Teredo furcifera, Lyrodus pedicellatus and Bankia companellate which are observed during the

high saline post-monsoon period, and Nausitora hedleyi during the low saline period. The most destructive of them are T. furcifera and N. hedleyi, as already mentioned in Chapter I.

Teredinids in general bore in the direction of the wood fibres. In the case of N. hedleyi, the initial course of the burrow is mostly found to be at an angle to the surface of the wood whereas in T. furcifera, it is perpendicular. However, at the cut ends, straight burrow of both species in the direction of the fibres are usually met with. Generally, the tunnels of T. furcifera are straight and more to the surface of the wood whereas those of N. hedleyi are comparatively deeper and twisted.

The presence of a calcareous lining between the animal and the burrow has been noticed and described by Jeffreys (1860) and later by Yonge (1927), Roch (1940), Dons (1946), Clapp (1951) and Turner (1966). In both T. furcifera and N. hedleyi, the calcareous lining was observed to be thicker towards the posterior end of the burrow, becomes thinner anteriorly and disappears at the boring end. If by accident any part of the tunnel gets exposed, the animal secretes a thick calcareous lining in that region. This probably explains the presence of comparatively thick walled calcareous tubes of N. hedleyi in partly damaged test panels. Even in heavily infested test panels, one shipworm is never found trespassed into the burrow of another. Some highly developed mechanism in the animals appears to help them in detecting the neighbouring burrow and preventing them from boring into it. In case they happen to come across the burrow of another, they withdraw from that direction and take a new course. In such cases, a thick cap of calcareous material is found deposited in the wrongly made excavation.

Extracted uninjured specimens of T. furcifera and N. hedleyi, when kept in aerated seawater started showing signs of tube building. White scattered patches of calcareous material towards the posterior end of the body joined together subsequently and extended forward as a tube. The tube grew as a tongue like extension between the body of the animal and the surface of the container while wing like calcareous structures appeared on either side of it, encircling the body, thus forming a tube. The secretion of calcareous lining was found faster on the side of the body which came in contact with the container and was found getting fused to it. If the animal was made to lie on the other side of the body, the secretion of the tube was found to be faster on that side. Therefore it appears that the contact of the body with the container stimulated faster secretion of calcareous material. In larger animals (75-150 mm length) the tube usually grew only upto half to three-fourth of the length of their body while in smaller animals (10-50 mm length) the tube completely covered the animal.

The siphons of shipworms have been described by Sigerfoos (1908), Roch (1940), Yonge (1948, 1957), Clapp (1951), Nair (1957), Bade et al. (1961), Turner (1966), Morton (1970) and Saraswathy and Nair (1971). In the aquarium tanks, undisturbed shipworms either keep their siphons just above or below the mouth of the burrow or extend and wave them in the surrounding water. If test panels containing shipworms were kept in a trough of seawater poor in oxygen, the extension of the inhalent siphons was enormous and the animals were found waving their siphons just beneath the surface of the water, probably in search of regions of higher oxygen content. But when the seawater in that trough was aerated fully, the siphons were found retracted upto the mouth of the burrow. It appears

that the fall in oxygen content in the medium is one of the factors which causes the abnormal extension of the inhalent siphons. No difference was observed in the siphonal activity between day and night.

Behavioural studies were conducted on animals to understand how the siphons reacted to various natural and artificial tactile stimuli. When the displayed siphons of T. furcifera and N. hedleyi were constantly pricked with a needle, they retracted their siphons and plugged the burrows with the pallets. However, it was observed that in the natural habitat, even when the siphons were constantly struck by sand and other particles carried by the high velocity water currents, the animals did not fully withdraw their siphons into the burrow and plug the opening. This adaptation is of survival value as otherwise the rain of sand and other particles will obstruct the siphons of their functions. In the laboratory, when small foreign particles were introduced into the comparatively large burrow opening of N. hedleyi, the siphons showed a trial and error reaction and a powerful jet of water threw away the unwanted particles. When a needle was kept at the entrance of the burrow, partly obstructing it, the siphons showed the usual probing for a few minutes and then extended out through the available space, unmindful of the needle. Another interesting observation was that, the amphipod, Melita Zeylanica, found in large numbers on the test panels have a tendency to aggregate at the mouth of the burrow of N. hedleyi. Some of them were found continuously probing the burrow. When the appendages of the amphipod first touched the siphons, the same trial and error reaction was shown and afterwards unmindful of the disturbance of these small creatures, the siphons were found extending. Sometimes, small M. zeylanica were observed moving over the siphons with the latter showing comparatively

little irritation. Of course, violent movements of M. zeylanica over the siphons caused sudden retraction and closure of the burrow.

The West Coast of India is gifted with numerous backwaters of which the largest one is the Vembanad lake. It extends from Cranganore in the north to Alleppey in the south. Geographically, it is positioned between latitudes $9^{\circ} 28'$ and $10^{\circ} 10'$ North and longitudes $76^{\circ} 13'$ and $76^{\circ} 31'$ East. Having a length of c. 115 km and a breadth of c. 15 km, it covers an area of c. 256 sq.km. The venue of Cochin Harbour is in the northern half of the lake. A 9.13 M deep approach channel communicates the lake with the sea and thus making it an estuary. The rivers - the Periyar, the Achankoil, the Pambai, the Manimala, the Meenachil and the Moovattupuzha, which originate from the Western Ghats are the principal ones in this region causing heavy freshwater runoff into the estuary. These rivers are of perennial nature, but the flow is considerably less during the dry season. During the monsoon period, due to high discharge of freshwater, the estuary is virtually converted into a freshwater basin. It is a positive estuary since the runoff and precipitation exceed evaporation. The tide is of a mixed semi-diurnal type, with the average tidal height of about 90 cm diminishing towards the north and south of the estuary. From December/January onwards, the estuary gets well mixed up and the increased tidal influence in the region is mainly responsible for the high salinity condition. During the monsoon period, the salt water penetration into the estuary is considerably diminished by the heavy freshwater flow from the rivers into the sea.

The hydrography of the Cochin Harbour region has been worked by Balakrishnan (1957), Cheriyan (1963, 1967a, 1973), George and Kartha (1963)

Ramamritham and Jayaraman (1963), Sankaranarayanan and Qasim (1969), Qasim and Gopinath^{an} (1969), Jesanto (1971), Manikoth and Salih (1974), etc. The hydrographic features like temperature, salinity, dissolved oxygen and pH are greatly influenced by tidal rhythm (Qasim and Gopinathan, 1969). In order to correlate the ecological studies with hydrographic conditions, the hydrography of the Cochin Harbour region was investigated for two years, January 1975 to December 1976, the period when ecological studies were conducted.

Bi-weekly surface water samples were collected from the jetty of the Department of Marine Sciences, situated on the eastern side of the Ernakulam shipping channel (Fig.1) and they were analyzed for salinity, dissolved oxygen, phosphate, nitrite, silicate and pH. The surface water temperature was measured using a Celsius thermometer. Salinity, dissolved oxygen, phosphate and silicate were analyzed by following Strickland and Parsons (1968) and nitrite, Lange (1972). The pH was measured using a pH meter. The rainfall data were collected from the Daily Weather Report published by the India Meteorological Department.

The monthly data of salinity, oxygen, rainfall and temperature are given in Table 1 and graphically represented in Fig.2. The monthly variations in phosphate, nitrite, silicate and pH are presented in Table 2.

From the analysis of the data presented in Table 1 and 2 and Fig.2, the prevalence of three hydrographic periods can be recognized, namely the pre-monsoon period (January to May), the monsoon period (June to September) and the post-monsoon period (October to December). Owing to the reduced freshwater flow into the estuary and increased tidal influence almost marine

Fig. 1 **Map of Cochin Harbour showing the test site at the jetty
of the Department of Marine Science.**

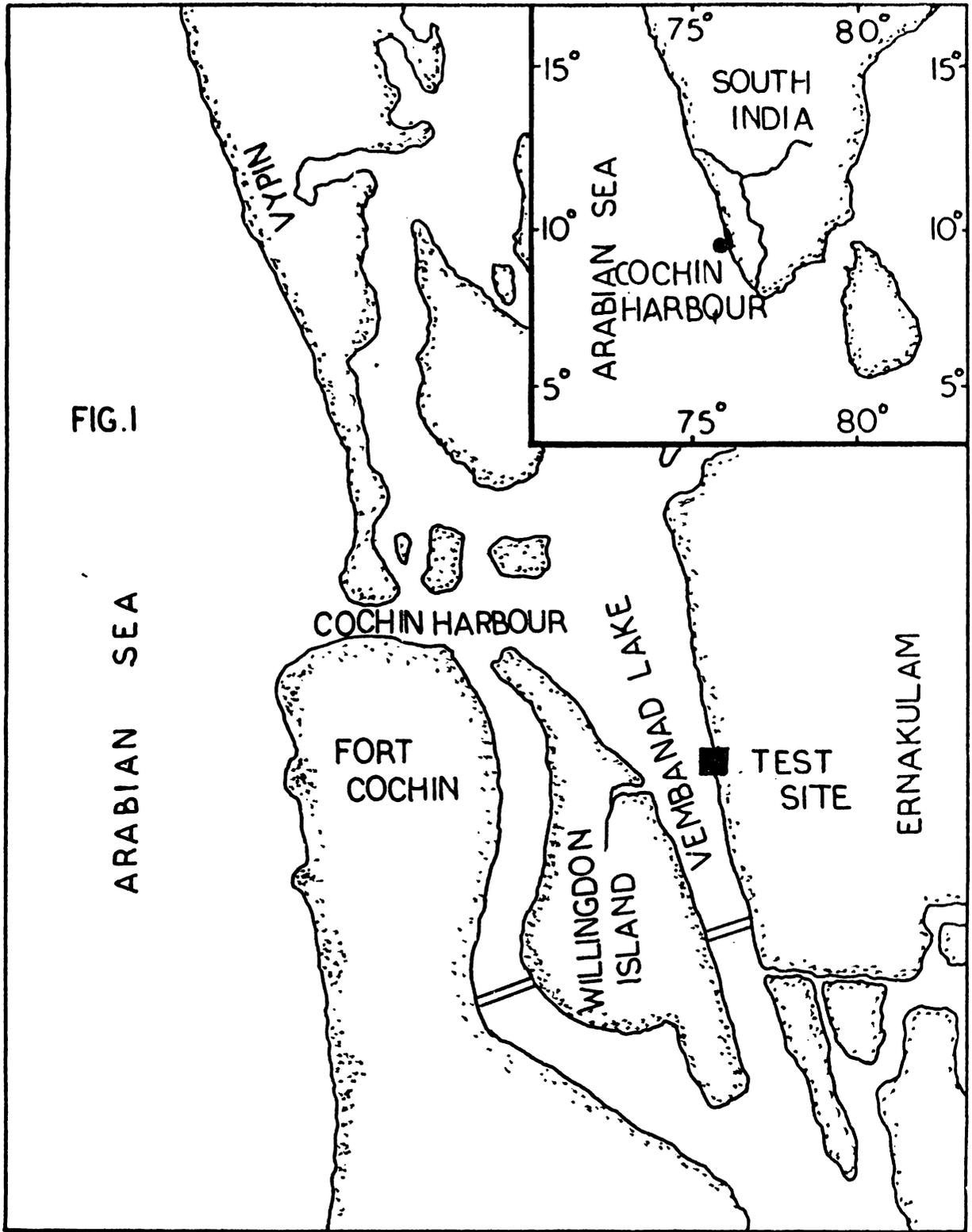


Table 1. Variations in salinity, oxygen temperature and rainfall at the test site during 1975 and 1976.

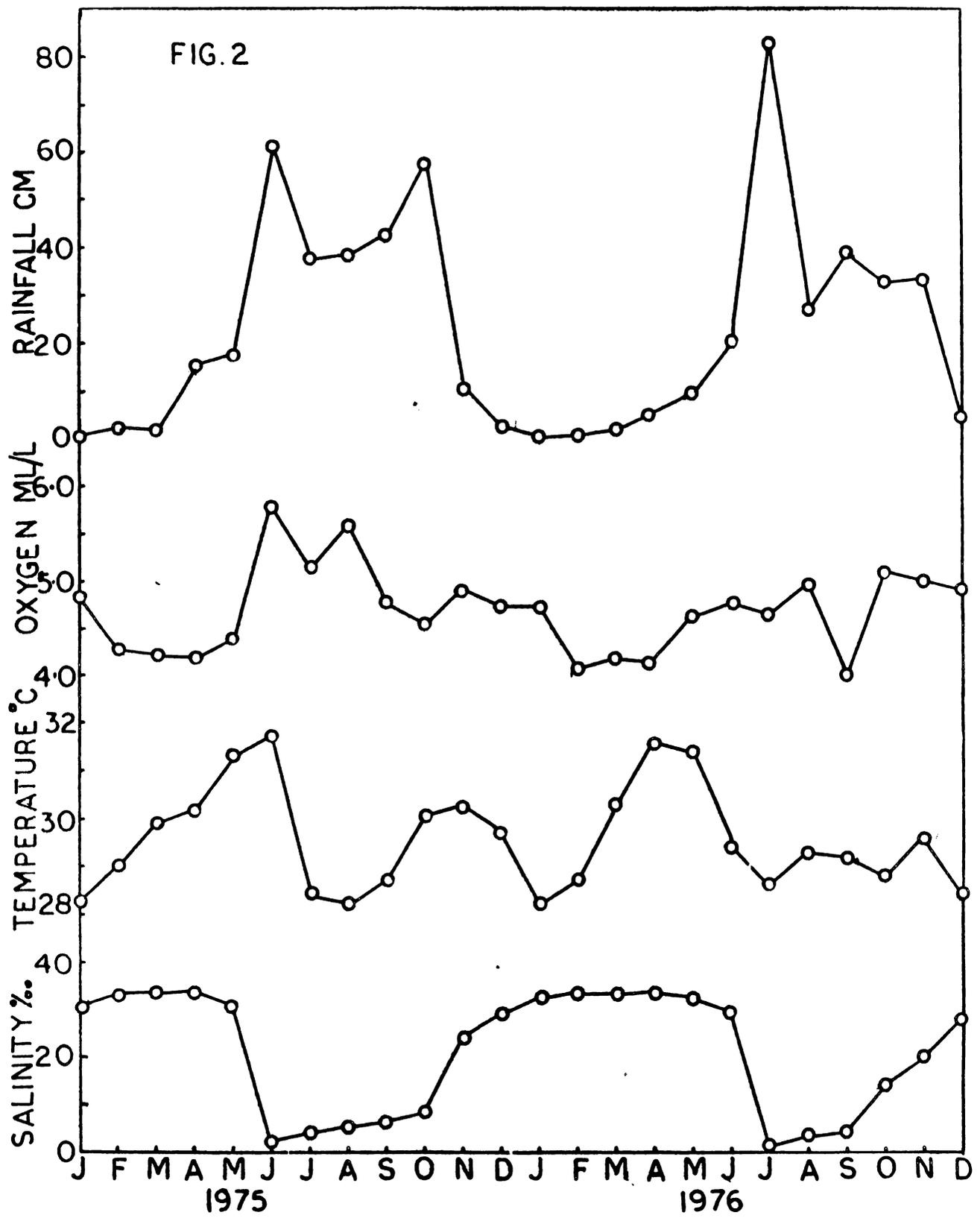
Months	Salinity ‰		Oxygen ml/L		Temperature °C		Rainfall CM	
	1975	1976	1975	1976	1975	1976	1975	1976
Jan	31.16	32.42	4.81	4.72	28.3	28.3	0.1	Nil
Feb	33.52	33.21	4.28	4.07	29.0	28.7	2.2	0.1
Mar	33.57	33.46	4.21	4.19	29.9	30.3	1.8	1.9
Apr	33.68	33.54	4.19	4.14	30.2	31.6	15.0	5.0
May	31.41	32.26	4.34	4.64	31.3	31.4	17.3	9.3
Jun	2.27	29.45	5.74	4.76	31.7	29.4	61.1	20.0
Jul	4.67	1.28	5.12	4.70	28.4	28.6	37.2	80.3
Aug	5.73	3.92	5.57	4.98	28.2	29.3	38.6	26.4
Sep	6.79	4.84	4.76	4.02	28.7	29.2	42.5	38.6
Oct	8.46	14.36	4.55	5.11	30.1	28.8	57.6	32.1
Nov	24.53	19.98	4.93	5.01	30.3	29.6	10.7	33.2
Dec	29.14	28.41	4.73	4.93	29.7	28.4	2.1	4.7

Table 2. Variations in phosphate, nitrite, silicate and pH at the test site during 1975 and 1976.

Months	Phosphate µg-at/L		Nitrite µg-at/L		Silicate µg-at/L		pH	
	1975	1976	1975	1976	1975	1976	1975	1976
Jan	0.66	0.58	0.25	0.58	20	22	8.2	8.2
Feb	0.84	0.70	0.30	0.70	9	10	8.2	8.4
Mar	0.68	0.94	0.62	0.94	8	7	8.4	8.4
Apr	0.83	0.88	0.58	0.88	17	8	8.4	8.4
May	0.87	0.90	0.60	0.90	16	10	8.4	8.2
Jun	1.25	0.95	0.75	0.95	25	15	7.2	8.0
Jul	1.18	1.00	0.75	1.00	27	25	7.4	7.2
Aug	1.00	1.32	0.70	1.32	25	24	7.4	7.2
Sep	0.92	1.14	0.72	1.14	22	20	8.0	7.4
Oct	0.94	0.98	0.74	0.98	17	18	8.0	8.0
Nov	0.83	0.86	0.58	0.84	13	15	8.2	8.0
Dec	0.95	0.72	0.40	0.72	14	10	8.4	8.2

Fig. 2 **Monthly variations in salinity, temperature, oxygen and
rainfall at the Cochin Harbour region during 1975 and 1976.**

FIG. 2



conditions prevail during the pre-monsoon period. The monsoon period is characterized by very low salinity in the harbour region due to the heavy influx of freshwater from the adjoining regions into estuary, which almost nullify the seawater influence. The salinity shows an upward trend during the post-monsoon period and the cycle is repeated. The fluctuations in temperature were comparatively small. Oxygen, phosphate, nitrite and silicate showed seasonal variation. In general, high values were observed during the low saline period. pH varied from 7.2 during the monsoon period to 8.4 during the post and pre-monsoon period.

Thus it can be seen from the preceding account that the Cochin Harbour region is subjected to great fluctuations in hydrographic conditions. In a tropical estuary, salinity is the most important environmental factor influencing the animals and therefore eco-physiological studies were conducted on teredinids in this region in relation to salinity.

CHAPTER III
ECOLOGICAL STUDIES
(i) INTRODUCTION

A thorough knowledge on the ecology of teredinids is of supreme consideration to devise suitable methods for their prevention, and also to interpret and understand the laboratory observations on the physiological studies. The occurrence, abundance and settlement of teredinids on wooden structures in a locality are mainly dependent on the hydrographic factors such as temperature, salinity, oxygen, etc. Ecological studies on teredinids of Cochin Harbour have been conducted by Nair (1965, 1966), Saraswathy and Nair (1969) and more recently by Santhakumari and Nair (1975 - data collected in 1965 and 1966). But the passing of time and changes in the environmental conditions can alter the period of appearance, abundance and even composition of the animal population. Hence, the present study was taken up to understand the occurrence, abundance and seasonal intensity of teredinids in the Cochin Harbour region in relation to hydrographic conditions along with Laboratory studies conducted on the salinity tolerance of N. hedleyi and oxygen consumption in both Teredo furcifera and N. hedleyi.

(ii) MATERIAL AND METHODS

The investigation on the occurrence, abundance and seasonal intensity of teredinids in Cochin Harbour was carried out by a system of short term and long term wooden test panels. Blocks of mango wood (Mangifera indica), an easily susceptible species to shipworm attack, of the size 15 x 10 x 5 cm, were used for this purpose. The test panels were fixed to iron frames covered with polythene, using nuts and bolts. The frames with test panels were suspended horizontally 30 cm below low tide level at the jetty of the Department of Marine Sciences (Cochin Harbour).

At an interval of one month, the exposed test panels were inspected, and replacement of test panels were made in such a way that it was possible to collect data of any particular month as well as that of a period preceeding to that month. Panels exposed for periods over five months were found completely destroyed by borers and hence the maximum period of exposure was restricted to five months. The incidence of teredinids was recorded by counting the entrance holes on the test panels. Following the above procedure, data were collected from January 1975 to December 1976.

(iii) RESULTS

Eventhough the data collected for two years on all shipworms are available, only those of T. furcifera and N. hedleyi are given in Figs. 3, 4, 5, 6 and 7 which represents monthly, bi-monthly, tri-monthly, four-monthly and five-monthly data, respectively. In the figures, the average number of the above shipworms is plotted against the last month of exposure in relation to salinity.

An analysis of the data presented in Fig.3 shows that fresh settlement of T. furcifera was noticed from January/February to May/June when the salinity ranged between 29.45 ‰ and 33.67 ‰, with the maximum intensity in February/March. In the case of N. hedleyi settlement started in July (salinity 4.67/1.28 ‰) and ended in December/January (salinity 28.41/32.42 ‰), with the maximum settlement in October/November.

A scrutiny of the bi-monthly data given in Fig.4 reveals that T. furcifera was noticed in the test panels examined in February to June/July, with the maximum attack in those inspected in March/April. The



occurrence of N. hedleyi was noticed in the panels examined in July/August to December/February with the maximum intensity in those examined in December.

From the tri-monthly data presented in Fig.5, it is evident that the occurrence of T. furcifera was noticed in the test panels collected in January/March to July/August with the maximum numbers in those examined in April/May. In the case of N. hedleyi panels examined in July to December/March showed the attack with the maximum intensity in the panels examined in December.

An analysis of the four-monthly data presented in Fig.6 shows that T. furcifera occurred in the test panels examined in January/April to August/September with the maximum in those examined in May/June. The attack of N. hedleyi was observed in the test panels collected in July to December/April with the maximum in those examined in November/December.

From the five-monthly data given in Fig.7, it is clear that the occurrence of T. furcifera was noticed in the test panels examined in January/May to September/October and the maximum intensity was found in those examined in July. In the case of N. hedleyi, test panels inspected in July to December/May showed its presence with the maximum attack in October/December.

The data of the long term panels presented in Figs.4 to 7, only show the occurrence of T. furcifera and N. hedleyi during the entire period of the test and do not reveal whether settlement was there in every month of their exposure. This difficulty is overcome by the pattern diagram

Fig. 3 Monthly settlement of Nausitora hedleyi and Teredo
furcifera in relation to salinity during 1975 and 1976.

FIG. 3

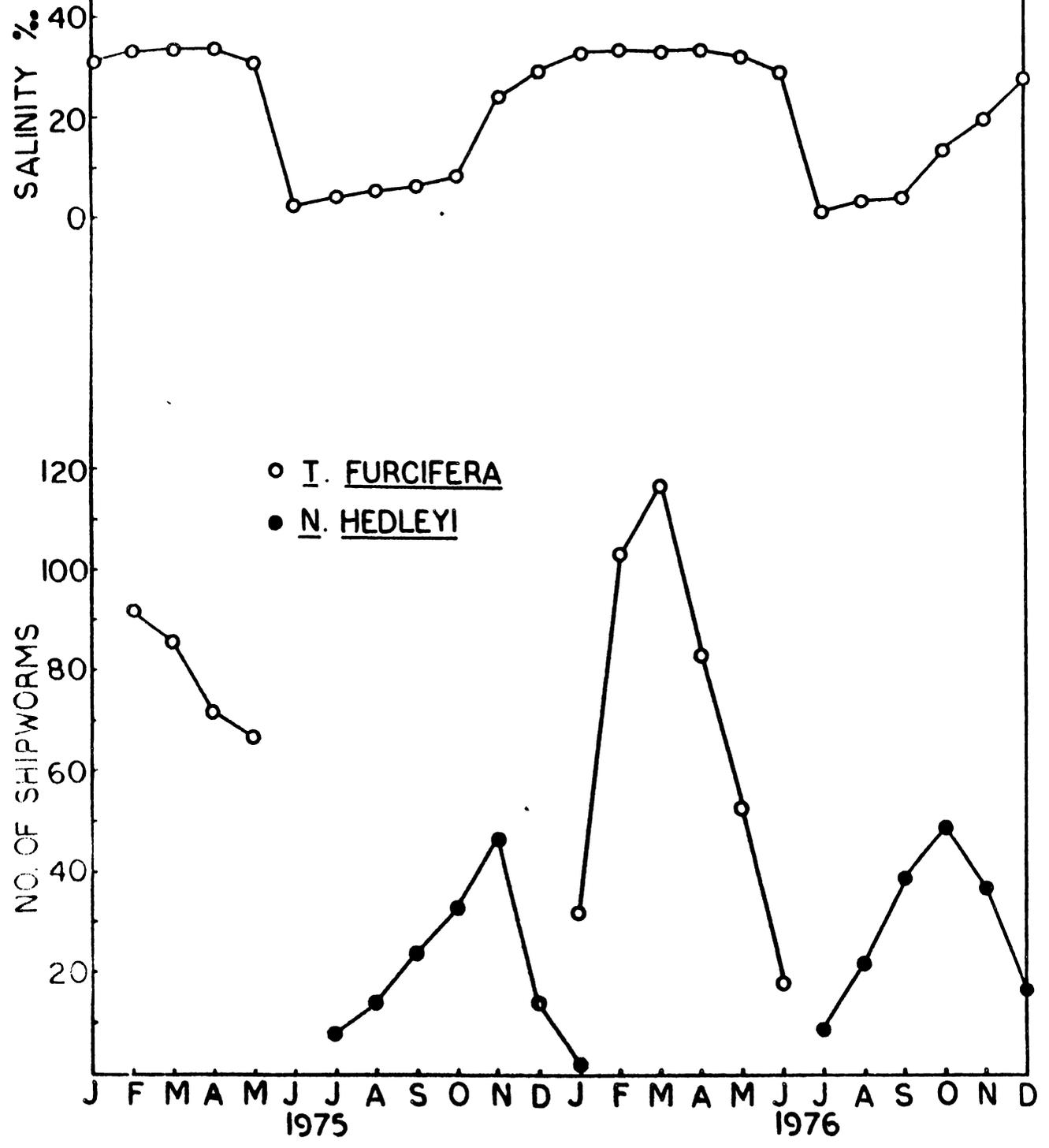
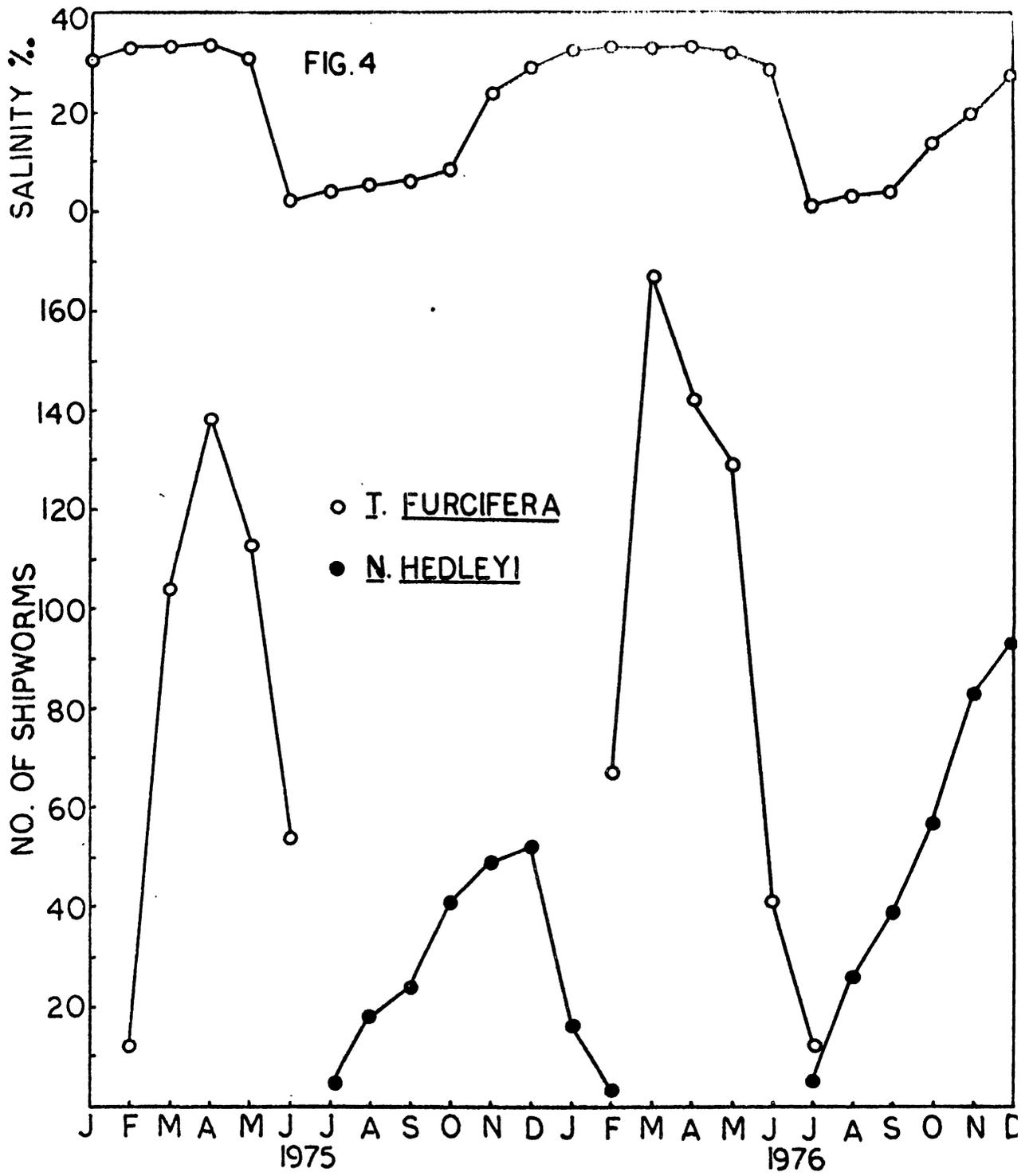
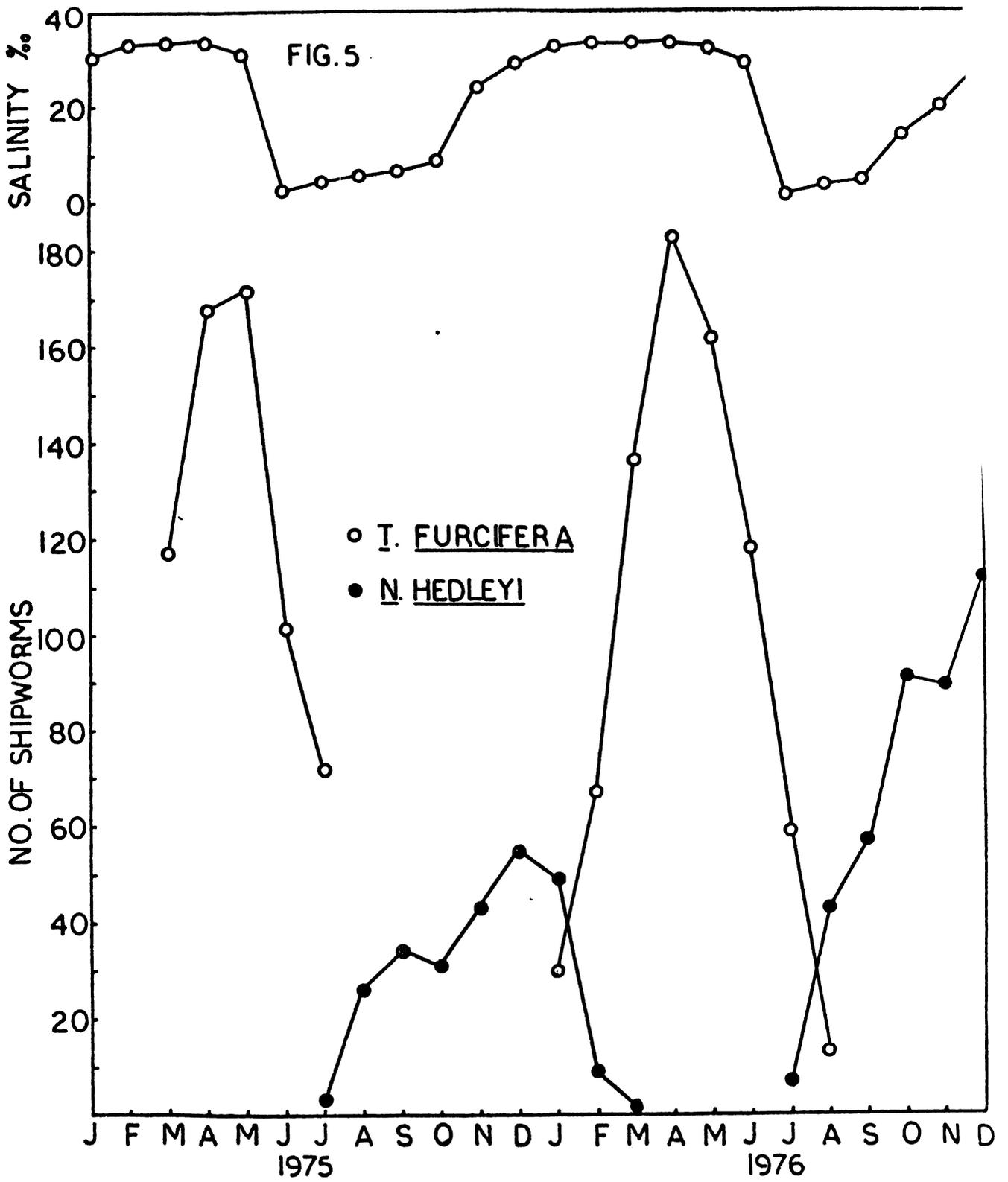
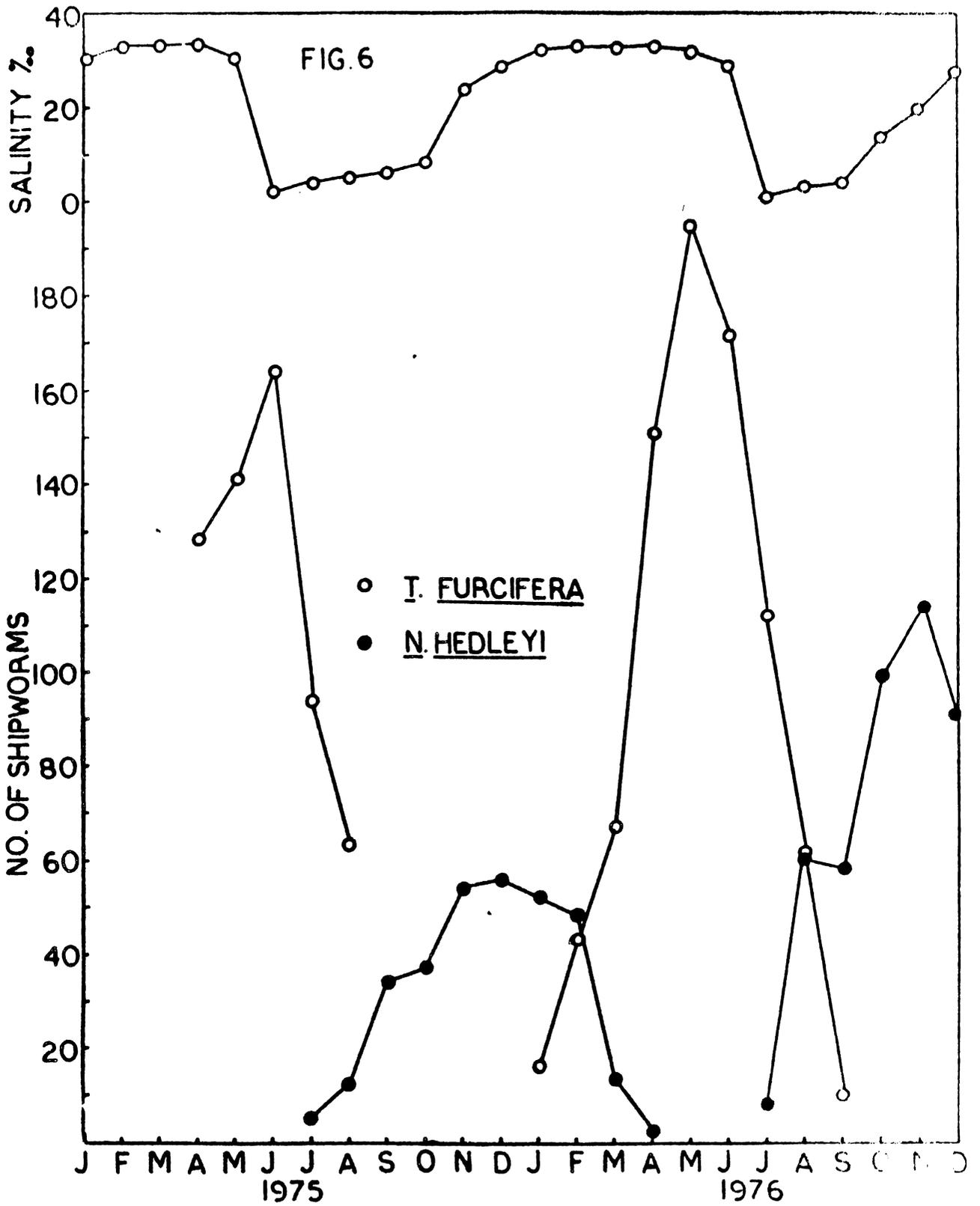
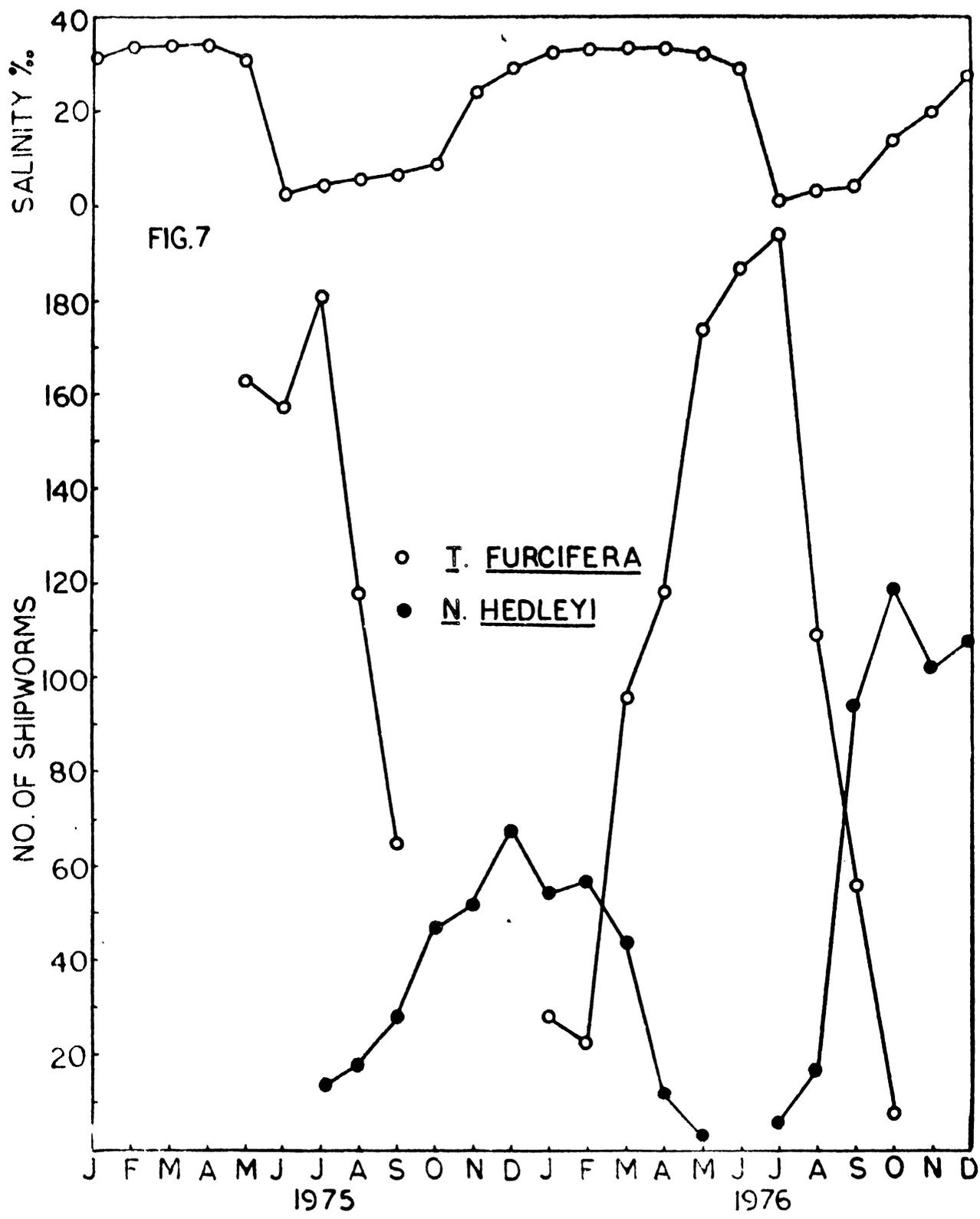


Fig. 4 Bi-monthly settlement of Nausitora hedleyi and Teredo furcifera in relation to salinity during 1975 and 1976.
(Average number of shipworms is plotted against the last month exposure of the long term panel)









presented in Fig.8 where the data on the settlement of the above two species in short and long term experiments are given on either side of the diagonal of the square diagram in relation to salinity. Here the values corresponding to T. furcifera are to be read horizontally and that of N. hedleyi, vertically. The period of settling and non-settling of each species as well as the period when both species settle simultaneously, can very easily be detected from this diagram. The diagram further reveals how the monthly settlement and intensity is modified by the exposure of test panels for more than one month.

Apart from T. furcifera and N. hedleyi, a few other teredinids were also obtained during the above study. They are L. pedicellatus, B. companellata and N. dunlopei. A tri-monthly test panel immersed in February 1975 showed the presence of two specimens of L. pedicellatus during a period when the salinity varied from 33.52 ‰ to 33.63 ‰. The shells and pallets of a single specimen of B. companellata were collected from a bi-monthly test panel exposed in June, 1976 when the salinity was 29.45 ‰. N. dunlopei, a new record from the West Coast of India is described below:

Nausitora dunlopei Wright

Nausitora dunlopei Wright, 1864, p. 453.

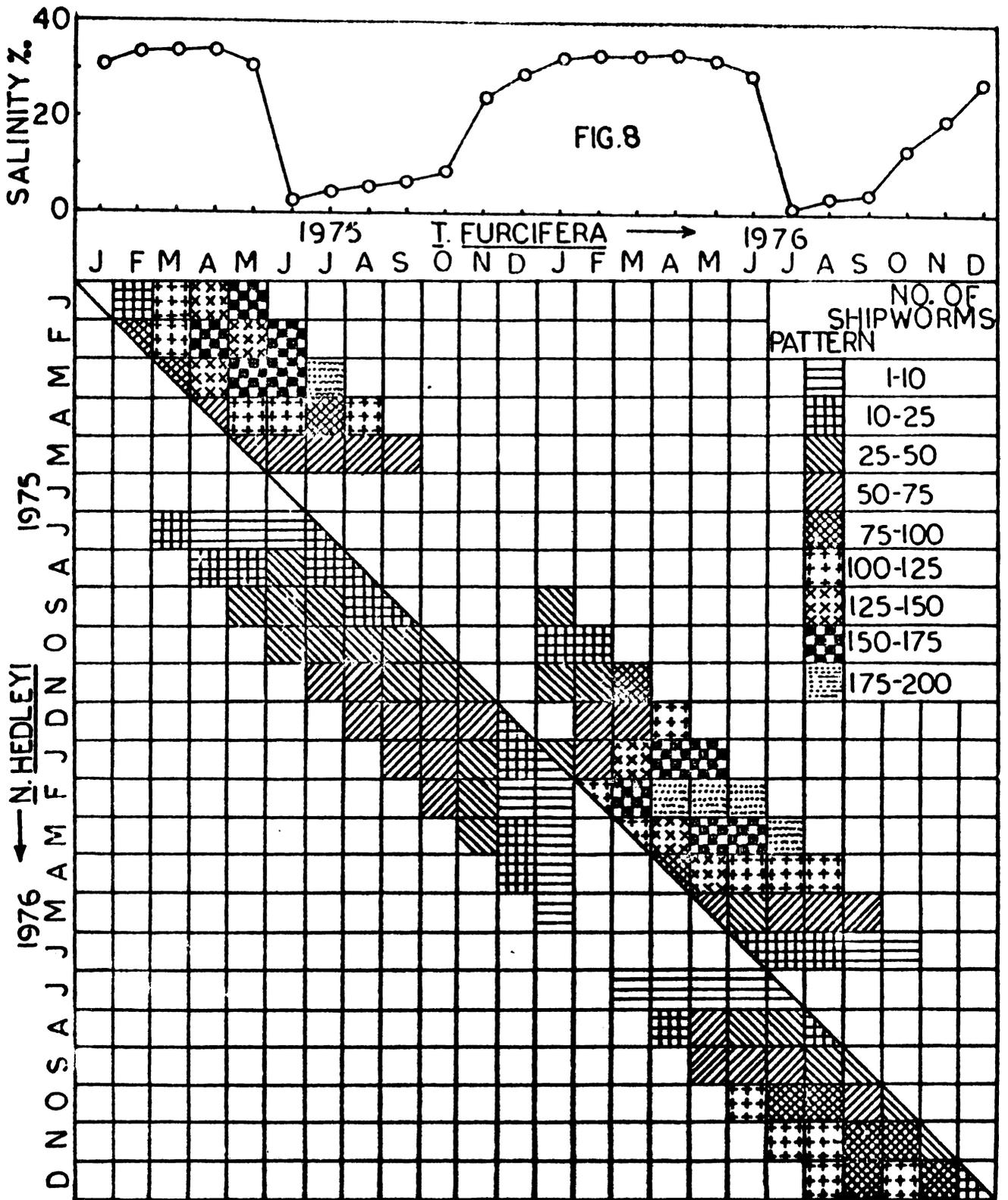
Calobates fluviatilis Hedley, 1898, p. 93.

Bankia (Nausitora) Smithi Bartsch, 1927, p. 61.

Bankia globosa Sivickis, 1928, p. 288.

Bankia quadrangularis Sivickis, 1928, p. 287.

Nausitora messeli Iredale, 1932, p. 37.



Nausitora madagassica Roch, 1935, p. 271.

Nausitora schneideri Moll, 1935, p. 271.

Bankia pennanseris Roch, 1935, p. 274.

Nausitora queenslandica Iredale, 1936, p. 37.

Bankia (Nausitora) madrasensis Nair, 1954, p. 399.

Nausitora lanceolata Rajgopal, 1964, p. 109.

Nausitora dunlopei Wright

Turner, 1966.

Two specimens of N. dunlopei, one adult and other young were obtained. The adult specimen was collected from a four-monthly test panel immersed in August 1975. The salinity during the above period varied from 5.73 ‰ to 24.53 ‰. The young specimen was obtained in October 1975 from a test panel exposed for one month. The salinity during the above month ranged between 5.72 ‰ to 10.56 ‰. The diagnostic features of the adult specimen are given below.

The pallet blade is elongate and composed of distinct segments which are closely packed and fused, with a central cylindrical stalk. The stalk protrudes beyond the tip of the blade due to the loss of early segments. On the convex outer side, the striations are transverse proximally, but distally they curve towards the tip of the blade on either side (Fig.9). On the inner side of the blade, the striations are transverse and the central stalk is clearly visible in the distal one third part (Fig.10). On the basal portion of the blade, periostracal covering is seen extending as awns.

The specimen collected measured 115 mm, pallet 12 mm with blade

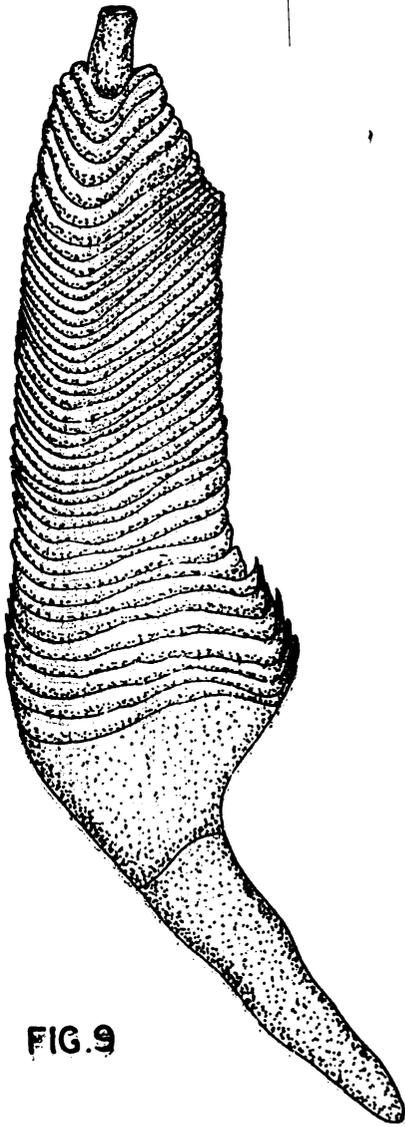


FIG. 9

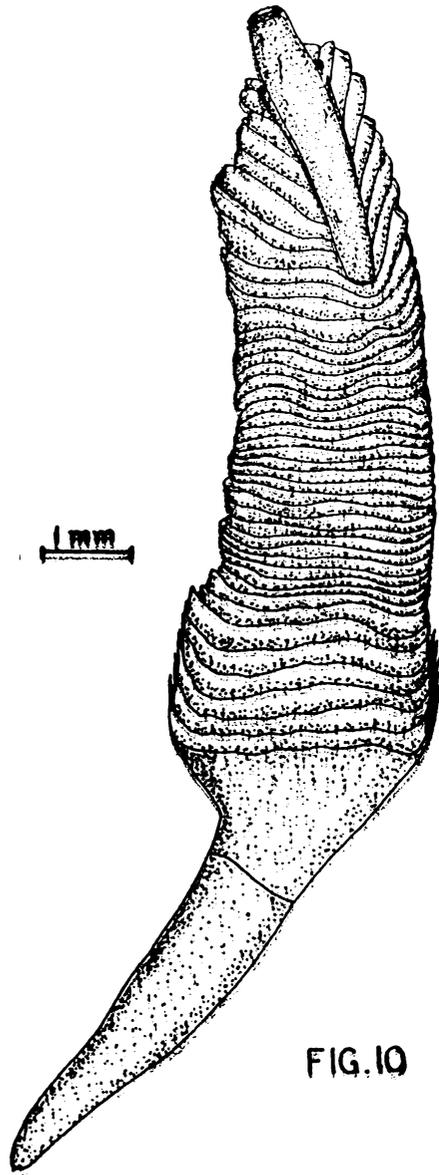


FIG. 10

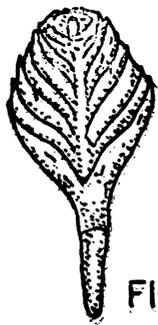


FIG. 11

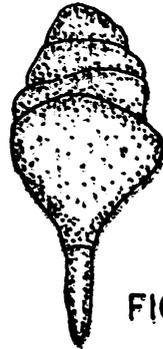


FIG. 12

8 mm and stalk 4 mm.

The characters of the present specimen compares well with those of Wright (1864).

The identifying features of the young specimen are given below.

The pallet blade is broadly oval shaped. On its convex outer face striations are seen branching from a median line and curving towards the tip of the blade (Fig.11). The cylindrical stalk protrudes out through the distal depression. On the inner face of the pallet, the striations are more or less transverse (Fig.12). The basal part of the pallet has a thin periostracal covering.

The specimen measured 21 mm, pallet 2.76 mm with blade 2.16 mm and stalk 0.60 mm.

The characters of the present specimen show close similarity to that of Bankia pennan^seris Roch and B. madrasensis Nair, both of which have later been identified as young N. dunlopei by Turner (1966).

From India N. dunlopei has earlier been reported from West Bengal, Andhra Pradesh and Madras Coast, and also from Madagasker, Australia, Fiji islands, Phillipine islands, Siam, Hawaiian islands and Bismark archepelago.

(iv) DISCUSSION

With the inclusion of N. dunlopei, the total strength of tredimids^e occurring in Cochin Harbour has been raised to 9 from 8 (Ref. Chapter I). Though nine species of shipworms are present in the Cochin Harbour region, the most prominent of them are T. furcifera and N. hedleyi, in terms of

abundance.

T. furcifera has been reported from Hawaiian islands, Midway islands, East Coast of America and Indian Ocean while N. hedleyi has been recorded from Indian Ocean region alone. In Indian Ocean, T. furcifera has been collected from East Coast of Africa, Madagasker, Red Sea, Persian Gulf, Burma, Malayasia, Indonesia, Indian Ocean islands and in India from Andhra Pradesh Coast, Tamil Nadu Coast, Bombay Coast and South West Coast, and N. hedleyi, from Burma, Malayasia, Indonesia, Indian Ocean islands and in India from Tamil Nadu Coast and the South West Coast. In addition to Cochin Harbour, T. furcifera and N. hedleyi have been reported from Ayiramthengu and Neendakara along the South West Coast of India (Santhakumari and Nair, 1975).

In Vizakhapatnam, T. furcifera occurred in the test panels throughout the year with the maximum attack in summer months (Nagabhushanam, 1962a). Nair (1965) has stated that in Cochin Harbour, T. furcifera settled mainly during the high saline pre-monsoon period with sparse settlement during the earlier part of the monsoon and later part of the post-monsoon. Similar observations were made by Saraswathy and Nair (1969) and Santhakumari and Nair (1975). Nair (1965) has reported that the settlement of N. hedleyi is confined to the low saline periods of monsoon and post-monsoon months. An investigation conducted in Cochin Harbour by Saraswathy and Nair (1969) revealed that fresh settlement of N. hedleyi began in July and continued until about February. Santhakumari and Nair (1975) observed that in Cochin Harbour settlement in short term panels was from August to January in 1965/66.

The results of the present investigation clearly show that the settlement of T. furcifera and N. hedleyi is very much related to the salinity of the habitat. Further, the results reveal that the settlement of T. furcifera is confined mainly to the high saline pre-monsoon months, starting in January/February and attaining a peak in February/March. The drastic fall in salinity due to the onset of the South West monsoon in June/July results in the extermination of the stenohaline species, T. furcifera. A short period after the commencement of the South West monsoon, the settlement of N. hedleyi begins, making use of the favourable low saline condition. The settlement of N. hedleyi usually begins in July and it continues in the subsequent months with gradually increasing intensity throughout the low saline period. However, the settlement declines and ultimately stops as high salinity conditions prevail in the region. It is almost at this time the settlement of T. furcifera begins, and this cycle of events is repeated. The pattern of settlement of the two species of shipworms in general agrees with the observations made by earlier workers. Nevertheless, minor changes with regard to the period of settlement, the month of intense attack as well as the yearly intensity of the attack are found to occur and the changes can clearly be correlated to the prevailing hydrographic conditions, especially salinity, in the habitat.

From the pattern diagram presented in Fig.8 it can be understood that the number of T. furcifera and N. hedleyi in the long term test panels, usually increased with the increase in the duration of submergence. This is mainly due to the settlement of waves of shipworm larvae and also due to the conditioning of wood by the activities of microflora, making it more

susceptible to shipworm attack (Becker and Kohlmeyer, 1958). It can also be seen from the same figure that in certain periods, the intensity of teredinid attack does not increase with the duration of exposure of the test panels. Four reasons may be attributed for this discrepancy. Firstly, an interruption or fall in the settlement of teredinid larvae can occur due to unfavourable hydrographic conditions. Secondly, even after the return of favourable conditions, a time factor is involved for the shipworms to repopulate the area, after a partial or complete destruction under unfavourable conditions. Thirdly, thick fouler growth may hinder the settlement of teredinid larvae. Fourthly, due to scarcity of surface area for the settlement of new broods of larvae in the already borer destroyed test panels, further exposure of such panels does not increase the intensity.

In the monthly test panels, the maximum settlement of T. furcifera was obtained in the panels examined in February/March. However, in the long term panels (bi-monthly, tri-monthly, four-monthly and five-monthly) the peak (maximum settlement) was observed in those examined in the subsequent months i.e. March, April, May, June and July (Figs.4 to 7). This is because of the repeated settlement of the larvae of the species on the long term panels in the subsequent months.

Long term panel experiments furnish information about the tolerance of shipworms to different salinity conditions in the harbour. During the pre-monsoon marine condition, T. furcifera leads an active and normal life in the region. Soon after the onset of the monsoon, all T. furcifera die out due to the sharp fall in salinity. On the other hand, examination of the harbour timber structures like jetty piles, fender piles, etc., shows

that at least a few of N. hedleyi can withstand the sudden fall in salinity. A short period after the starting of the South West monsoon, fresh settlement of N. hedleyi is found to occur and continues throughout the low saline period and the adult animals are encountered in the post and pre-monsoon high saline period. Thus, it can be inferred that while T. furcifera is a stenohaline species restricted to the high saline period, N. hedleyi is euryhaline and can endure both high and low salinity conditions.

Further, it can be seen that the settlement of the two dominant species of shipworms in Cochin Harbour namely, the stenohaline T. furcifera and the euryhaline N. hedleyi, alternates, which is conditioned by the salinity variations. Due to the differences in the period of occurrence and abundance of these two species in this region, competition between them is avoided and the underwater timber structures in the harbour region are continually being destroyed almost throughout the year. Ecologically speaking, in Cochin Harbour, where the hydrographic conditions, especially salinity fluctuates seasonally, these two species of shipworms have adjusted themselves in such a way that they are quite successful in fully exploiting the realm throughout the year.

CHAPTER IV

DESCRIPTION OF SPECIES

The diagnostic features of Teredo furcifera and Nausitora hedleyi, including that at generic level, are given below. In shipworm taxonomy, pallets are mainly relied on for identification though shell valves are used occasionally in conjunction with the pallets. The information from the soft parts are employed only to supplement the characters of the pallets and valves or when essential for identification (Turner, 1966). The classification given by Turner (1966) is mainly followed.

Class - Bivalvia
Sub class - Lamellibranchia
Order - Adapedonta
Family - Teredinidae
Sub family - Teredininae
GENUS - TEREDO Linnaeus

Teredo Linnaeus 1758 - Teredo navalis Linnaeus
Austroteredo Habe 1952 - Teredo parksi Bartsch
Coeloteredo Bartsch 1923 - Teredo mindanensis Bartsch
Pingoteredo Iredale 1932 - Teredo shawi Iredale (-bartschi Clapp)
Zopoteredo Bartsch 1923 - Teredo clappi Bartsch

Teredo Linnaeus

Turner, 1966

Diagnostic Features : "Pallets variable, but with the blade always in one piece, usually with a small cup which may be divided medially.

Periostracum usually thin and closely adhering to the calcareous portion, but if extending beyond the calcareous portion as a border, it is never in the form of a cup as in Lyrodus. Blade usually sheathing the stalk for a short distance, the stalk varying in length but solid. The shells cannot be distinguished between those of Lyrodus and Bankia. The siphons are long and separate. The young are retained within the female until the veliger stage".

Teredo furcifera von Martens (Fig.13)

Teredo furcifera von Martens, 1894, p. 95.

Teredo furcillatus Miller, 1924, p. 149.

Teredo (Teredo) bensoni Edmondson, 1946, p. 214.

Teredo (Teredo) parksi madrasensis Nair, 1955, p. 265.

Teredo australasiatica Roch, 1935, p. 268.

Teredo furcata Moll, 1935, p. 267.

Teredo krappei Moll, 1935, p. 268.

Teredo laciniata Roch, 1935, p. 269.

Teredo (Teredo) parksi Bartsch, 1921, p. 28.

Turner furcifera von Martens

Turner, 1966.

Diagnostic Features : Pallet blade always in one piece, shorter than the stalk and running gradually into it. Outer face of the pallet is convex and inner face flat. Distal margin is deeply 'V' shaped on the outer face and inner margin shallowly excavated. Periostracum is usually yellow to pale brown covering the distal portion of the blade.

Fig. 13 Pallet of Teredo furcifera
A. Outer face of the pallet.
B. Inner face of the pallet.

Fig. 14 Pallet of Nausitora hedleyi
A. Outer face of the pallet.
B. Inner face of the pallet.



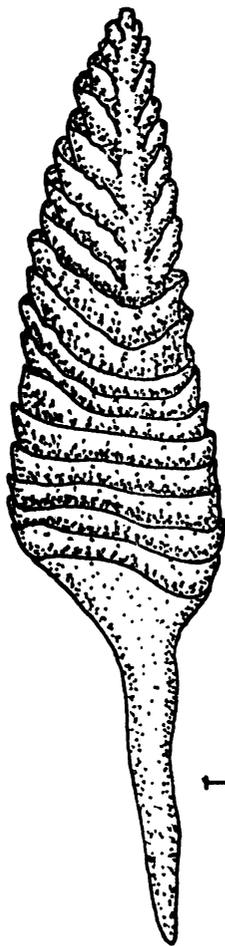
A

2 mm



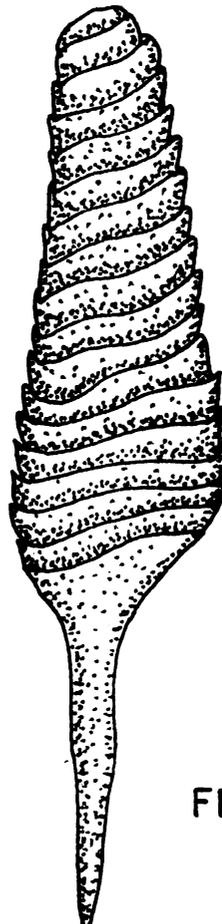
B

FIG.13



A

3 mm



B

FIG.14

The important anatomic features of T. furcifera are given below: Siphons separate, gills blade-like, branchial groove well developed, labial palps attached, stomach elongate, ceacum moderate, intestine not looping over the style stalk, anal canal open, heart median and auricles not pigmented.

The geographic distribution of the species and other aspects are described in Chapter III.

Sub family - Bankiinae

Genus - Nausitora Wright

Nausitora Wright 1864 - Nausitora dunlopei Wright

Inequarista Iredale 1932 - Nausitora messeli Iredale
(= dunlopei Wright)

Nausitorella Moll 1952 - Teredo fusticulus Jeffreys

Nausitora Wright

Turner, 1966

Diagnostic Features : "Pallets elongate, composed of closely packed and fused cone like elements built upon a central stalk. Periostracal covering often extending as awns on the basal portion of the blade of many and perhaps all species with a papillose, calcareous covering which may be worn out in old specimens. Valves large. Siphons short, united for at least half their length".

Nausitora hedleyi Schepman (Fig.14)

Nausitora (sic) hedleyi Schepman, 1919, p. 195.

Bankia (Nausitora) gabrieli Nair, 1955, p. 262.

Nausitora hedleyi Schepman

Turner, 1966.

Diagnostic Features : Pallet stalk is stout, cylindrical and shorter than the blade. The blade is elongate and composed of distinct cone-like segments which are closely packed and fused, with the horizontal curved line marking the margin of each cone. On the outer side of the pallet, the cone ridges are straight proximally, but distally they are curved towards the tip of the blade on either side. Periostracal covering is seen towards the basal part of the blade. On the flat inner side, ridges are almost straight.

The more important anatomical features of N. hedleyi are siphons partially separate, gills blade-like, branchial groove weak, labial palps attached, stomach elongate, caecum large, intestine not looping over style stalk, anal canal open, heart posterior and auricles lightly pigmented.

The geographic distribution of N. hedleyi and other related aspects are discussed in Chapter III.

CHAPTER V

STUDIES ON SALINITY TOLERANCE

(i) INTRODUCTION

In an estuary, salinity is the most conspicuously changing hydrographic factor. Salinity affects the organisms through changes in the total osmoconcentration, relative proportion of solutes, coefficients of absorption and saturation of dissolved gases, density and viscosity of the medium (Kinne, 1971). In the Cochin Harbour region, which is a typical estuary, the size and composition of animal populations are largely dependent on the hydrographic conditions. In this region, the fluctuation of salinity is more marked than that of temperature (Table 1). Hence, the teredinids inhabiting this region are subjected to high variations in salinity. Apart from the seasonal changes, short-term fluctuations in salinity also occur. Shipworms can tide over short period lethal salinities by virtue of their capacity to shut themselves in their burrows using the pallets. But when the adverse effects of sub- or supra-normal salinity continue indefinitely, other physiological mechanisms of salinity tolerance become important.

The salinity tolerance of different bivalves has been investigated by several authors. Blum (1922) studied the effects of salinity on Teredo navalis. Similar investigations were conducted by Allen and Carter (1924) on Bankia gouldi and Abraham (1953) on Meretrix casta. Nagabhusanam (1955) studied the tolerance of Martesia striata in different salinities. Investigations on the salinity tolerance of several marine and brackish-water lamellibranchs were conducted by Davis (1958) and Stickney (1964).

Schleiper et al. (1960) and Reshoft (1961) have studied similar aspects of several other bivalves. The salinity tolerance at sub individual levels of bivalves has been studied by Vernberg et al. (1963). Cheriyan (1966) conducted studies on the salinity tolerance of Nausitora hedleyi in situ. Pierce (1970) investigated the degree of tolerance of Modiolus demissus to different salinities. The optimum range of salinity in Cellana radiata was determined by Balaparameswara Rao and Ganapati (1972). Mane (1974) has studied the adaptations of Katelysia opima to salinity fluctuations. The salinity tolerance of Crassostrea madrasensis, Meretrix meretrix and Mytilus viridis has been studied by Sundaram and Shafee (1975) and Crassostrea cuculata by Nagabhushanam and Bidarkar (1975). Recently, Sivankutty Nair and Shynamma (1978) and Salih (1978) conducted studies on the salinity tolerance of Villorita cyprinoidea var. cochinensis and Meretrix casta, respectively.

From the seasonal intensity studies on teredinids conducted in the Cochin Harbour region, it was observed that in its habitat N. hedleyi could tolerate extreme salinity variations from almost freshwater to marine conditions. But an inference on the salinity tolerance of an animal based on the observations in the field alone will not be complete because the effects of salinity may be modified by other environmental factors in the habitat. Hence, experiments were conducted in laboratory, under controlled conditions, in which the salinity tolerance of N. hedleyi to sub-and supra-normal salinities was investigated.

(ii) MATERIAL AND METHODS

Test panels containing N. hedleyi were collected from the Cochin

Harbour region when the salinity was about 5 ‰ and the animals were acclimated in aquaria containing seawater of 5 ‰ salinity for 18 days. In the same way animals were collected from the same site when the salinity was about 20 ‰ and they were acclimated for 18 days in aquaria containing seawater of 20 ‰ salinity. The seawater in the aquaria was aerated and filtered daily by employing the device described by Cheriyan (1967). In the aquaria the animals were found to extend their siphons and eject excreta which are signs of active boring and feeding.

For the salinity tolerance experiments, animals were carefully extracted from their burrows and kept overnight in air saturated acclimation medium, filtered through 42 Whatman filter paper. Those uninjured healthy and active animals, as judged by the activity of their siphons and visual examination were only used for the tolerance experiments.

The desirability of using extracted animals were proved by the fact that they lived for more than 28 days in the acclimation salinities of 5 ‰ and 20 ‰. Eight series of experiments were conducted by transferring animals of two size groups, 15 to 50 mm and 100 to 150 mm (burrow length) acclimated in a particular salinity, to lower and higher salinities. The two size groups were fixed after running pilot salinity tolerance experiments. No perceptible difference was noticed within each size group. However, differences existed between the two size groups. Animals acclimated in 5 ‰ and 20 ‰ salinities were tested in salinities 0.60 ‰, 3 ‰, 5 ‰, 10 ‰, 15 ‰, 20 ‰, 25 ‰, 30 ‰ and 33.65 ‰. Sea water filtered through 42 Whatman filter paper was used for the various experiments. Experimental media of lower salinities were prepared by diluting filtered seawater with

distilled water. Animals extracted and selected for the experiments were transferred abruptly or gradually, as the case may be, to lower and higher salinities. In abrupt transfers, animals were suddenly transferred to the test salinity while in gradual transfers, they were passed through the intermediate salinities, in each of which they were kept for 24 hours.

The experiments were conducted in 5 litre glass troughs containing 3 litres of filtered water of experimental salinity. Two animals were kept at a time in a trough. The temperature of the test medium was maintained at $28.5^{\circ} \pm 0.5^{\circ}\text{C}$ in all the experiments. The loss of water due to evaporation was compensated by adding distilled water. The water in the trough was changed once in two days and aerated twice a day, giving least disturbance to the animal and that was found to be enough to keep the animals in good condition. In each series 20 animals were experimented and the duration of the experiment was fixed as 10 days. The rate of mortality was taken as the criterion of tolerance of the animals. Observations were made at an interval of 12 hours. Mortality was decided by the lack of response of the siphons to tactile stimuli, cessation of heart beat and the development of pale yellow colour over the body surface. The salinity in which at least 50 % of the animals died within a period of 10 days was considered as the lethal salinity. The formula of Lance (1963) was used for the calculation of percentage of survival:

$$\begin{array}{l} \text{Per cent survival after} \\ \text{exposure to various} \\ \text{salinities for 10 days} \end{array} = \frac{a_1}{b_2} \times \frac{b_1}{a_2} \times 100$$

where

a1 = the number of survivors in the experimental medium

a2 = the number of animals initially placed in the experimental medium

- b1 = the number of survivors in the control (acclimation medium)
b2 = the number of animals initially placed in the control
(acclimation medium)

(iii) EXPERIMENTS AND RESULTS

1. Abrupt transfer of N. hedleyi of the size group 15-50 mm, acclimated in 5 ‰ salinity, to lower and higher salinity media.

Animals of the size group 15-50 mm acclimated in 5 ‰ salinity were transferred abruptly to 0.60 ‰, 3 ‰, 5 ‰, 10 ‰, 15 ‰, 20 ‰, 25 ‰, 30 ‰ and 33.65 ‰ salinities. No mortality was observed in salinities 0.60 ‰ to 20 ‰. Survival was nil in salinities 30 ‰ and 33.65 ‰. The higher lethal salinity was 25 ‰ (Table 3).

2. Abrupt transfer of N. hedleyi of the size group 100-150 mm, acclimated in 5 ‰ salinity, to lower and higher salinity media.

Animals of the size group 100-150 mm acclimated in 5 ‰ salinity were transferred abruptly to 0.60 ‰, 3 ‰, 5 ‰, 10 ‰, 15 ‰, 20 ‰, 25 ‰, 30 ‰ and 33.65 ‰ salinities. Survival was 100 % in salinities 0.60 ‰ to 20 ‰ and nil in salinities 30 ‰ and 33.65 ‰. The higher lethal salinity was found to be 25 ‰ (Table 4).

3. Gradual transfer of N. hedleyi of the size group 15-50 mm, acclimated in 5 ‰ salinity, to lower and higher salinity media.

Animals of the size group 15-50 mm acclimated in 5 ‰ salinity were transferred gradually to 0.60 ‰, 3 ‰, 5 ‰, 10 ‰, 15 ‰, 20 ‰, 25 ‰, 30 ‰ and 33.65 ‰ salinities. Survival was 100 % in salinities

0.60 ‰ to 25 ‰. No lower and higher lethal salinity was observed (Table 5).

4. Gradual transfer of *N. hedleyi* of the size group 100-150 mm, acclimated in 5 ‰ salinity to lower and higher salinity media.

Animals of the size group 100-150 mm acclimated in 5 ‰ salinity were transferred gradually to 0.60 ‰, 3 ‰, 5 ‰, 10 ‰, 15 ‰, 20 ‰, 25 ‰, 30 ‰, and 33.65 ‰ salinities. There was no mortality in salinities 0.60 ‰ to 25 ‰. No lower or higher lethal salinities were observed (Table 6).

5. Abrupt transfer of *N. hedleyi* of the size group 15-50 mm, acclimated in 20 ‰ salinity, to lower and higher salinity media.

Animals of the size group 15-50 mm acclimated in 20 ‰ salinity were transferred abruptly to 0.60 ‰, 3 ‰, 5 ‰, 10 ‰, 15 ‰, 20 ‰, 25 ‰, 30 ‰ and 33.65 ‰ salinities. Cent percent survival was observed in salinities 10 ‰ to 30 ‰. The lower lethal salinity was 3 ‰. No higher lethal salinity was observed (Table 7).

6. Abrupt transfer of *N. hedleyi* of the size group 100-150 mm, acclimated in 20 ‰ salinity, to lower and higher salinity media.

Animals of the size group 100-150 mm acclimated in 20 ‰ salinity were transferred abruptly to 0.60 ‰, 3 ‰, 5 ‰, 10 ‰, 15 ‰, 20 ‰, 25 ‰, 30 ‰, and 33.65 ‰ salinities. Survival was 100 % in salinities 10 ‰ to 30 ‰. The lower lethal salinity was found to be 3 ‰. No higher lethal salinity was observed (Table 8).

Table 6. Per cent survival of N. hedleyi of the size group 100-150 mm at time intervals (days) when transferred gradually to lower and higher salinities from the acclimation salinity of 5 ‰.

Days	Salinity ‰								
	0.60	3	5	10	15	20	25	30	33.65
1	100	100	100	100	100	100	100	100	100
2	100	100	100	100	100	100	100	100	80
3	100	100	100	100	100	100	100	80	65
4	100	100	100	100	100	100	100	80	50
5-10	100	100	100	100	100	100	100	60	50

Table 7. Per cent survival of N. hedleyi of the size group 15-50 mm at time intervals (days) when transferred abruptly to lower and higher salinities from the acclimation salinity of 20 ‰.

Days	Salinity ‰								
	0.60	3	5	10	15	20	25	30	33.65
1	100	100	100	100	100	100	100	100	100
2	20	70	100	100	100	100	100	100	100
3	5	60	90	100	100	100	100	100	90
4	0	45	80	100	100	100	100	100	90
5-10	0	30	80	100	100	100	100	100	90

Table 8. Per cent survival of N. hedleyi of the size group 100-150 mm at time intervals (days) when transferred abruptly to lower and higher salinities from the acclimation salinity of 20 ‰.

Days	Salinity ‰								
	0.60	3	5	10	15	20	25	30	33.65
1	60	80	100	100	100	100	100	100	100
2	0	35	70	100	100	100	100	100	100
3	0	20	70	100	100	100	100	100	80
4	0	20	70	100	100	100	100	100	70
5-10	0	20	55	100	100	100	100	100	70

7. Gradual transfer of *N. hedleyi* of the size group 15-50 mm, acclimated in 20 ‰ salinity, to lower and higher salinity media.

Animals of the size group 15-50 mm acclimated in 20 ‰ salinity were transferred gradually to 0.60 ‰, 3 ‰, 5 ‰, 10 ‰, 15 ‰, 20 ‰, 25 ‰, 30 ‰ and 33.65 ‰ salinities. No mortality was recorded in salinities 5 ‰ to 33.65 ‰. No lower lethal salinity was found to exist (Table 9).

8. Gradual transfer of *N. hedleyi* of the size group 100-150 mm, acclimated in 20 ‰ salinity, to lower and higher salinities

Animals of the size group 100-150 mm acclimated in 20 ‰ salinity were transferred gradually to 0.60 ‰, 3 ‰, 5 ‰, 10 ‰, 15 ‰, 20 ‰, 25 ‰, 30 ‰ and 33.65 ‰ salinities. Survival was 100 % in salinities 5 ‰ to 30 ‰. No lower and higher lethal salinities were observed (Table 10).

(iv) DISCUSSION

Estuarine organisms possess a number of biological mechanism like escape, reduction of contact, regulation and acclimation for compensating the adverse effects of their environment (Kinne, 1971). Shipworms plug their burrows with pellets as a reaction to sudden changes in salinity. Cutting of direct contact with the environment is a temporary rather than permanent measure to tide over adverse conditions. If the change in salinity is prolonged, shipworms respond by employing different physiological mechanisms. The degree of tolerance of shipworms to salinity limits its occurrence and distribution.

Due to the complex interaction which exists between salinity and other environmental factors, salinity tolerance of the same species of shipworms may differ geographically. Thus in the case of Bankia setacea, the lower salinity limit has been determined at 20 ‰ in California (Kofoid, 1921), 16 ‰ at San Francisco bay (Miller, 1926) and 7.5 to 13.7 ‰ at Strait of Georgia (White, 1929). In British Columbia, salinities below 9 ‰ was not optimum for B. setacea (Black and Elsey, 1948). The normal activity of Teredo navalis was affected at 18 ‰ salinity at Nevo Scottia (M'Gonigle, 1926) and in Onagawa Bay, Japan (Imai et al., 1950), and 9 ‰ salinity at San Francisco Bay (Blum, 1922; Miller, 1926). The lowest salinity for normal activity of Bankia gouldi at Beufort was found to be 14 ‰ (Allen and Carter, 1924).

Shipworms react differently to different salinities. Some being tolerant of high salinities, others endure very low salinities and even fresh water. Some other tolerate wide ranges while others, only narrow ranges. The attack of Bankia companellata decreased with decrease in salinity (Nagabhushanam, 1961b). Roch (1940) found that the normal activity of B. minima was affected at salinities below 32 ‰. T. navalis, at San Francisco Bay, could tolerate a salinity range from normal sea water to 4 ‰ (Miller, 1926). From fresh water conditions N. dunlopei has been collected (Wright, 1864; Putnam, 1880, etc.). N. hedleyi is known to be typically euryhaline (Cheriyān, 1966). The genus Nausitora in general is confined to brackish water though a few species have invaded the sea (Nair, 1954; Nagabhushanam, 1960).

The present study showed that in the acclimation salinities of 5 ‰ and 20 ‰, all N. hedleyi of both size groups survived for 10 days.

N. hedleyi of small and large size groups acclimated in 5 ‰ could be successfully transferred abruptly to 0.60 ‰ to 20 ‰ salinities. The higher lethal salinity was found to be 25 ‰ for animals of both size groups in abrupt transfers. However, at least 10 % of the smaller animals survived on the second day of transfer to 25 ‰ salinity, whereas none of the larger animals survived in this medium (Table 3 and 4). N. hedleyi of small and large size groups acclimated in 20 ‰ salinity withstood a sudden salinity fall up to 15 ‰ salinity. The lower lethal salinity was observed to be 3 ‰. The smaller animals were found to be less sensitive to fluctuations in salinity since at least 5 % survived on the third day of transfer to 0.60 ‰ salinity whereas none of the larger size groups survived on that day in the same salinity (Table 7 and 8). Therefore, it may be inferred that N. hedleyi can tolerate even a 15 ‰ sudden salinity variation without any adverse effects and that the smaller animals are more tolerant than larger ones.

In experiments where N. hedleyi were transferred gradually to lower and higher salinities, the animals were found capable of tolerating much lower and higher salinity media. Thus N. hedleyi acclimated in 5 ‰ or 20 ‰ salinity can be gradually transferred to 0.60 ‰ and 33.65 ‰ salinities without any apparent adverse effects on the animals (Tables 5, 6, 9 and 10).

Kinne (1964) has pointed out that acclimation to lower and higher salinities tends to shift the lower lethal salinity limit downwards and higher lethal salinity limit upwards, respectively. The present finding is in agreement with the above generalization. Smaller animals are found

to tolerate fluctuations in salinities better than larger ones. Gradual transfer of animals to lower and higher salinities extended the tolerance limit. This may be because of the chances the animals are getting to acclimatize gradually to changes in salinities. From the results of the present study it can be presumed that N. hedleyi is capable of tolerating a sudden salinity variation up to 15 ‰ and if the change is gradual, it can endure salinities from 0.60 ‰ to 33.65 ‰. This explains why N. hedleyi is observed in the Cochin Harbour region throughout the year. These observations were taken into consideration while planning the metabolic studies, discussed in Chapter 6.

CHAPTER VI

STUDIES ON OXYGEN CONSUMPTION

(i) INTRODUCTION

The rate of metabolism in animals varies widely depending upon intrinsic and extrinsic factors (Vernberg and Vernberg, 1972). The intrinsic factors are size, activity, nutritive state, sex, etc. The extrinsic factors are categorized into controlling factors and limiting factors (Blackman, 1906; Fry, 1947; Newell, 1970). Salinity, temperature, light and other factors which operate individually and in combination producing minimum and maximum metabolic rates are included in the controlling factors. Factors like oxygen availability and substrate supply which directly interfere with the metabolic processes are included in the limiting factors. Since intrinsic and extrinsic factors interact together and determine the metabolic rate, it is necessary to find out oxygen consumption as a function of a single parameter, while keeping all other factors constant (Ghiretti, 1966 and Vernberg and Vernberg, 1972).

Generally oxygen consumption is an exponential function of body weight (Zeuthen, 1947, 1953; Hemmingsen, 1950, 1960) and can be expressed in the form of an allometric equation:

$$\frac{dO_2}{dt} = a W^b$$

where dO_2/dt is rate of oxygen consumption, 'W' is the weight, 'a' is the y intercept and 'b' is the slope. In the linearized form it can be written as

$$\log \frac{dO_2}{dt} = \log a + b \log W$$

In a double logarithmic coordinate system in which oxygen consumption on

the ordinate is plotted against weight on the abscissa, a straight line rather than an exponential curve is obtained.

The metabolic rate i.e. oxygen uptake per unit body weight per unit time is obtained by dividing the above equation by weight, and is expressed as

$$QO_2 = \frac{dO_2}{wdt} = a W^{b-1}$$

i.e. in the linearized form

$$\log \frac{dO_2}{wdt} = \log a + b - 1 \log W$$

where $b-1$ is the slope. Usually the 'b' value is less than 1 and hence $b-1$ has a negative value. Negative 'b' values (Newell and Northcroft, 1967) as well as 'b' values greater than 1 are also encountered (Ansell, 1973).

Zeuthen (1953) suggested that a 'b' value of $2/3$ or 0.67 indicates a metabolism proportional to the surface area. A proportionality of metabolism, not to cell surface but to vascularization and development of complex respiratory system was indicated by Hemingsen (1950, 1960). He proposed that metabolism varies with $3/4$ or 0.751 power of the body weight-power rule. Reviewing the variation of 'b' values, Bertalanffy (1957) stated that "in the various animal classes, three metabolic types i.e. form of dependence of metabolic rate on body size can be distinguished: proportionality of metabolic rate to surface area, or to weight, or one intermediate between surface and weight proportionality". However, many other metabolic types other than the three types of Bertalanffy (1957) do exist.

'b' values were found to vary depending upon changes in intrinsic and extrinsic factors. Thus Zeuthen (1953) found that in the early developmental stages, the 'b' ranges between 0.7 and 0.8 and during development it varies from 0.9 to 1 and in larger mature individuals it is low again. Depending upon variations in salinity, changes in the 'b' values were observed by Rao (1958) in Metapenaeus monoceros; Kennedy and Mihursky (1972) in Mya arenaria, Macoma balthica and Mulinia lateralis, Shafee (1976) in Mytilus viridis and Salih (1978a) in Meretrix casta. Kuenzler (1961), Hughes (1970) and Ansell (1973) observed different 'b' values for bivalves in media of different temperature. Variation of 'b' values with changes in oxygen tension was noticed by Subrahmanyam (1962) in Panaeus indicus, Cheriyan (1973) in Sphaeroma terebrans and Cherian (1978a) in Sphaeroma amandalei, Cirolana willeyi and C. fluviatilis. Seasonal changes of 'b' values were noticed by Bayne et al. (1973) in Mytilus edulis.

Since fluctuation in salinity is the most important characteristic feature of estuaries, estuarine organisms exhibit various metabolic patterns as a response to variation in salinity. The short term overshoot and undershoot responses as well as long term responses of stabilized animals are deviations from the basic pattern of metabolism due to changes in salinity (Kimme, 1971). Following a change in salinity, a new steady rate is attained which is influenced by its past history as well as intrinsic and extrinsic factors acting on the animal (Vernberg and Vernberg, 1972). Within the tolerance range of salinity the new steady level in marine and brackishwater invertebrates may (1) increase in subnormal salinities and/or decrease in supranormal salinities (2) increase in sub - and supranormal

salinities (3) decrease in sub - and supranormal salinities (4) remain essentially unaffected. Euryhaline invertebrates are representatives of the first two types of metabolic responses. The third and fourth types are represented by stenohaline and extremely euryhaline animals, respectively (Kinne, 1971 and Vernberg and Vernberg, 1972).

Potts and Parry (1964) have objected the view of Schlieper, (c.f. Remane and Schlieper, 1958) that increased metabolic rate in subnormal salinities is due to increased energy demands for active ion transport and have put forward several arguments in support of their view. The different ways by which salinity affects the metabolic rate has been discussed by Kinne (1971). He, further, generalized the modifying effects of salinity on the respiratory rate.

The oxygen consumption of bivalves in relation to salinity has been studied by several workers. Kinne (1964) has cited the response of Mytilus viridis acclimated in low salinity and transferred to high salinity and vice versa. Nagabhushanam (1962) has studied the respiration of Martesia striata in different salinities. Ranade (1973) investigated the metabolism of Katylisia opima and Meretrix meretrix in various salinities. Shafee (1976) studied the oxygen consumption of Mytilus viridis in 100 %, 75 % and 50 % salinities (100 % salinity = 35 ‰). Very recently, Salih (1978a) investigated the effect of salinity variation on the oxygen consumption of Meretrix casta.

In an estuary, the oxygen may fluctuate from hypoxic to hyperoxic conditions. This results in corresponding response by the animal population inhabiting the region. Thus some oxygen 'sensitive' animals are restricted

to highly oxygenated waters while others have evolved adaptive mechanisms by which they live in hypoxic conditions. Depending upon the metabolic response of the animals to oxygen tension, organisms are classified either as 'conformers' which have oxygen consumption directly proportional to the oxygen tension of the medium, or 'regulators' which have oxygen consumption steady over a wide range of oxygen tension. Below a critical oxygen tension (P_c), the oxygen independent metabolic rate becomes oxygen dependent (Prosser and Brown, 1961; Vernberg and Vernberg 1972). The shift in P_c values as well as change of oxygen independent metabolic rate to oxygen dependent metabolism can occur due to the action of extrinsic and intrinsic factors (Vernberg and Vernberg, 1972).

Oxygen consumption of bivalves in relation to oxygen tension has been studied by a few authors - Mytilus edulis by Bruce (1926) and Rotthauwe (1958) Ostrea edulis by Galstoff and Whipple (1930), Anodonta cygnea by Hers (1943), Pecten grandis and P. irradiusⁿ by Van Dam (1954), Martesia striata by Nagabhushanam (1962) and in a few other bivalves by Bayne (1971, 1973) and Taylor (1975, 1975a).

From the foregoing account it can be understood that the oxygen consumption of bivalves is dependent on body size, salinity and oxygen content of the medium. In the Cochin Harbour region, Teredo furcifera occurs during the high saline period while Nausitora hedleyi is observed almost throughout the year. The closing of the burrows of shipworms with their pallets to tide over unfavourable conditions will naturally result in a fall in oxygen tension in the burrows. To have a clear understanding on the effect of the above three parameters on the metabolic rate of the two

species, experiments were conducted by subjecting the animals to variations in one of the parameters, keeping constant the others. Oxygen consumption experiments were conducted on N. hedleyi in relation to body weight and ^{salinity} and oxygen tension, and in T. furcifera in relation to body size, ~~salinity~~ and oxygen tension.

(ii) MATERIAL AND METHODS

To determine the rate of oxygen consumption in Nausitora hedleyi and Teredo furcifera under falling oxygen tension, a respiratory apparatus was designed and fabricated in the laboratory. As shown in Fig.15, the apparatus consists of a respiratory chamber with an air tight lid carrying a 30 ml syringe, two inlets and an outlet. The inlet 'A' which reaches the bottom of the respiratory chamber is connected to a constant level overflow tank 'R' and the inlet 'C' is connected to a burette 'B'. The outlet 'D' is to draw out water samples. The total internal volume of the rubber tube connections is less than 0.5 ml. The apparatus is maintained at $28 \pm 1^\circ \text{C}$ by keeping it in an electrically controlled waterbath 'W' provided with a thermometer 'T'. The respiratory chamber is covered with a black paper jacket 'J' having a window to observe the activity of the animal.

To begin the experiment, the animal was carefully introduced into the respiratory chamber containing sufficient quantity of sea water and the chamber was closed with the lid without the plunger 'P'. The apparatus was then placed in the waterbath as shown in the figure and it was slowly filled with sea water from the overflow tank keeping the outlet closed. The column of air in the rubber tube connection between the apparatus and the burette was removed by running a few ml of water from the latter. When water over-

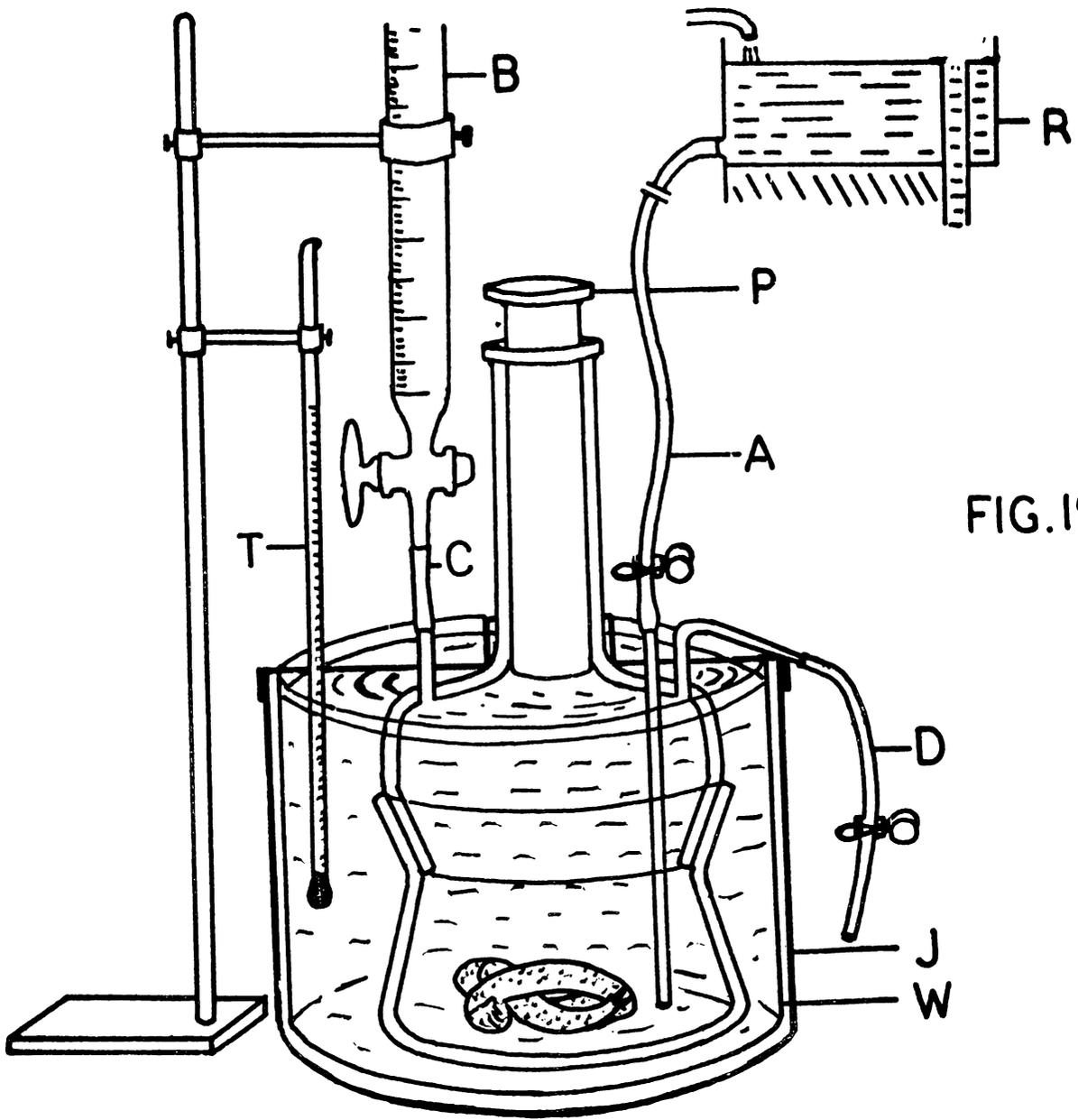
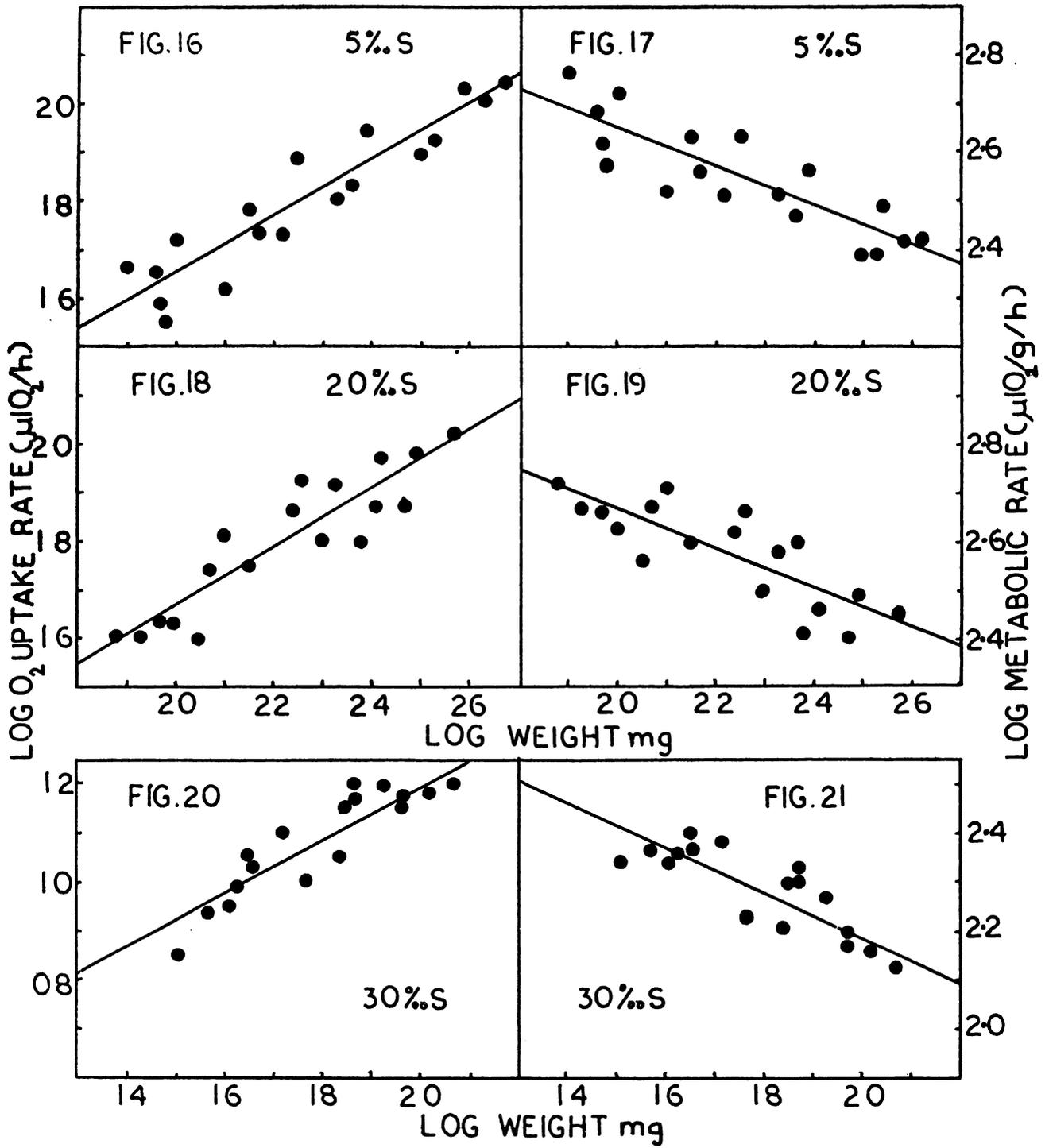


FIG. 15

- Figs. 16 and 18** Relationship between O_2 uptake rate ($\mu l O_2/h$) and body weight (mg) of Nausitora hedleyi in the acclimation salinities of 5 ‰ and 20 ‰.
- Figs. 17 and 19** Relationship between metabolic rate ($\mu l O_2/g/h$) and body weight (mg) of Nausitora hedleyi in the acclimation salinities of 5 ‰ and 20 ‰.
- Fig. 20** Relationship between O_2 uptake rate ($\mu l O_2/h$) and body weight (mg) of Teredo furcifera in the acclimation salinity of 30 ‰.
- Fig. 21** Relationship between metabolic rate ($\mu l O_2/g/h$) and body weight (mg) of Teredo furcifera in the acclimation salinity of 30 ‰.



flowed the barrel, the inflow was cut off, the outlet was opened and the plunger was then carefully replaced and gently pressed down completely to expel all the air trapped in the outlet. After filling the apparatus without any air bubbles, a continuous flow of well aerated seawater from the overflow tank at a constant flow rate was maintained, such that there was no fall in the oxygen tension inside the respiratory chamber, in order to acclimate the animal to the apparatus. A sample of water flowing through the respiratory chamber was then collected for the determination of the initial oxygen content. Then the outlet was closed and the continuous flow was cut off. From the burette exactly 10 ml of seawater was let into the apparatus which raised the plunger of the syringe. 10 ml water samples were drawn out at definite intervals through the outlet and at each time the capacity of the respiratory chamber was restored to the original volume by letting in water from the burette. The intervals between samplings was fixed by running pilot experiments with animals of different size. Sampling bottles of 9 ml capacity were used. Employing this apparatus, any number of 10 ml water samples could be drawn out. A control experiment was run without animal under identical conditions. Preparation of different test media was done as described in Chapter V.

The dissolved oxygen content in water samples was determined by Winkler's micromethod (Welsh and Smith, 1953). A 1 ml tuberculine syringe fitted with necessary screwing arrangements which can be read upto 5 μ l was employed for titration. The normality of sodium thiosulphate used ranged between 0.005 and 0.007 and it was verified everytime before use.

Respiratory chambers of 125 and 250 ml capacities were used depending

upon the size of the animals experimented. In calculating the volume of the test medium in the respiratory chamber, the volume of the experimental animal was taken into consideration. No significant variation of pH in the experimental medium was noticed before and after the experiment. A stirrer was not incorporated in the apparatus as the animal was found to be capable of setting in a circulation of water through siphonal activity, sufficient enough to ensure homogenous mixing of water.

The collection, acclimation, preparation and selection of N. hedleyi specimens for oxygen consumption studies were done as described in Chapter V. In the case of T. furcifera, the same procedure as for N. hedleyi was followed with the exception that the former was collected when the salinity in the harbour was about 30 ‰ and that they were acclimated in the same salinity.

The oxygen consumption of N. hedleyi acclimated in 5 ‰ S was determined in 0.60 ‰, 3 ‰, 5 ‰, 10 ‰, 15 ‰, 20 ‰ and 25 ‰ salinities and that of animals acclimated in 20 ‰ S was measured in 3 ‰, 5 ‰, 10 ‰, 15 ‰, 20 ‰, 25 ‰, 30 ‰ and 33.65 ‰ salinities. The choice of the experimental salinities was based on the results obtained from the salinity tolerance studies on the animals. (Ref. Chapter V). In the case of T. furcifera, oxygen consumption experiments were conducted in the acclimation salinity (30 ‰) alone. The dry weight of N. hedleyi specimens experimented varied from 64.87 to 515.7 mg and that of T. furcifera from 32.36 to 120.2 mg. The experiments had to be restricted to the above weight groups as bigger animals were uncommon in the test panels operated and moreover extraction of larger animals without injury was difficult.

The following are the aspects studied.

1. Oxygen consumption of N. hedleyi and T. furcifera in relation to body weight in the acclimation salinities.
2. Oxygen consumption of N. hedleyi in relation to salinity.
3. Oxygen consumption of N. hedleyi and T. furcifera in relation to oxygen tension.

The regression coefficients obtained for animals under different experimental conditions were compared using students 't'.

(iii) EXPERIMENTS AND RESULTS

A. Oxygen consumption of N. hedleyi and T. furcifera in relation to body weight in the acclimation media at 140 mm Hg partial pressure of oxygen (pO₂)

1. Oxygen consumption of N. hedleyi in the acclimation salinities of 5 ‰ and 20 ‰

1.a. Oxygen consumption in animals acclimated in 5 ‰ salinity

The oxygen uptake rate and metabolic rate of different sizes of N. hedleyi are given in Table 11. The dry weight of the animals experimented varied from 79.62 to 417.80 mg and their oxygen uptake rate from 38.73 to 104.00 $\mu\text{lO}_2/\text{h}$. The rate of oxygen uptake was found to increase with increase in body size and the relationship could be represented by the formula $\text{O}_2 = a W^b$. A double logarithmic plot of oxygen uptake rate and body weight is shown in Fig.16. The estimated values of the regression coefficients 'b' and log 'a' are 0.5959 and 0.4560, respectively.

The weight specific oxygen consumption or metabolic rate i.e. oxygen uptake per unit body weight in unit time showed a decrease with increasing

Table 11. Oxygen uptake rate and metabolic rate of *N. hedleyi* in the acclimation medium of 5 ‰ salinity at 140 mm Hg pO₂ (Values taken from the Figs.16-17)

Body weight mg	O ₂ uptake rate μlO ₂ /h	Metabolic rate μlO ₂ /g/h
79.62	38.73	486.44
91.64	42.07	459.08
93.44	42.56	455.48
95.57	43.25	452.55
100.30	44.46	443.27
125.30	50.93	406.47
141.50	54.58	385.72
157.40	56.10	356.42
166.50	60.12	361.08
177.00	62.66	354.01
214.90	69.82	324.90
229.00	72.78	317.82
244.20	75.68	309.91
316.80	88.31	278.76
339.40	91.83	270.57
343.70	93.11	270.91
382.80	98.40	257.05
417.80	104.00	248.92

Table 12. Oxygen uptake rate and metabolic rate of *N. hedleyi* in the acclimation medium of 20 ‰ salinity at 140 mm Hg pO₂ (Values taken from the Figs.18-19)

Body weight mg	O ₂ uptake rate μlO ₂ /h	Metabolic rate μlO ₂ /g/h
76.82	39.17	509.89
85.34	41.98	491.92
93.51	44.36	474.39
100.90	46.24	458.28
112.40	49.66	441.82
116.30	51.05	438.95
126.80	53.21	419.64
140.40	57.02	406.13
174.10	64.57	370.88
183.20	66.37	362.28
200.00	70.31	351.55
214.50	73.28	341.63
234.00	77.45	330.98
240.60	78.52	326.35
254.30	81.85	321.86
296.50	88.92	299.90
311.40	91.41	293.55
372.10	102.30	274.93

body weight and it could be represented by the equation $O_2/W = aW^{b-1}$. The metabolic rate ranged between 486.44 and 248.92 $\mu\text{l/g/h}$. In Fig.17 is shown the double logarithmic plot of metabolic rate against body weight which showed a negative linear relationship with $b-1$, $- 0.4041$.

1.b. Oxygen consumption of animals acclimated in 20 ‰ salinity

The oxygen uptake rate and metabolic rate of N. hedleyi of different sizes acclimated in 20 ‰ S are presented in Table 12. The oxygen uptake rate varied from 39.17 to 102.30 $\mu\text{lO}_2/\text{h}$ and metabolic rate 509.89 to 274.93 $\mu\text{lO}_2/\text{g/h}$ of animals whose dry weight ranged between 76.82 and 372.10 mg. In Fig.18 logarithm of oxygen uptake rate is plotted against logarithm of body weight and in Fig.19 logarithm of metabolic rate is plotted against logarithm of body weight. The 'b', log 'a' and 'b-1' values estimated are 0.6043, 0.4567 and $- 0.3957$, respectively.

The regression coefficients, the correlation coefficients, the standard errors of 'b', the student's 't's and their probabilities for animals acclimated in 5 ‰ S and 20 ‰ S are given in Table 13.

2. Oxygen consumption of T. furcifera acclimated in 30 ‰ salinity

The rate of oxygen uptake and metabolic rate for different weights of T. furcifera acclimated in 30 ‰ S are presented in Table 14. The oxygen uptake rate varied from 8.34 to 17.10 $\mu\text{lO}_2/\text{h}$ and the metabolic rate 257.63 to 142.26 $\mu\text{lO}_2/\text{g/h}$ in animals whose dry weight ranged between 32.36 and 120.20 mg. The double logarithmic plot of oxygen uptake rate against body weight is shown in Fig.20. The 'b' and log 'a' values estimated are 0.5461 and 0.0973, respectively. In Fig.21 a double logarithmic plot of

Table 13. Regression coefficients, correlation coefficients, Student's 't' values of 'b' probabilities and metabolic rate obtained for N. hedleyi in the acclimation medium of 5 ‰ and 20 ‰ salinities at 140 mm Hg pO₂.

Acclimation Salinity ‰	No	b	b-1	r	S _b	t _b	p	μlO ₂ /h for lg animal
5	18	0.5959	-0.4041	0.9270	0.0603	9.8823	< 0.001	175.2
20	18	0.6043	-0.3957	0.9117	0.0688	8.7858	< 0.001	186.1

Table 14. Oxygen uptake rate and metabolic rate of T. furcifera in the acclimation medium of 30 ‰ salinity at 140 mm Hg pO₂ (Values taken from Figs.20-21)

Body weight mg	O ₂ uptake rate μlO ₂ /h	Metabolic rate μlO ₂ /g/h
32.36	8.34	257.63
37.45	9.00	240.19
40.44	9.46	233.98
42.96	9.71	225.91
44.97	9.95	221.35
46.01	10.07	218.87
52.88	10.86	205.37
58.68	11.56	197.00
69.67	12.65	181.57
71.29	12.79	179.41
73.73	13.12	177.95
74.49	13.13	176.27
85.71	14.16	165.21
93.53	14.89	159.20
93.91	14.93	158.98
105.20	15.89	151.05
118.50	16.87	142.36
120.20	17.10	142.26

Table 15. Regression coefficients, correlation coefficient, Student's 't' value of 'b' probability and metabolic rate obtained for T. furcifera in the acclimation medium of 30 ‰ salinity at 140 mm Hg pO₂

Acclimation Salinity ‰	No	b	b-1	r	S _b	t _b	p	μlO ₂ /h for lg animal
30	18	0.5461	-0.4539	0.9064	0.0650	8.3967	< 0.001	54.41

metabolic rate against body weight is shown. The weight specific regression coefficient is -0.4539.

The regression coefficients, the correlation coefficient, the standard error of 'b', the students 't' and its probability are given in the Table 15.

B. Oxygen consumption of *N. hedleyi* in relation to salinity at 140 mm Hg pO₂.

Animals were directly transferred to higher and lower salinities from the acclimation media of 5 ‰ S and 20 ‰ S and their oxygen consumption rates were studied.

1. Oxygen consumption of animals acclimated in 5 ‰ salinity and experimented in different salinities

Animals acclimated in 5 ‰ S were transferred directly to 0.60 ‰, 3 ‰, 5 ‰, 10 ‰, 15 ‰, 20 ‰ and 25 ‰ salinities and their metabolic rates were studied. Experiments in 30 ‰ S and 33.65 ‰ S were not conducted as the animals did not survive in the above media for any length of time.

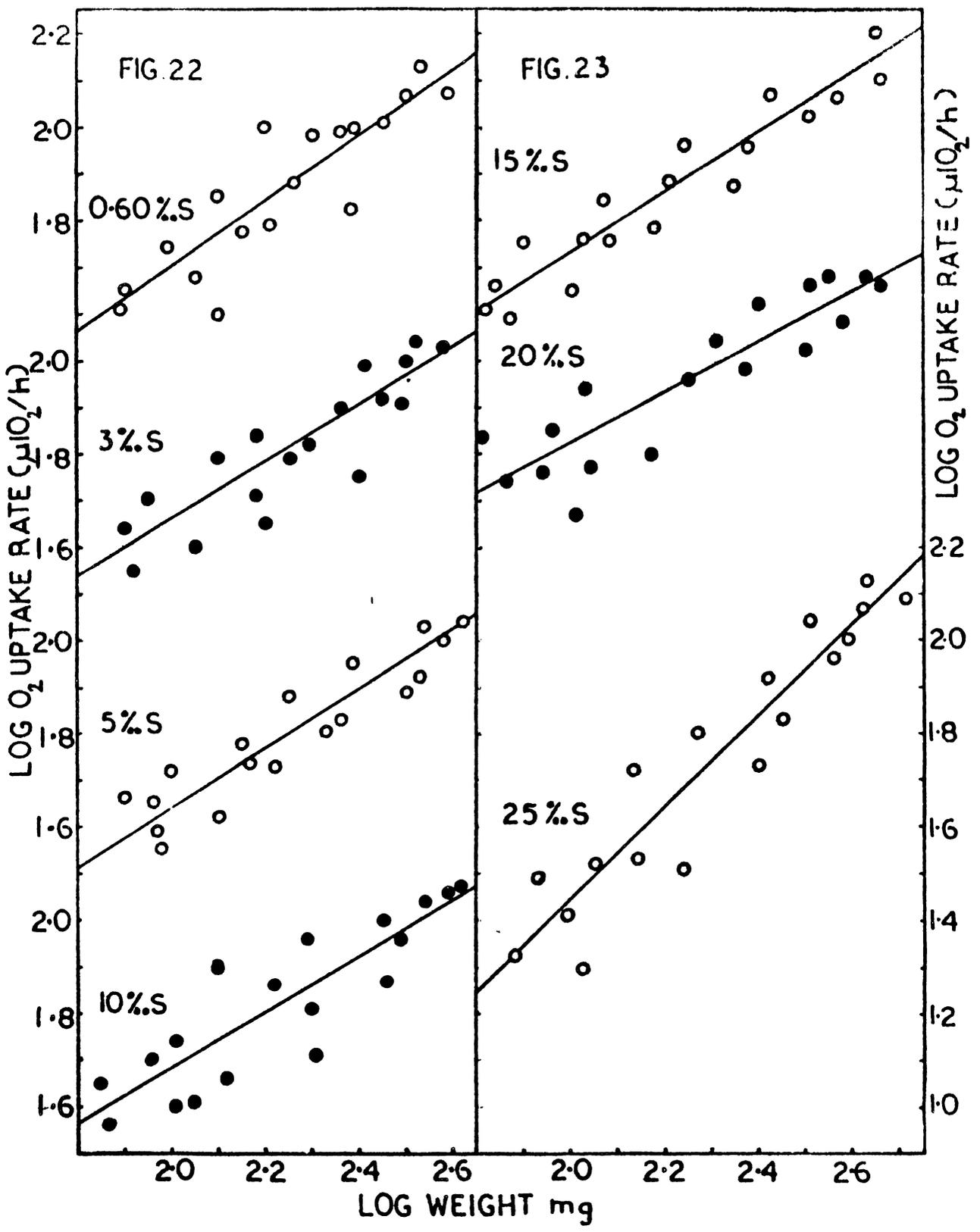
1.a. Oxygen consumption in 0.60 ‰ salinity

The oxygen uptake rate and metabolic rate of animals varied from 42.56 to 130.00 $\mu\text{lO}_2/\text{h}$ and 546.41 to 332.82 $\mu\text{lO}_2/\text{g/h}$, respectively. The dry weight of the animals ranged between 77.89 and 390.6 mg. The values of log 'a', 'b' and 'b-1' obtained are 0.3197, 0.6923 and - 0.3077, respectively (Fig.22).

1.b. Oxygen consumption in 3 ‰ salinity

The oxygen uptake rate and metabolic rate varied from 39.72 to

Figs. 22 and 23 Relationship between oxygen uptake rate ($\mu\text{lO}_2/\text{h}$) and body weight (mg) of Nausitora hedleyi acclimated in 5 ‰S and experimented in 0.60 ‰S, 3 ‰S, 5 ‰S, 10 ‰S, 15 ‰S, 20 ‰S and 25 ‰S at 140 mm Hg pO_2



104.5 $\mu\text{lO}_2/\text{h}$ and 497.74 to 275.44 $\mu\text{lO}_2/\text{g/h}$, respectively. The dry weight of the animals ranged between 79.80 and 379.4 mg. The values of log 'a', 'b' and 'b-1' obtained are 0.4214, 0.6195 and - 0.3805, respectively (Fig.22).

1.c. Oxygen consumption in 5 ‰ salinity

The oxygen uptake rate and metabolic rate varied from 38.73 to 104.0 $\mu\text{lO}_2/\text{h}$ and 486.44 to 248.92 $\mu\text{lO}_2/\text{g/h}$, respectively. The dry weight of the animals ranged between 79.62 and 417.8 mg. The values of log 'a', 'b' and 'b-1' obtained are 0.4557, 0.5959 and - 0.4041, respectively (Fig.22).

1.d. Oxygen consumption in 10 ‰ salinity

The oxygen uptake rate and metabolic rate varied from 38.9 to 112.5 $\mu\text{lO}_2/\text{h}$ and 545.58 to 269.53 $\mu\text{lO}_2/\text{g/h}$, respectively. The dry weight of the animals ranged between 71.3 and 417.4 mg. The values of log 'a', 'b' and 'b-1' are 0.4787, 0.5999 and - 0.4010, respectively (Fig.22).

1.e. Oxygen consumption in 15 ‰ salinity

The oxygen uptake rate and metabolic rate varied from 41.78 to 138.4 $\mu\text{lO}_2/\text{h}$ and 629.41 to 301.72 $\mu\text{lO}_2/\text{g/h}$, respectively. The dry weight of the animals ranged between 66.38 and 458.7 mg. The values of log 'a', 'b' and 'b-1' are 0.4925, 0.6195 and - 0.3805, respectively (Fig.23).

1.f. Oxygen consumption in 20 ‰ salinity

The oxygen uptake rate and metabolic rate varied from 52.72 to 149.6 $\mu\text{lO}_2/\text{h}$ and 812.70 to 327.35 $\mu\text{lO}_2/\text{g/h}$, respectively. The dry weight of the animals ranged between 64.87 and 457.0 mg. The values of log 'a', 'b' and 'b-1' are 0.7539, 0.5342 and - 0.4658, respectively (Fig.23).

1.g. Oxygen consumption in 25 ‰ salinity

The oxygen uptake and metabolic rate varied from 21.48 to 137.7 $\mu\text{lO}_2/\text{h}$ and 277.38 to 267.02 $\mu\text{lO}_2/\text{g/h}$, respectively. The dry weight of the animals ranged between 77.44 and 515.7 mg. The values of log 'a', 'b' and 'b-1' are - 0.5184, 0.9798 and - 0.0202, respectively (Fig.23).

The regression coefficients, the standard errors and other statistical details of N. hedleyi acclimated in 5 ‰ S and experimented in different salinities are presented in Table 16.

Table 16 Statistical analysis of the regression coefficients obtained for N. hedleyi acclimated in 5 ‰ salinity, in different salinities at 140 mm Hg pO₂.

Salinity medium ‰	No	b	r	S _b	t _b	p
0.60	18	0.6923	0.8856	0.0919	7.5361	< 0.001
3	18	0.6195	0.8787	0.0826	7.4962	< 0.001
5	18	0.5959	0.9270	0.0603	9.8823	< 0.001
10	18	0.5999	0.8777	0.0804	7.4614	< 0.001
15	18	0.6195	0.9527	0.0479	12.9330	< 0.001
20	18	0.5342	0.8929	0.0671	7.9613	< 0.001
25	18	0.9798	0.9456	0.0837	11.6876	< 0.001

2. Oxygen consumption of animals acclimated in 20 ‰ salinity and experimented in different salinities

Animals acclimated in 20 ‰ salinity were transferred directly to 3 ‰, 5 ‰, 10 ‰, 15 ‰, 20 ‰, 25 ‰, 30 ‰ and 33.65 ‰ salinities and their respiratory rates were studied. Experiments in 0.60 ‰ S was not conducted as the animals did not survive in the medium for any length of time.

2.a. Oxygen consumption in 3 ‰ salinity

The oxygen uptake rate and metabolic rate varied from 56.36 to

134.3 $\mu\text{lO}_2/\text{h}$ and 616.16 to 368.05 $\mu\text{lO}_2/\text{g/h}$, respectively. The dry weight of the animals ranged between 91.47 and 364.9 mg. The values of log 'a', 'b' and 'b-1' are 0.5215, 0.6269 and - 0.3731, respectively (Fig.24).

2.b. Oxygen consumption in 5 ‰ salinity

The oxygen uptake rate and metabolic rate varied from 45.5 to 165.2 $\mu\text{lO}_2/\text{h}$ and 675.17 to 330.99 $\mu\text{lO}_2/\text{g/h}$, respectively. The dry weight of the animals ranged between 67.39 and 499.1 mg. The values of log 'a', 'b' and 'b-1' are 0.4804, 0.6440 and - 0.3560, respectively (Fig.24).

2.c. Oxygen consumption in 10 ‰ salinity

The oxygen uptake ^{rate} and metabolic rate varied from 41.5 to 130.3 $\mu\text{lO}_2/\text{h}$ and 629.46 to 341.91 $\mu\text{lO}_2/\text{g/h}$, respectively. The dry weight of the animals ranged between 65.93 and 381.1 mg. The values of log 'a', 'b' and 'b-1' are 0.4299, 0.6533 and - 0.3467, respectively (Fig.24).

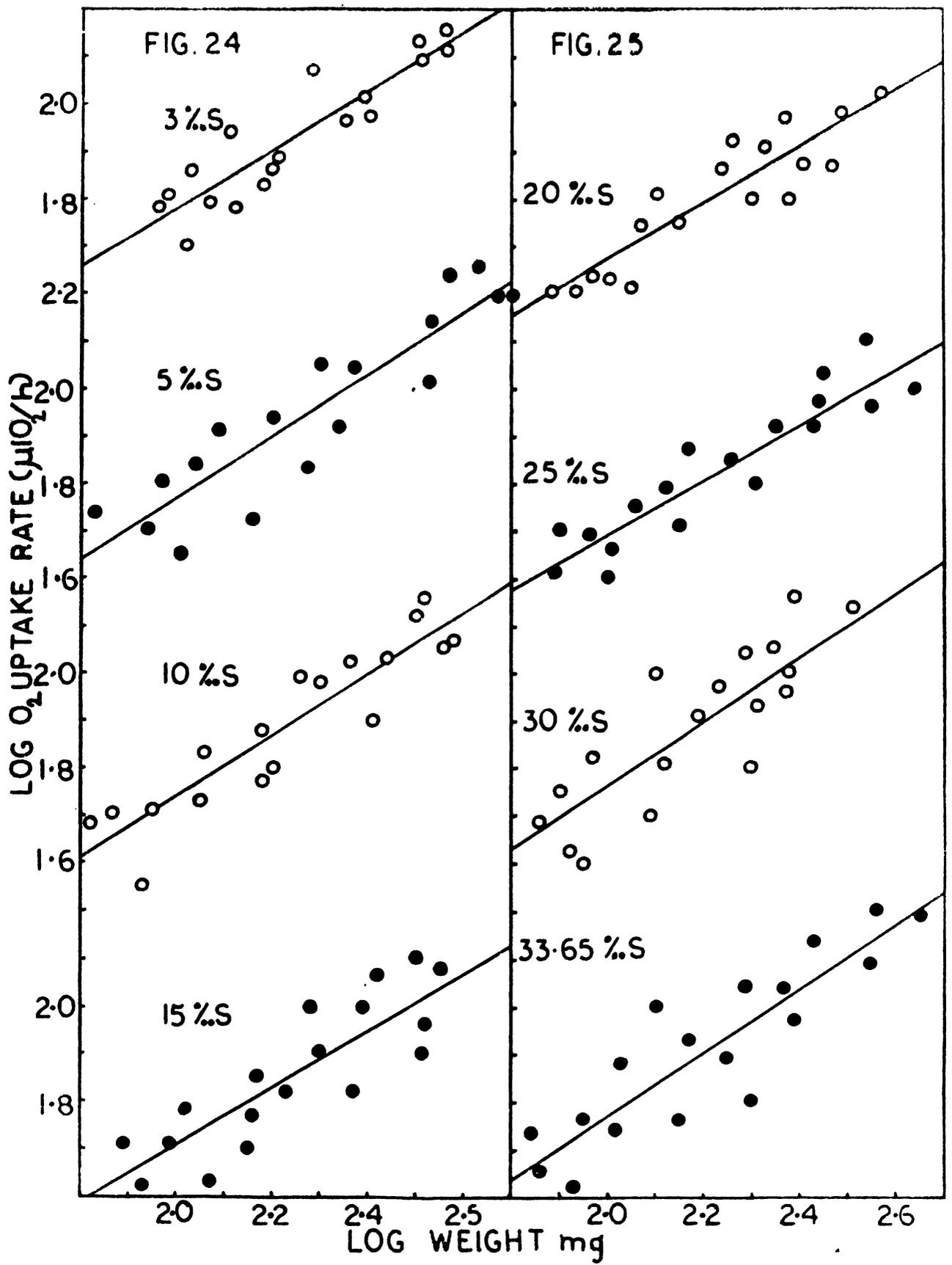
2.d. Oxygen consumption in 15 ‰ salinity

The oxygen uptake rate and metabolic rate varied from 43.45 to 109.9 $\mu\text{lO}_2/\text{h}$ and 559.27 to 310.63 $\mu\text{lO}_2/\text{g/h}$, respectively. The dry weight of animals ranged between 77.69 to 353.8 mg. The values of log 'a', 'b' and 'b-1' are 0.4815, 0.6117 and - 0.3883, respectively (Fig.24).

2.e. Oxygen consumption in 20 ‰ salinity

The oxygen uptake rate and metabolic rate varied from 39.17 to 102.3 $\mu\text{lO}_2/\text{h}$ and 509.89 to 274.93 $\mu\text{lO}_2/\text{g/h}$, respectively. The dry weight of the animals ranged between 79.82 and 371.1 mg. The values of log 'a', 'b' and 'b-1' are 0.4567, 0.6043 and - 0.3957, respectively (Fig. 25).

Figs. 24 and 25 Relationship between oxygen uptake rate ($\mu\text{lO}_2/\text{h}$) and body weight (mg) of Nausitora hedleyi acclimated in 20 ‰ S and experimented in 3 ‰ S, 5 ‰ S, 10 ‰ S, 15 ‰ S, 20 ‰ S, 25 ‰ S, 30 ‰ S and 33.65 ‰ S at 140 mm Hg pO_2



2.f. Oxygen consumption in 25 ‰ salinity

The oxygen uptake rate and metabolic rate varied from 42.56 to 115.9 $\mu\text{lO}_2/\text{h}$ and 544.45 to 267.24 $\mu\text{lO}_2/\text{g/h}$, respectively. The dry weight of the animals ranged between 78.17 and 433.7 mg. The values of log 'a', 'b' and 'b-1' are 0.5243, 0.5840 and - 0.4160, respectively (Fig.25).

2.g. Oxygen consumption in 30 ‰ salinity

The oxygen uptake rate and metabolic rate varied from 46.13 to 127.6 $\mu\text{lO}_2/\text{h}$ and 633.31 to 393.34 $\mu\text{lO}_2/\text{g/h}$, respectively. The dry weight of the animals ranged between 72.84 and 324.4 mg. The values of log 'a', 'b' and 'b-1' are 0.3950, 0.6813 and - 0.3187, respectively (Fig.25).

2.h. Oxygen consumption in 33.65 ‰ salinity

The oxygen uptake rate and metabolic rate varied from 46.67 to 159.2 $\mu\text{lO}_2/\text{h}$ and 671.32 to 356.23 $\mu\text{lO}_2/\text{g/h}$, respectively. The dry weight of the animals ranged between 69.52 and 446.9 mg. The values of log 'a', 'b' and 'b-1' are 0.4576, 0.6581 and - 0.3419, respectively (Fig.25).

The regression coefficients, the standard errors and other statistical details of N. hedleyi acclimated in 20 ‰ S and experimented in different media are presented in Table 17.

Table 17 Statistical analysis of the regression coefficients obtained for N. hedleyi acclimated in 20 ‰ salinity, and in different salinities at 140 mm Hg pO_2 .

Salinity medium ‰	No	b	r	S _b	t _b	p
3	18	0.6269	0.9143	0.0699	8.9607	< 0.001
5	18	0.6440	0.9091	0.0733	8.7858	< 0.001
10	18	0.6533	0.9202	0.0715	9.1371	< 0.001
15	18	0.6117	0.8517	0.0943	6.4867	< 0.001
20	18	0.6043	0.9119	0.0688	8.7834	< 0.001
25	18	0.5840	0.9273	0.0601	9.7171	< 0.001
30	18	0.6813	0.8248	0.1053	6.4701	< 0.001
33.65	18	0.6581	0.8839	0.0867	7.5905	< 0.001

C. Oxygen consumption of *N. hedleyi* and *T. furcifera* in relation to oxygen tension

Oxygen consumption in relation to pO_2 , salinity variation and body weight has been studied in *N. hedleyi* acclimated in 5 ‰ S and 20 ‰ S. In *T. furcifera* respiratory studies have been conducted in relation to pO_2 and body weight only in the acclimation medium of 30 ‰ S.

1. Oxygen consumption of *N. hedleyi* acclimated in 5 ‰ salinity under declining pO_2 in different salinities

The regression lines fitted for $\log O_2$ uptake rate- \log body weight under various pO_2 in different salinities for animals acclimated in 5 ‰ S are shown in Figs. 26-32.

The oxygen uptake rate and metabolic rate obtained for 100 mg, 200 mg, 300 mg and 400 mg weight groups of animals under various pO_2 and in different salinities are presented in Tables 18-24. (Values taken from Figs. 26-32).

1.a. Rate of respiration at 140 mm Hg pO_2

The rate of oxygen uptake in 0.60 ‰ S varied from 50.62 to 132.20 $\mu l O_2/h$, in 3 ‰ S 45.75 to 108.00 $\mu l O_2/h$, in 5 ‰ S 44.49 to 101.50 $\mu l O_2/h$, in 10 ‰ S 47.49 to 109.50 $\mu l O_2/h$, in 15 ‰ S 53.89 to 127.2 $\mu l O_2/h$, in 20 ‰ S 66.42 to 139.30 $\mu l O_2/h$ and in 25 ‰ S 27.62 to 107.40 $\mu l O_2/h$.

The metabolic rate in 0.60 ‰ S varied from 506.2 to 330.50 $\mu l O_2/g/h$, in 3 ‰ S 457.50 to 270.00 $\mu l O_2/g/h$, in 5 ‰ S 444.90 to 253.75 $\mu l O_2/g/h$, in 10 ‰ S 474.90 to 273.75 $\mu l O_2/g/h$, in 15 ‰ S 538.90 to

Figs. 26-29 Relationship between oxygen uptake rate ($\mu\text{lO}_2/\text{h}$) and body weight (mg) of Nausitora hedleyi acclimated in 5 ‰S and experimented in 0.60 ‰S, 3 ‰S, 5 ‰S and 10 ‰S under declining oxygen tension ($p\text{O}_2$)

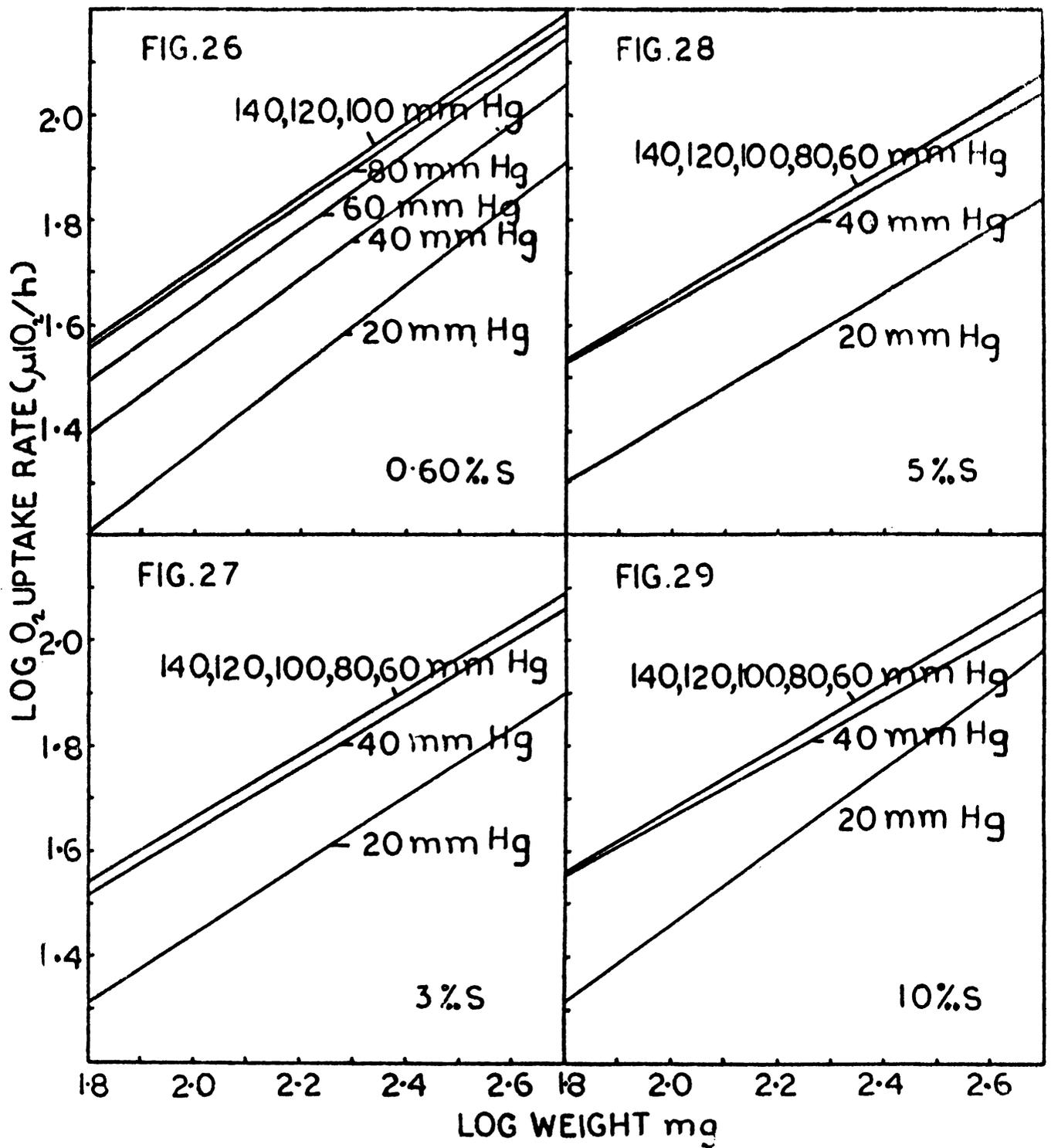


Table 18. Oxygen uptake rate and metabolic rate under declining pO_2 for 100 mg, 200 mg, 300 mg and 400 mg weight groups of *N. hedleyi* acclimated in 5 ‰ salinity and experimented in 0.60 ‰ salinity. (Values taken from Fig. 26)

pO_2 mm Hg	Body weight mg	O_2 uptake rate $\mu l O_2/h$	Metabolic rate $\mu l O_2/g/h$
140	100	50.62	506.20
	200	81.79	408.95
	300	108.20	360.67
	400	132.20	330.50
120	100	50.62	506.20
	200	81.79	408.95
	300	108.20	360.67
	400	132.20	330.50
100	100	50.62	506.20
	200	81.79	408.95
	300	108.20	360.67
	400	132.20	330.50
80	100	49.73	497.30
	200	79.29	396.45
	300	105.80	352.67
	400	126.40	316.00
60	100	43.37	433.70
	200	70.94	354.70
	300	94.62	315.40
	400	116.10	290.25
40	100	34.89	348.90
	200	57.98	289.90
	300	78.03	260.10
	400	96.34	240.85
20	100	22.75	227.50
	200	39.07	195.35
	300	53.64	178.80
	400	67.01	167.53

Table 19. Oxygen uptake rate and metabolic rate under declining pO_2 for 100 mg, 200 mg, 300 mg and 400 mg weight groups of *N. hedleyi* acclimated in 5 ‰ salinity and experimented in 3 ‰ salinity. (Values taken from Fig.27)

pO_2 mm Hg	Body weight mg	O_2 uptake rate $\mu l O_2/h$	Metabolic rate $\mu l O_2/g/h$
140	100	45.75	457.50
	200	70.30	351.50
	300	90.36	301.20
	400	108.00	270.00
120	100	45.75	457.50
	200	70.30	351.50
	300	90.36	301.20
	400	108.00	270.00
100	100	45.75	457.50
	200	70.30	351.50
	300	90.36	301.20
	400	108.00	270.00
80	100	45.75	457.50
	200	70.30	351.50
	300	90.36	301.20
	400	108.00	270.20
60	100	45.75	457.50
	200	70.30	351.50
	300	90.36	301.20
	400	108.00	270.00
40	100	43.81	438.10
	200	66.12	330.60
	300	84.10	280.33
	400	99.77	249.43
20	100	27.38	273.80
	200	43.20	216.00
	300	56.40	188.00
	400	68.17	170.43

Table 20. Oxygen uptake rate and metabolic rate under declining pO_2 for 100 mg, 200 mg, 300 mg and 400 mg weight groups of N. hedleyi in the acclimation medium of 5 ‰ salinity. (Values taken from Fig.28)

pO_2 mm Hg	Body weight mg	O_2 uptake rate $\mu l O_2/h$	Metabolic rate $\mu l O_2/g/h$
140	100	44.49	444.90
	200	67.13	335.65
	300	85.47	284.90
	400	101.50	253.75
120	100	44.49	444.90
	200	67.13	335.65
	300	85.47	284.90
	400	101.50	253.75
100	100	44.49	444.90
	200	67.13	335.65
	300	85.47	284.90
	400	101.50	253.75
80	100	44.49	444.90
	200	67.13	335.65
	300	85.47	284.90
	400	101.50	253.75
60	100	44.49	444.90
	200	67.13	335.65
	300	85.47	284.90
	400	101.50	253.75
40	100	43.50	435.00
	200	64.59	322.95
	300	81.37	271.23
	400	95.90	239.75
20	100	26.19	261.90
	200	39.83	199.15
	300	50.90	169.67
	400	60.57	151.43

Table 21. Oxygen uptake rate and metabolic rate under declining pO_2 for 100 mg, 200 mg, 300 mg and 400 mg weight groups of *N. hedleyi* acclimated in 5 ‰ salinity and experimented in 10 ‰ salinity. (Values taken from Fig.29)

pO_2 mm Hg	Body weight mg	O_2 uptake rate $\mu l O_2/h$	Metabolic rate $\mu l O_2/g/h$
140	100	47.49	474.90
	200	71.96	359.80
	300	92.39	307.97
	400	109.50	273.75
120	100	47.49	474.90
	200	71.96	359.80
	300	92.39	307.97
	400	109.50	273.75
100	100	47.49	474.90
	200	71.96	359.80
	300	92.39	307.97
	400	109.50	273.75
80	100	47.49	474.90
	200	71.96	359.80
	300	92.39	307.97
	400	109.50	273.75
60	100	47.49	474.90
	200	71.96	359.80
	300	92.39	307.97
	400	109.50	273.75
40	100	46.65	466.50
	200	68.47	342.35
	300	85.70	285.67
	400	100.60	251.50
20	100	29.10	291.00
	200	48.38	241.90
	300	65.12	217.07
	400	80.41	201.03

Figs. 30-32 Relationship between oxygen uptake rate ($\mu\text{lO}_2/\text{h}$) and body weight (mg) of Nausitora hedleyi acclimated in 5 ‰S and experimented in 15 ‰S, 20 ‰S and 25 ‰S under declining oxygen tension ($p\text{O}_2$)

Fig. 33 Relationship between oxygen uptake rate ($\mu\text{lO}_2/\text{h}$) and body weight (mg) of Nausitora hedleyi acclimated in 20 ‰S and experimented in 3 ‰S under declining oxygen tension ($p\text{O}_2$)

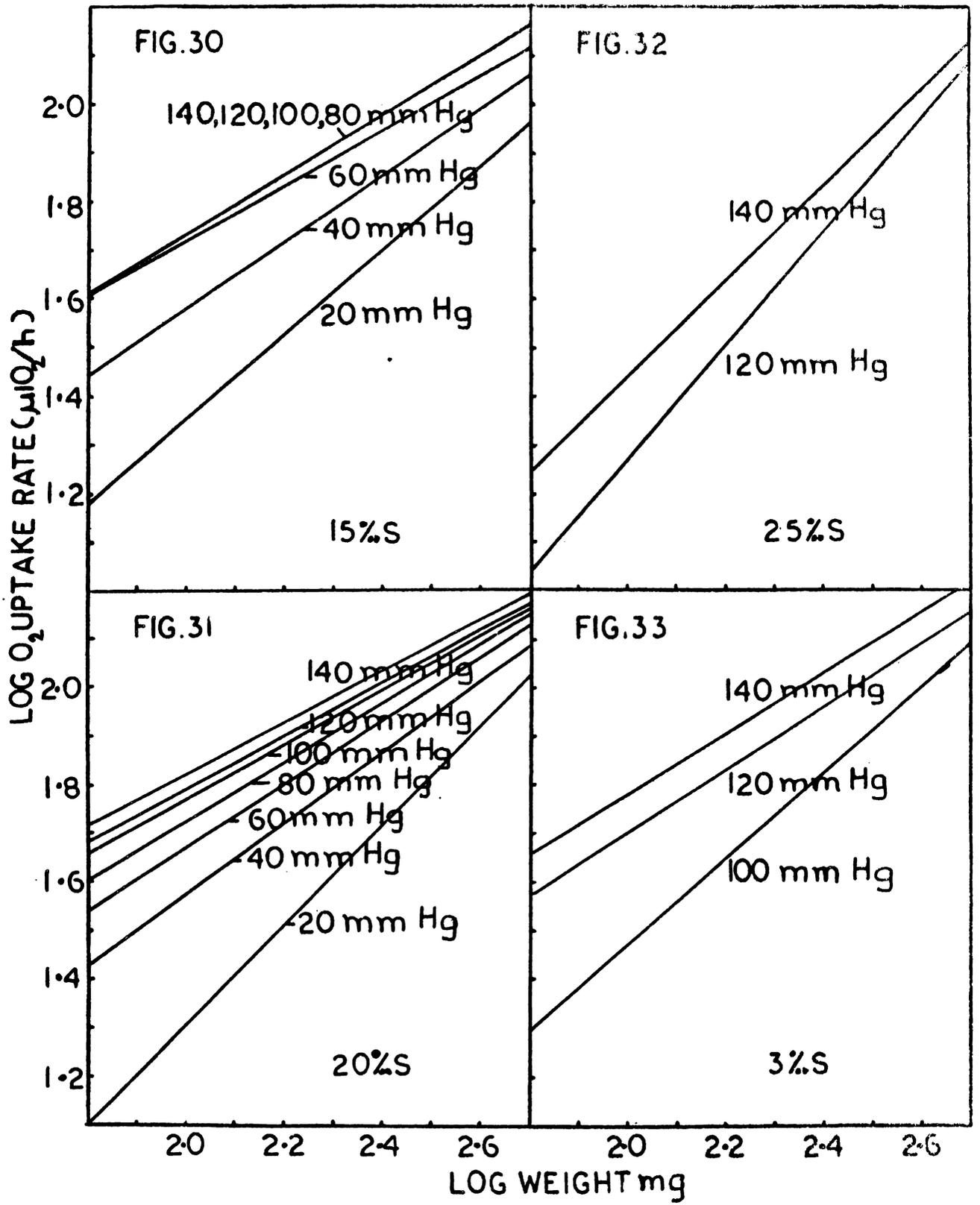


Table 22. Oxygen uptake rate and metabolic rate under declining pO_2 for 100 mg, 200 mg, 300 mg and 400 mg weight groups of *N. hedleyi* acclimated in 5 ‰ salinity and experimented in 15 ‰ salinity. (Values taken from Fig.30)

pO_2 mm Hg	Body weight mg	O_2 uptake rate $\mu lO_2/h$	Metabolic rate $\mu lO_2/g/h$
140	100	53.89	538.90
	200	82.79	413.95
	300	106.40	354.67
	400	127.20	318.00
120	100	53.89	538.90
	200	82.79	413.95
	300	106.40	354.67
	400	127.20	318.00
100	100	53.89	538.90
	200	82.79	413.95
	300	106.40	354.67
	400	127.20	318.00
80	100	53.89	538.90
	200	82.79	413.95
	300	106.40	354.67
	400	127.20	318.00
60	100	52.88	528.80
	200	77.64	388.20
	300	97.18	323.93
	400	114.00	285.00
40	100	37.76	377.60
	200	61.02	305.10
	300	80.81	269.37
	400	98.65	246.63
20	100	22.25	222.50
	200	40.37	201.85
	300	57.22	190.73
	400	73.28	183.20

Table 23. Oxygen uptake rate and metabolic rate under declining pO_2 for 100 mg, 200 mg, 300 mg and 400 mg weight groups of *N. hedleyi* acclimated in 5 ‰ salinity and experimented in 20 ‰ salinity. (Values taken from Fig.31)

pO_2 mm Hg	Body weight mg	O_2 uptake rate $\mu l O_2/h$	Metabolic rate $\mu l O_2/g/h$
140	100	66.42	664.20
	200	96.18	480.90
	300	119.50	398.33
	400	139.30	348.25
120	100	62.01	620.10
	200	90.74	453.70
	300	113.30	377.67
	400	132.80	332.60
100	100	59.30	593.00
	200	88.20	441.00
	300	111.30	371.00
	400	131.20	328.00
80	100	52.84	528.40
	200	80.85	404.25
	300	103.70	345.67
	400	123.70	309.25
60	100	46.95	469.50
	200	73.13	365.65
	300	94.77	315.90
	400	114.60	286.50
40	100	36.76	367.60
	200	61.51	307.55
	300	83.10	277.00
	400	103.10	257.75
20	100	20.01	200.10
	200	36.35	181.75
	300	51.54	171.80
	400	66.06	165.15

Table 24. Oxygen uptake rate and metabolic rate under declining pO₂ for 100 mg, 200 mg, 300 mg and 400 mg weight groups of N. hedleyi acclimated in 5 ‰ salinity and experimented in 25 ‰ salinity (Values taken from Fig.32)

pO ₂ mm Hg	Body weight mg	O ₂ uptake rate μlO ₂ /h	Metabolic rate μlO ₂ /g/h
140	100	27.62	276.20
	200	54.46	272.30
	300	81.04	270.13
	400	107.40	268.50
120	100	18.45	184.50
	200	41.73	208.65
	300	67.25	224.17
	400	94.36	235.90

318.00 μlO₂/g/h, in 20 ‰ S 664.20 to 348.25 μlO₂/g/h and in 25 ‰ S 276.20 to 268.50 μlO₂/g/h.

The 'b' value ranged between 0.5342 (in 20 ‰ S) and 0.9798 (in 25 ‰ S).

1.b. Rate of respiration at 120 mm Hg pO₂

The rate of oxygen uptake in all the salinities except in 20 ‰ S and 25 ‰ S in the same as that at 140 mm Hg pO₂. In 20 ‰ S the rate varied from 62.01 to 132.80 μlO₂/h and in 25 ‰ S 18.45 to 94.36 μlO₂/h.

The metabolic rate in all the salinities is the same as that at 140 mm Hg pO₂, except in 20 ‰ S and 25 ‰ S. In 20 ‰ S the rate varied from 620.10 to 332.60 μlO₂/g/h and in 25 ‰ S 184.50 to 235.90 μlO₂/g/h.

The 'b' values varied from 0.5493 (in 20 ‰ S) to 1.1770 (in 25 ‰ S).

1.c. Rate of respiration at 100 mm Hg pO₂

The rate of oxygen uptake is the same as that at 140 and 120 mm Hg pO₂ in all the salinities except in 20 ‰ S. In 20 ‰ S, the rate varied from 59.30 to 131.20 $\mu\text{lO}_2/\text{h}$. In 25 ‰ S, no readings could be obtained for reasons already mentioned.

The metabolic rate is the same as that at 140 and 120 mm Hg pO₂ in all the salinities except in 20 ‰ S. In 20 ‰ S the rate varied from 593.00 to 328.00 $\mu\text{lO}_2/\text{g/h}$.

The 'b' values ranged between 0.5727 (in 20 ‰ S) and 0.6923 (in 0.60 ‰ S).

1.d. Rate of respiration at 80 mm Hg pO₂

The rate of oxygen uptake is the same as that at 140-100 mm Hg pO₂ in all the salinities except in 0.60 ‰ S and 20 ‰ S. In 0.60 ‰ S, the rate varied from 49.73 to 126.40 $\mu\text{lO}_2/\text{h}$ and in 20 ‰ S 52.84 to 123.70 $\mu\text{lO}_2/\text{h}$.

The metabolic rate is the same as that at 140-100 mm Hg pO₂ in all the salinities except in 0.60 ‰ S and 20 ‰ S. In 0.60 ‰ S the rate varied from 497.30 to 316.00 $\mu\text{lO}_2/\text{g/h}$ and in 20 ‰ S 528.40 to 309.25 $\mu\text{lO}_2/\text{g/h}$.

The 'b' values ranged between 0.5959 (in 5 ‰ S) and 0.6727 (in 0.60 ‰ S).

1.e. Rate of respiration at 60 mm Hg pO₂

The rate of oxygen uptake in all the salinities is the same as that at 140-80 mm Hg pO₂ except in 0.60 ‰ S, 15 ‰ S and 20 ‰ S. In 0.60 ‰ S

the rate varied from 43.37 to 116.10 $\mu\text{lO}_2/\text{h}$, in 15 ‰ S 52.88 to 114.00 $\mu\text{lO}_2/\text{h}$ and 20 ‰ S 46.95 to 114.60 $\mu\text{lO}_2/\text{h}$.

The metabolic rate in all the salinities is the same as that at 140-80 mm Hg pO_2 except in 0.60 ‰ S, 15 ‰ S and 20 ‰ S. In 0.60 ‰ S the rate varied from 433.70 to 290.25 $\mu\text{lO}_2/\text{g/h}$, in 15 ‰ S 528.80 to 285.00 $\mu\text{lO}_2/\text{g/h}$ and in 20 ‰ S 469.50 to 286.50 $\mu\text{lO}_2/\text{g/h}$.

The 'b' values ranged between 0.5540 (in 15 ‰ S) and 0.7100 (in 0.60 ‰ S).

1.f. Rate of respiration at 40 mm Hg pO_2

The rate of oxygen uptake in 0.60 ‰ S varied from 34.89 to 96.34 $\mu\text{lO}_2/\text{h}$, in 3 ‰ S 43.81 to 99.77 $\mu\text{lO}_2/\text{h}$, in 5 ‰ S 43.50 to 95.90 $\mu\text{lO}_2/\text{h}$, in 10 ‰ S 46.65 to 100.60 $\mu\text{lO}_2/\text{h}$, in 15 ‰ S 37.76 to 98.65 $\mu\text{lO}_2/\text{h}$ and in 20 ‰ S 36.76 to 103.10 $\mu\text{lO}_2/\text{h}$.

The metabolic rate in 0.60 ‰ S varied from 348.90 to 240.85 $\mu\text{lO}_2/\text{g/h}$, in 3 ‰ S 438.10 to 249.43 $\mu\text{lO}_2/\text{g/h}$, in 5 ‰ S 435.00 to 239.75 $\mu\text{lO}_2/\text{g/h}$, in 10 ‰ S 466.50 to 251.50 $\mu\text{lO}_2/\text{g/h}$, in 15 ‰ S 377.60 to 246.63 $\mu\text{lO}_2/\text{g/h}$ and in 20 ‰ S 367.60 to 257.75 $\mu\text{lO}_2/\text{g/h}$.

The 'b' values ranged between 0.5537 (in 10 ‰ S) and 0.7424 (in 20 ‰ S).

1.g. Rate of respiration at 20 mm Hg pO_2

The rate of oxygen uptake in 0.60 ‰ S varied from 22.75 to 67.01 $\mu\text{lO}_2/\text{h}$, in 3 ‰ S 27.38 to 68.17 $\mu\text{lO}_2/\text{h}$, in 5 ‰ S 26.19 to 60.57 $\mu\text{lO}_2/\text{h}$,

in 10 ‰ S 29.10 to 80.41 $\mu\text{lO}_2/\text{h}$, in 15 ‰ S 22.25 to 73.28 $\mu\text{lO}_2/\text{h}$ and in 20 ‰ S 20.01 to 66.06 $\mu\text{lO}_2/\text{h}$.

The metabolic rate in 0.60 ‰ S varied from 227.50 to 167.53 $\mu\text{lO}_2/\text{g/h}$, in 3 ‰ S 273.8 to 170.43 $\mu\text{lO}_2/\text{g/h}$, in 5 ‰ S 261.90 to 151.43 $\mu\text{lO}_2/\text{g/h}$, in 10 ‰ S 291.00 to 201.03 $\mu\text{lO}_2/\text{g/h}$, in 15 ‰ S 222.50 to 183.20 $\mu\text{lO}_2/\text{g/h}$, and in 20 ‰ S 200.10 to 165.15 $\mu\text{lO}_2/\text{g/h}$.

The 'b' values ranged between 0.6049 (in 5 ‰ S) and 0.8615 (in 20 ‰ S).

2. Oxygen consumption of *N. hedleyi* acclimated in 20 ‰ S under declining $p\text{O}_2$ in different salinities

The regression lines fitted for log oxygen uptake rate-log body weight under various $p\text{O}_2$ in different salinities for animal acclimated in 20 ‰ S are shown in Figs.33-40. The oxygen uptake rate and metabolic rate obtained for 100 mg, 200 mg, 300 mg and 400 mg weight groups of animals under various $p\text{O}_2$ and in different salinities are given in Tables 25-32.

(Values obtained from Figs.33-40)

Table 25. Oxygen uptake rate and metabolic rate under declining $p\text{O}_2$ for 100 mg, 200 mg, 300 mg and 400 mg weight groups of *N. hedleyi* acclimated in 20 ‰ salinity and experimented in 3 ‰ salinity (Values taken from Fig.33)

$p\text{O}_2$ mm Hg	Body weight mm	O_2 uptake rate $\mu\text{lO}_2/\text{h}$	Metabolic rate $\mu\text{lO}_2/\text{g/h}$
140	100	59.61	596.10
	200	92.04	460.20
	300	118.70	395.67
	400	142.20	355.50
120	100	50.21	502.10
	200	78.74	393.70
	300	102.40	341.33
	400	123.50	308.75
100	100	29.77	297.70
	200	53.88	266.90
	300	77.36	257.87
	400	99.38	248.45

Figs. 34-37 Relationship between oxygen uptake rate ($\mu\text{lO}_2/\text{h}$) and body weight (mg) of Nausitora hedleyi acclimated in 20 ‰S and experimented in 5 ‰S, 10 ‰S, 15 ‰S and 20 ‰S under declining oxygen tension ($p\text{O}_2$)

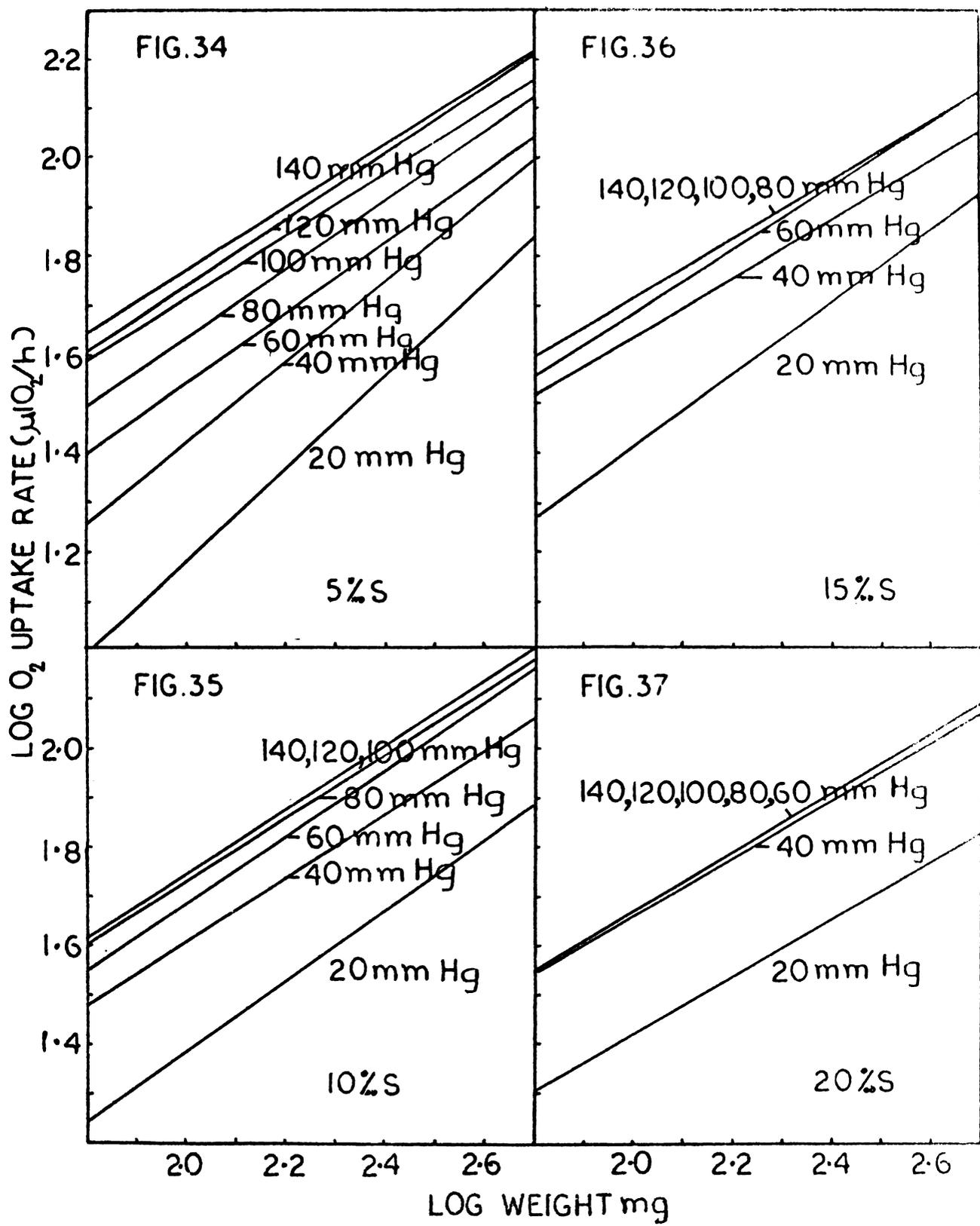


Table 26. Oxygen uptake rate and metabolic rate under declining pO_2 for 100 mg, 200 mg, 300 mg and 400 mg weight groups of *N. hedleyi* acclimated in 20 ‰ salinity and experimented in 5 ‰ salinity. (Values taken from Fig.34)

pO_2 mm Hg	Body weight mg	O_2 uptake rate $\mu l O_2/h$	Metabolic rate $\mu l O_2/g/h$
140	100	58.56	585.60
	200	91.66	458.30
	300	119.10	397.00
	400	143.30	358.25
120	100	54.73	547.30
	200	86.48	432.40
	300	113.00	376.67
	400	136.70	341.75
100	100	51.23	512.30
	200	79.73	398.65
	300	103.40	344.67
	400	124.30	310.75
80	100	42.57	425.70
	200	68.68	343.40
	300	90.86	362.87
	400	110.90	277.25
60	100	34.99	349.90
	200	57.24	286.20
	300	76.35	254.50
	400	93.69	234.23
40	100	26.30	263.00
	200	46.39	231.95
	300	64.68	215.60
	400	81.85	204.63
20	100	15.03	150.30
	200	28.76	143.80
	300	42.33	141.10
	400	55.10	137.75

Table 27. Oxygen uptake rate and metabolic rate under declining pO_2 for 100 mg, 200 mg, 300 mg and 400 mg weight groups of *N. hedleyi* acclimated in 20 ‰ salinity and experimented in 10 ‰ salinity. (Values taken from Fig.35)

pO_2 mm Hg	Body weight mg	O_2 uptake rate $\mu l O_2/h$	Metabolic rate $\mu l O_2/g/h$
140	100	54.51	545.10
	200	85.70	428.50
	300	111.80	372.67
	400	134.90	337.25
120	100	54.51	545.10
	200	85.70	428.50
	300	111.80	372.67
	400	134.90	337.25
100	100	54.51	545.10
	200	85.70	428.50
	300	111.80	372.67
	400	134.90	337.25
80	100	53.27	532.70
	200	82.81	414.05
	300	107.20	357.33
	400	128.70	321.75
60	100	47.31	473.10
	200	75.93	379.65
	300	102.10	340.33
	400	122.00	305.00
40	100	40.12	401.20
	200	62.69	313.45
	300	81.62	272.07
	400	98.19	245.48
20	100	23.75	237.50
	200	39.29	196.45
	300	52.73	175.77
	400	65.00	162.50

Table 28. Oxygen uptake rate and metabolic rate under declining pO_2 for 100 mg, 200 mg, 300 mg and 400 mg weight groups of N. hedleyi acclimated in 20 ‰ salinity and experimented in 15 ‰ salinity. (Values taken from Fig.36)

pO_2 mm Hg	Body weight mg	O_2 uptake rate $\mu l O_2/h$	Metabolic rate $\mu l O_2/g/h$
140	100	50.69	506.90
	200	77.45	387.25
	300	99.31	331.03
	400	118.40	296.00
120	100	50.69	506.90
	200	77.45	387.25
	300	99.31	331.03
	400	118.40	296.00
100	100	50.69	506.90
	200	77.45	387.25
	300	99.31	331.03
	400	118.40	296.00
80	100	50.69	506.90
	200	77.45	387.25
	300	99.31	331.03
	400	118.40	296.00
60	100	48.16	481.60
	200	75.86	379.30
	300	98.95	329.83
	400	117.60	294.00
40	100	42.55	425.50
	200	64.48	322.40
	300	82.22	274.07
	400	97.72	244.30
20	100	25.65	256.50
	200	42.37	211.85
	300	56.83	189.43
	400	70.10	175.25

Table 29. Oxygen uptake rate and metabolic rate under declining pO_2 for 100 mg, 200 mg, 300 mg and 400 mg weight groups of *N. hedleyi* in the acclimation medium of 20 ‰ salinity. (Values taken from Fig.37)

pO_2 mm Hg	Body weight mg	O_2 uptake rate $\mu l O_2/h$	Metabolic rate $\mu l O_2/g/h$
140	100	46.28	462.80
	200	70.34	351.70
	300	89.86	299.53
	400	106.40	266.00
120	100	46.28	462.80
	200	70.34	351.70
	300	89.86	299.53
	400	106.40	266.00
100	100	46.28	462.80
	200	70.34	351.70
	300	89.86	299.53
	400	106.40	266.00
80	100	46.28	462.80
	200	70.34	351.70
	300	89.86	299.53
	400	106.40	266.00
60	100	46.28	462.80
	200	70.34	351.70
	300	89.86	299.53
	400	106.40	266.00
40	100	45.92	459.20
	200	68.21	341.05
	300	85.94	286.47
	400	101.30	253.25
20	100	26.53	265.30
	200	39.62	198.10
	300	50.09	166.97
	400	59.17	147.93

Figs. 38-40 Relationship between oxygen uptake rate ($\mu\text{lO}_2/\text{h}$) and body weight (mg) of Nausitora hedleyi acclimated in 20 ‰S and experimented in 25 ‰S, 30 ‰S and 33.65 ‰S under declining oxygen tension ($p\text{O}_2$)

Fig. 41 Relationship between oxygen uptake rate ($\mu\text{lO}_2/\text{h}$) and body weight (mg) of Teredo furcifer in the acclimation salinity of 30 ‰ under declining oxygen tension ($p\text{O}_2$)

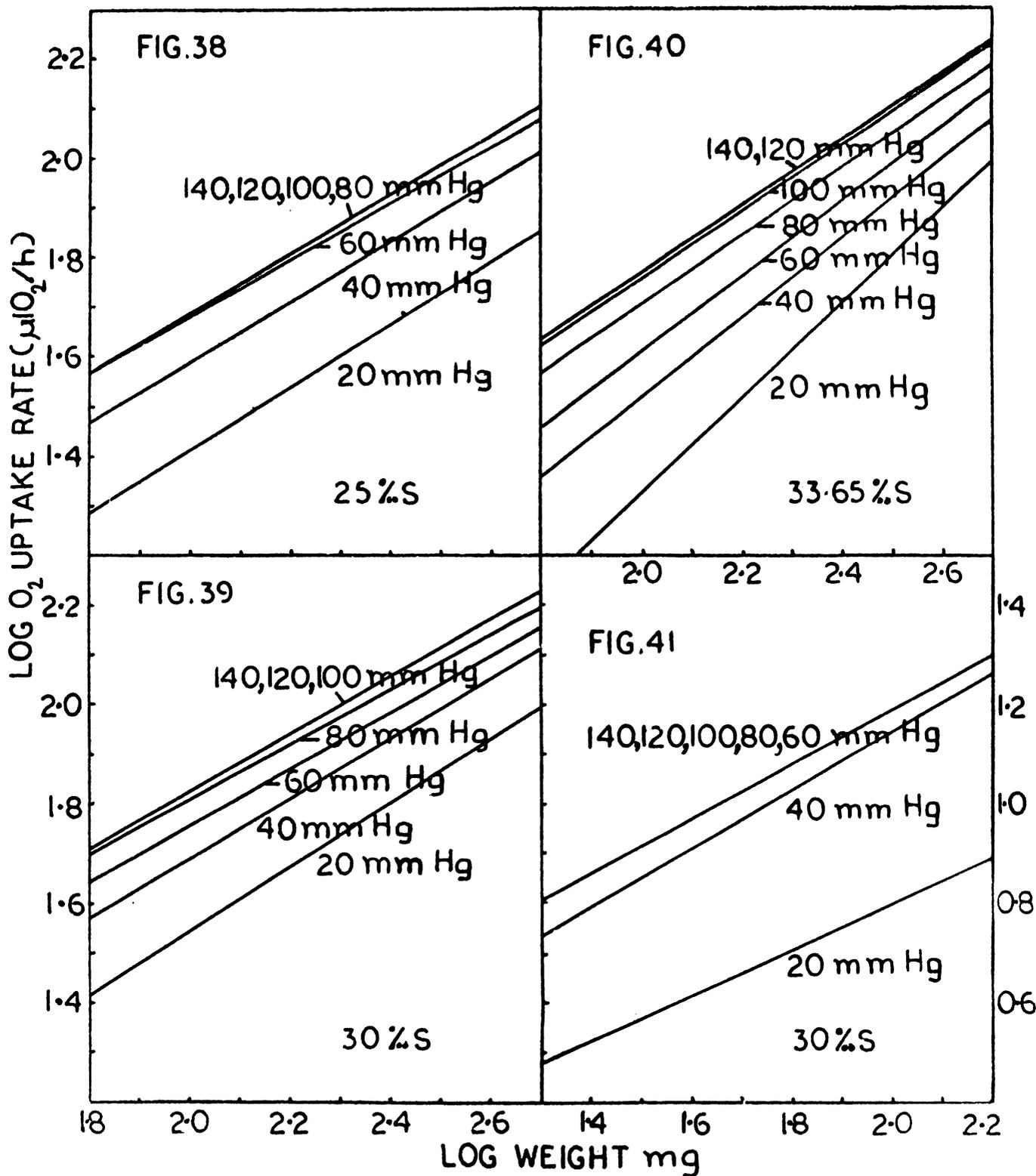


Table 30. Oxygen uptake rate and metabolic rate under declining pO_2 for 100 mg, 200 mg, 300 mg and 400 mg weight groups of *N. hedleyi* acclimated in 20 ‰ salinity and experimented in 25 ‰ salinity. (Values taken from Fig.38)

pO_2 mm Hg	Body weight mg	O_2 uptake rate $\mu l O_2/h$	Metabolic rate $\mu l O_2/g/h$
140	100	49.23	492.30
	200	73.62	368.10
	300	93.50	316.67
	400	110.60	276.50
120	100	49.23	492.30
	200	73.62	368.10
	300	93.50	316.67
	400	110.60	276.50
100	100	49.23	492.30
	200	73.62	368.10
	300	93.50	316.67
	400	110.60	276.50
80	100	49.23	492.30
	200	73.62	368.10
	300	93.50	316.67
	400	110.60	276.50
60	100	47.81	478.10
	200	71.03	355.15
	300	89.54	298.47
	400	105.50	263.75
40	100	39.23	392.30
	200	59.20	296.00
	300	75.30	251.00
	400	89.33	223.33
20	100	25.48	254.80
	200	39.80	199.00
	300	51.70	172.33
	400	62.20	155.50

Table 31. Oxygen uptake rate and metabolic rate under declining pO_2 for 100 mg, 200 mg, 300 mg and 400 mg weight groups of *N. hedleyi* acclimated in 20 ‰ salinity and experimented in 30 ‰ salinity. (Values taken from Fig.39)

pO_2 mm Hg	Body weight mg	O_2 uptake rate $\mu l O_2/h$	Metabolic rate $\mu l O_2/g/h$
140	100	57.23	572.30
	200	91.77	458.85
	300	121.00	403.33
	400	147.20	368.00
120	100	57.23	572.30
	200	91.77	458.85
	300	121.00	403.33
	400	147.20	368.00
100	100	57.23	572.30
	200	91.77	458.85
	300	121.00	403.33
	400	147.20	368.00
80	100	55.82	558.20
	200	87.28	436.40
	300	113.30	377.67
	400	136.50	341.25
60	100	49.63	496.30
	200	78.83	394.15
	300	103.40	344.67
	400	125.20	313.00
40	100	42.23	422.30
	200	68.42	342.10
	300	90.95	303.17
	400	111.20	278.00
20	100	30.19	301.90
	200	50.74	253.70
	300	68.74	229.13
	400	85.27	213.18

Table 32. Oxygen uptake rate and metabolic rate under declining pO_2 for 100 mg, 200 mg, 300 mg and 400 mg weight groups of *N. hedleyi* acclimated in 20 ‰ salinity and experimented in 33.65 ‰ salinity. (Values taken from Fig.40)

pO_2 mm Hg	Body weight mg	O_2 uptake rate $\mu l O_2/h$	Metabolic rate $\mu l O_2/g/h$
140	100	59.40	594.00
	200	93.67	468.35
	300	122.30	407.67
	400	147.90	369.75
120	100	59.40	594.00
	200	93.67	468.35
	300	122.30	407.67
	400	147.90	369.75
100	100	58.01	580.10
	200	91.14	455.70
	300	118.70	395.67
	400	143.20	358.00
80	100	51.80	518.00
	200	82.37	411.85
	300	108.10	360.33
	400	131.00	327.50
60	100	41.05	410.50
	200	68.63	343.15
	300	92.72	309.07
	400	114.80	287.00
40	100	32.97	329.70
	200	57.53	287.65
	300	79.69	265.63
	400	100.40	251.00
20	100	21.61	216.10
	200	40.26	201.30
	300	57.93	193.10
	400	75.01	187.53

2.a. Rate of respiration at 140 mm Hg pO₂

The rate of oxygen uptake in 3 ‰ S varied from 59.61 to 142.20 $\mu\text{lO}_2/\text{h}$, in 5 ‰ S 58.56 to 143.30 $\mu\text{lO}_2/\text{h}$, in 10 ‰ S 54.51 to 134.90 $\mu\text{lO}_2/\text{h}$, in 15 ‰ S 50.69 to 118.40 $\mu\text{lO}_2/\text{h}$, in 20 ‰ S 46.28 to 106.40 $\mu\text{lO}_2/\text{h}$, in 25 ‰ S 49.23 to 110.60 $\mu\text{lO}_2/\text{h}$, in 30 ‰ S 57.23 to 147.20 $\mu\text{lO}_2/\text{h}$ and in 33.65 ‰ S 59.40 to 147.90 $\mu\text{lO}_2/\text{h}$.

The metabolic rate in 3 ‰ S varied from 596.10 to 355.50 $\mu\text{lO}_2/\text{g/h}$, in 5 ‰ S 585.60 to 358.25 $\mu\text{lO}_2/\text{g/h}$, in 10 ‰ S 545.10 to 337.25 $\mu\text{lO}_2/\text{g/h}$, in 15 ‰ S 506.9 to 296.00 $\mu\text{lO}_2/\text{g/h}$, in 20 ‰ S 462.80 to 266.00 $\mu\text{lO}_2/\text{g/h}$, in 25 ‰ S 492.30 to 276.50 $\mu\text{lO}_2/\text{g/h}$, in 30 ‰ S 572.30 to 368.00 $\mu\text{lO}_2/\text{g/h}$ and in 33.65 ‰ S 594.00 to 369.75 $\mu\text{lO}_2/\text{g/h}$.

The 'b' values ranged between 0.5840 (in 25 ‰ S) and 0.6813 (in 30 ‰ S).

2.b. Rate of respiration at 120 mm Hg pO₂

The rate of oxygen uptake in all the salinities is the same as that at 140 mm Hg pO₂ except in 3 ‰ S and 5 ‰ S. In 3 ‰ S the rate varied from 50.21 to 123.50 $\mu\text{lO}_2/\text{h}$ and in 5 ‰ S 54.73 to 136.70 $\mu\text{lO}_2/\text{h}$.

The metabolic rate is the same in all the salinities as that at 140 mm Hg pO₂ except in 3 ‰ S and 5 ‰ S. In 3 ‰ S the rate varied from 502.10 to 308.75 $\mu\text{lO}_2/\text{g/h}$ and in 5 ‰ S 547.30 to 341.75 $\mu\text{lO}_2/\text{g/h}$.

The 'b' values ranged between 0.5840 (in 25 ‰ S) and 0.6813 (in 30 ‰ S).

2.c. Rate of respiration at 100 mm Hg pO₂

The rate of oxygen uptake is the same as that at 140 and 120 mm Hg pO₂ in all the salinities except in 3 ‰ S, 5 ‰ S and 33.65 ‰ S. In 3 ‰ S the rate varied from 29.77 to 99.38 $\mu\text{lO}_2/\text{h}$, in 5 ‰ S 51.23 to 124.30 $\mu\text{lO}_2/\text{h}$ and 33.65 ‰ S 58.01 to 143.20 $\mu\text{lO}_2/\text{h}$.

The metabolic rate is the same in all salinities as that at 140 and 120 mm Hg pO₂ except in 3 ‰ S, 5 ‰ S and 33.65 ‰ S. In 3 ‰ S the rate varied from 297.70 to 248.45 $\mu\text{lO}_2/\text{g/h}$ and in 5 ‰ S 512.30 to 310.75 $\mu\text{lO}_2/\text{g/h}$ and in 33.65 ‰ S 580.10 to 358.00 $\mu\text{lO}_2/\text{g/h}$.

The 'b' values ranged between 0.5840 (in 25 ‰ S) and 0.8695 (in 3 ‰ S).

2.d. Rate of respiration at 80 mm Hg pO₂

The rate of oxygen uptake is the same as that at 140-100 mm Hg pO₂ in all the salinities, except in 5 ‰ S, 10 ‰ S, 30 ‰ S and 33.65 ‰ S. The measurement in 3 ‰ S could not be continued below 100 mm Hg pO₂ for reasons already mentioned. In 5 ‰ S the rate varied from 42.57 to 110.90 $\mu\text{lO}_2/\text{h}$, in 10 ‰ S, 53.27 to 128.70 $\mu\text{lO}_2/\text{h}$, in 30 ‰ S 55.82 to 136.50 $\mu\text{lO}_2/\text{h}$ and in 33.65 ‰ S 51.80 to 131.00 $\mu\text{lO}_2/\text{h}$.

The metabolic rate is the same as that at 140-100 mm Hg pO₂ in all the salinities except in 5 ‰ S, 10 ‰ S, 30 ‰ S and 33.65 ‰ S. In 5 ‰ S the rate varied from 425.70 to 277.25 $\mu\text{lO}_2/\text{g/h}$, in 10 ‰ S 532.70 to 321.75 $\mu\text{lO}_2/\text{g/h}$, in 30 ‰ S 558.20 to 341.25 $\mu\text{lO}_2/\text{g/h}$ and in 33.65 ‰ S 518.00 to 327.50 $\mu\text{lO}_2/\text{g/h}$.

The 'b' values ranged between 0.5840 (in 25 ‰ S) and 0.6901 (in 5 ‰ S).

2.e. Rate of respiration at 60 mm Hg pO₂

The same rate of oxygen uptake is found from 140 to 60 mm Hg pO₂ in the acclimation salinity of 20 ‰. In 5 ‰ S, the rate varied from 34.99 to 93.69 $\mu\text{lO}_2/\text{h}$, in 10 ‰ S 47.31 to 122.00 $\mu\text{lO}_2/\text{h}$, in 15 ‰ S 48.16 to 117.60 $\mu\text{lO}_2/\text{h}$, in 25 ‰ S 47.81 to 105.50 $\mu\text{lO}_2/\text{h}$, in 30 ‰ S 49.63 to 125.20 $\mu\text{lO}_2/\text{h}$ and in 33.65 ‰ S 41.05 to 114.80 $\mu\text{lO}_2/\text{h}$.

The metabolic rate is the same from 140 to 60 mm Hg pO₂ in the acclimation salinity of 20 ‰. The rate in 5 ‰ S varied from 349.90 to 234.23 $\mu\text{lO}_2/\text{g/h}$, in 10 ‰ S 473.10 to 305.00 $\mu\text{lO}_2/\text{g/h}$, in 15 ‰ S 481.60 to 294.00 $\mu\text{lO}_2/\text{g/h}$, in 25 ‰ S 478.10 to 263.75 $\mu\text{lO}_2/\text{g/h}$, in 30 ‰ S 496.30 to 313.00 $\mu\text{lO}_2/\text{g/h}$ and in 33.65 ‰ S 410.50 to 287.00 $\mu\text{lO}_2/\text{g/h}$.

The 'b' values ranged between 0.5709 (in 25 ‰ S) and 0.7419 (in 33.65 ‰ S).

2.f. Rate of respiration at 40 mm Hg pO₂

The rate of oxygen uptake in 5 ‰ S varied from 26.30 to 81.85 $\mu\text{lO}_2/\text{h}$, in 10 ‰ S 40.12 to 98.19 $\mu\text{lO}_2/\text{h}$, in 15 ‰ S 42.55 to 97.72 $\mu\text{lO}_2/\text{h}$, in 20 ‰ S 45.92 to 101.30 $\mu\text{lO}_2/\text{h}$, in 25 ‰ S 39.23 to 89.33 $\mu\text{lO}_2/\text{h}$, in 30 ‰ S 42.23 to 112.20 $\mu\text{lO}_2/\text{h}$ and in 33.65 ‰ S 32.97 to 100.40 $\mu\text{lO}_2/\text{h}$.

The metabolic rate in 5 ‰ S varied from 263.00 to 204.63 $\mu\text{lO}_2/\text{g/h}$, in 10 ‰ S 401.20 to 245.48 $\mu\text{lO}_2/\text{g/h}$, in 15 ‰ S 425.50 to 244.30 $\mu\text{lO}_2/\text{g/h}$, in 20 ‰ S 459.20 to 253.25 $\mu\text{lO}_2/\text{g/h}$, in 25 ‰ S 392.30 to 223.33 $\mu\text{lO}_2/\text{g/h}$,

in 30 ‰ S 422.30 to 278.00 $\mu\text{lO}_2/\text{g}/\text{h}$ and in 33.65 ‰ S 329.70 to 251.00 $\mu\text{lO}_2/\text{g}/\text{h}$.

The 'b' values ranged between 0.5706 (in 20 ‰ S) and 0.8188 (in 5 ‰ S).

2.g. Rate of respiration at 20 mm Hg pO₂

The rate of oxygen uptake in 5 ‰ S varied from 15.03 to 55.10 $\mu\text{lO}_2/\text{h}$, in 10 ‰ S 23.75 to 65.00 $\mu\text{lO}_2/\text{h}$, in 15 ‰ S 25.65 to 70.10 $\mu\text{lO}_2/\text{h}$, in 20 ‰ S 26.53 to 59.17 $\mu\text{lO}_2/\text{h}$, in 25 ‰ S 25.48 to 62.20 $\mu\text{lO}_2/\text{h}$, in 30 ‰ S 30.19 to 85.27 $\mu\text{lO}_2/\text{h}$ and in 33.65 ‰ S 21.61 to 75.01 $\mu\text{lO}_2/\text{h}$.

The metabolic rate in 5 ‰ S varied from 150.30 to 137.75 $\mu\text{lO}_2/\text{g}/\text{h}$, in 10 ‰ S 237.50 to 162.50 $\mu\text{lO}_2/\text{g}/\text{h}$, in 15 ‰ S 256.50 to 175.25 $\mu\text{lO}_2/\text{g}/\text{h}$, in 20 ‰ S 265.30 to 147.93 $\mu\text{lO}_2/\text{g}/\text{h}$, in 25 ‰ S 254.80 to 155.50 $\mu\text{lO}_2/\text{g}/\text{h}$, in 30 ‰ S 301.90 to 213.18 $\mu\text{lO}_2/\text{g}/\text{h}$ and in 33.65 ‰ S 216.10 to 187.53 $\mu\text{lO}_2/\text{g}/\text{h}$.

The 'b' values ranged between 0.5786 (in 20 ‰ S) and 0.9356 (in 5 ‰ S).

3. Oxygen consumption of *T. furcifera* acclimated in 30 ‰ salinity under declining pO₂

The regression lines drawn at different pO₂ for animals acclimated in 30 ‰ S are shown in Fig.40. The rate of oxygen uptake and metabolic rate obtained for 40 mg, 60 mg, 80 mg, 100 mg and 120 mg weight groups of animals under declining pO₂ are given in Table 33. (Values taken from the Fig.41).

Table 33. Oxygen uptake rate and metabolic rate under declining pO_2 for 40 mg, 60 mg, 80 mg, 100 mg and 120 mg weight groups of T. furcifera in the acclimation medium of 30 ‰ salinity. (Values taken from Fig.41)

pO_2 mm Hg	Body weight mg	O_2 uptake rate $\mu l O_2/h$	Metabolic rate $\mu l O_2/g/h$
140	40	9.38	234.50
	60	11.70	195.60
	80	13.70	171.25
	100	15.47	154.70
	120	17.10	142.50
120	40	9.38	234.50
	60	11.70	195.60
	80	13.70	171.25
	100	15.45	154.70
	120	17.10	142.50
100	40	9.38	234.50
	60	11.70	195.60
	80	13.70	171.25
	100	15.47	154.70
	120	17.10	142.50
80	40	9.38	234.50
	60	11.70	195.60
	80	13.70	171.25
	100	15.47	154.70
	120	17.10	142.50
60	40	9.38	234.50
	60	11.70	195.60
	80	13.70	171.25
	100	15.47	154.70
	120	17.10	142.50
40	40	8.09	202.25
	60	10.38	173.00
	80	12.39	154.88
	100	14.20	142.00
	120	15.86	132.17
20	40	4.03	100.75
	60	4.89	81.50
	80	5.60	70.00
	100	6.24	62.40
	120	6.80	56.67

3.a. Rate of respiration at 140 to 60 mm Hg pO₂

The same oxygen uptake rate and metabolic rate were obtained in the species from 140 to 60 mm Hg pO₂. The rate of oxygen uptake varied from 9.38 to 17.10 $\mu\text{lO}_2/\text{h}$ and metabolic rate 234.50 to 142.50 $\mu\text{lO}_2/\text{g/h}$. The 'b' value obtained is 0.5461.

3.b. Rate of respiration at 40 mm Hg pO₂

The rate of oxygen uptake varied from 8.09 to 15.86 $\mu\text{lO}_2/\text{h}$ and metabolic rate 202.25 to 132.17 $\mu\text{lO}_2/\text{g/h}$. The 'b' value obtained is 0.6141.

3.c. Rate of respiration at 20 mm Hg pO₂

The rate of oxygen uptake varied from 4.03 to 6.80 $\mu\text{lO}_2/\text{h}$ and metabolic rate 100.75 to 56.67 $\mu\text{lO}_2/\text{g/h}$. The 'b' value obtained is 0.4758.

(iv) DISCUSSION

A. Oxygen consumption in relation to body weight at 140 mm Hg pO₂

From the results presented above it is evident that the rate of oxygen uptake in Nausitora hedleyi increases with increasing body weight while the weight specific oxygen consumption decreases with increasing body weight in both the acclimation salinities, 5 ‰ and 20 ‰. In the case of animals acclimated in 5 ‰ S, oxygen uptake rate increases with 0.5959th power of body weight and the metabolic rate decreases with 0.4041th power of body weight at 140 mm Hg pO₂. In animals acclimated in 20 ‰ S, the rate of oxygen uptake increases with 0.6043th power of body weight and the metabolic rate decreases with 0.3957th power of body weight.

In Teredo furcifera acclimated in 30 ‰ S the rate of oxygen uptake increases with 0.5461th power of body weight and the metabolic rate decreases with 0.4539th power of body weight.

In bivalves the 'b' value is reported to vary from 0.24 to 0.95. Rothauwe (1958) has shown that Mytilus edulis obeyed the surface area law of Zeuthen (1953). Kuenzler (1961) has observed that in Modiolus demissus the 'b' value varied from 0.31 to 0.69 in the range of temperature 8°C to 26.5°C. Srinivasan (1965) has reported a 'b' value of 0.55 for Martesia fragilis. An average 'b' value of 0.74 has been obtained for Scrobicularia plana when the temperature varied from 0.5°C to 22.5°C (Hughes, 1970). Kennedy and Mihursky (1972) have stated that the 'b' value ranged between 0.31 and 0.95 for several bivalves. They have further reported that for Mya arenaria, Macoma balthica and Mulinia lateralis, the 'b' value is between 0.24 and 0.85. Vahl (1972) has given 0.77 as the 'b' value for Cardium edule and 0.75 for M. edulis (Vahl, 1973). For Donax vittatus, in the range of temperature between 2.9°C and 20.0°C, the 'b' value is found to be 0.87 (Ansell, 1973). An average 'b' value of 0.70 has been observed for 16 species of bivalves from the West Coast of Scotland at 10°C (Cited by Ansell, 1973). Bayne et al. (1973) have observed that in M. edulis the 'b' values in winter and summer are 0.72 and 0.67, respectively. For Chlamys (Aequipecten) opercularis, McLusky (1973) has obtained an average 'b' value of 0.65 in temperature 5°C, 10°C and 15°C. Mangapathi Rao et al. (1974) have given a 'b' value of 0.59 for Congeria sallei in 35 ‰ salinity. Shafee (1976) has stated that the 'b' value for

Mytilus viridis varied from 0.70 to 0.90 in different salinities. Seasonal variation of 'b' value from 0.75 to 0.93 has been noticed for Chlamys islandica (Vahl, 1978). Salih (1978a) has observed that in Meretrix casta the 'b' value ranged between 0.42 and 0.75 when the salinity varied from 5 ‰ to 40 ‰.

Comparison of the 'b' values obtained for N. hedleyi in the two acclimation media (5 ‰S and 20 ‰S) shows that the difference between the regression coefficients is statistically insignificant (Table 34). Zar (1974) has stated that in such cases the average of the 'b' values may be taken for further discussion. Hence, 0.6001 will represent the regression coefficient for N. hedleyi. A comparison of the 'b' value obtained for T. furcifera in the acclimation salinity (30 ‰) with that for N. hedleyi in the two acclimation salinities (5 ‰ and 20 ‰) also shows that the values are not statistically different (Table 35).

Statistically same 'b' value for N. hedleyi in the two acclimation salinities of 5 ‰ and 20 ‰ evidently shows that in both the acclimation media, the different size groups of animals have the same proportion of oxygen consumption. In the Cochin Harbour region, the euryhaline N. hedleyi is reported to occur throughout the year. However, they are known to lead an active reproductive life in salinities between 5 ‰ and 20 ‰, as evidenced by the gonad index studies (Saraswathy, 1967) and seasonal intensity studies (Ref. Chapter III). This suggests that a variation in salinity from 5 ‰ to 20 ‰ and vice-versa in the natural habitat does not affect the normal activity of the animal and this probably explains the existence of same

Table 34. Comparison of regression coefficients obtained for N. hedleyi in the acclimation salinities of 5 ‰ and 20 ‰ at 140 mm Hg pO₂

Comparing media ‰	Probability
5 and 20	N.S. *

* N.S. - Not significant.

Table 35. Comparison of regression coefficients obtained for N. hedleyi in the acclimation media of 5 ‰ and 20 ‰ salinities with that of T. furcifera acclimated in 30 ‰ salinity at 140 mm Hg pO₂

Comparing media ‰	Probability
5 and 30	N.S. *
20 and 30	N.S. *

* N.S. - Not significant.

relationship between oxygen consumption and body weight in the two acclimation salinities. In the case of T. furcifera, even though it is a stenohaline form occurring during the high saline period of the year, the O₂ uptake rate - body weight relationship (metabolic type) is not different from that of the euryhaline N. hedleyi. This observation is of much significance as it brings out the existence of similar metabolic types in two species of shipworms - the euryhaline N. hedleyi and the stenohaline T. furcifera with different settling period and salinity tolerance ranges.

As already mentioned Bertalanffy (1957) has postulated three types of metabolic types - metabolic rate proportional to surface area ('b' value is 0.67), metabolic rate proportional to weight ('b' value is 1) and

metabolic rate intermediate between surface area and weight proportionality ('b' value is 0.67 - 1). The 'b' values of N. hedleyi (0.6001) and T. furcifera (0.5461) obtained in the acclimation salinities do not strictly come within the range proposed by Bertalanffy (1957). However, the existence of many metabolic types other than those proposed by Bertalanffy (1957) has been reported by many workers (Ganapati and Rao, 1960; Kuenzler, 1961; Kennedy and Mihursky, 1972, etc.).

The metabolic rate (for 1 g animal) obtained for N. hedleyi in the acclimation media of 5 ‰ and 20 ‰ salinities are $175.2 \mu\text{lO}_2/\text{g/h}$ and $186.1 \mu\text{lO}_2/\text{g/h}$, respectively (Table 13) and that for T. furcifera in the acclimation medium of 30 ‰ S is $54.41 \mu\text{lO}_2/\text{g/h}$ (Table 15). Comparison of the metabolic rates of the above two shipworms with those of other bivalves is difficult due to the differences in the conditions like temperature, salinity, etc., under which the experiments were conducted and also due to the variations in the environmental history of the animals experimented. Further, some workers have presented metabolic rates based on wet body weight. It is known that the water content of the body varies from species to species (Nicol, 1960) and within the species it shows seasonal variation also (Saraswathy, 1967). Hence it is difficult to convert wet weight to dry weight for the purpose of comparison. The metabolic rate of those bivalves which are more relevant to the present study alone are discussed below. Lane and Tierney (1951) have stated that for Teredo sp, the metabolic rate varied from $272.5 \mu\text{lO}_2/\text{g/h}$ to $161 \mu\text{lO}_2/\text{g/h}$ when the dry weight of the animals ranged between 27.6 mg and 75.3 mg. Moon and Pritchard (1970) have observed that for Mytilus californianus, the metabolic rate was $261 \mu\text{lO}_2/\text{g/h}$

for low (tide) level forms and $347 \mu\text{lO}_2/\text{g/h}$ for high (tide) level forms. In Donax vittatus, the metabolic rate varied from 226.03 to $2356.2 \mu\text{lO}_2/\text{g/h}$ when the temperature ranged between 2.9°C and 20°C (Ansell, 1973). In Chlamys (Aequipecten) opercularis acclimated for one week the metabolic rate varied from 214 to $743 \mu\text{lO}_2/\text{g/h}$ in the temperature range, 5°C to 20°C (McLusky, 1973) Vahl (1972) has reported that the rate in Cardium edule is $370 \mu\text{lO}_2/\text{g/h}$. In Mytilus edulis Vahl (1973) has reported a metabolic rate of $370 \mu\text{lO}_2/\text{g/h}$ in 15.5 ‰S at $10 \pm 0.5^\circ\text{C}$. A seasonal variation of metabolic rate from 81 to $256 \mu\text{lO}_2/\text{g/h}$ has been noticed in Chlamys islandica by Vahl (1978). Bayne et al. (1973) have reported that the metabolic rate of Mytilus edulis in winter and summer were $263 \mu\text{lO}_2/\text{g/h}$ and $164 \mu\text{lO}_2/\text{g/h}$, respectively. In Mytilus viridis a metabolic rate of $800 \mu\text{lO}_2/\text{g/h}$ in 35 ‰S at $28 \pm 1^\circ\text{C}$ has been obtained by Shafee (1976). Comparison of the metabolic rates obtained for N. hedleyi in both the acclimation salinities (5 ‰ and 20 ‰) with those of other bivalves referred to above shows that the values obtained for the former fall within the range of the metabolic rate reported for Chlamys islandica (Vahl, 1978). For the purpose of comparison, the calculated values of metabolic rates in T. furcifera for the same weight groups reported for Teredo sp. (Lane and Tierney, 1951) are given below. In T. furcifera the rate ranged between $277.57 \mu\text{lO}_2/\text{g/h}$ and $175.96 \mu\text{lO}_2/\text{g/h}$ when the dry weight of animals varied from 27.6 to 75.3 mg and these values compare well with those reported for Teredo sp.

An attempt has been made to compare the oxygen uptake rate and metabolic rate in N. hedleyi in the two acclimation salinities of 5 ‰ and 20 ‰. The calculated values of oxygen uptake rate and metabolic rate

for different weight groups, 80 mg, 90 mg, 100 mg, 110 mg, 120 mg, 200 mg, 300 mg and 400 mg animals acclimated in 5 ‰S are given in Table 36 (Values taken from Figs.16-17) and those of animals acclimated in 20 ‰S are presented in Table 37 (Values taken from Figs.18-19). From the above tables it can be seen that for N. hedleyi acclimated in 5 ‰S, the rate of oxygen uptake varied from 39.90 to 101.50 $\mu\text{lO}_2/\text{h}$ and the metabolic rate, 498.75 to 253.75 $\mu\text{lO}_2/\text{g/h}$ for the weights 80 to 400 mg. For similar weight of animals acclimated in 20 ‰S, the rate of oxygen uptake varied from 40.46 to 106.40 $\mu\text{lO}_2/\text{h}$ and the metabolic rate 505.75 to 266.00 $\mu\text{lO}_2/\text{g/h}$.

It can be seen from the above that the oxygen consumption rates of N. hedleyi in the two acclimation salinities of 5 ‰ and 20 ‰ are almost comparable. Comparable rates of respiration in the two widely different acclimation salinities suggest the capacity of the euryhaline species to adjust itself gradually to changes in salinity and carry on normal activities without any appreciable difference in the respiratory rate.

In order to compare the oxygen consumption rates of the stenohaline T. furcifera with those of the euryhaline N. hedleyi, the oxygen uptake rate and metabolic rate of 80 mg, 90 mg, 100 mg, 110 mg and 120 mg weight groups of T. furcifera acclimated in 30 ‰S are given in Table 38 (Values taken from Figs.20-21). The oxygen uptake rate and metabolic rate varied from 13.70 to 17.10 $\mu\text{lO}_2/\text{h}$ and 171.25 to 142.50 $\mu\text{lO}_2/\text{g/h}$, respectively for the weight groups 80 to 120 mg.

Comparison of the oxygen consumption rates of N. hedleyi with those

Table 36. Oxygen uptake rate and metabolic rate for 80 mg, 90 mg, 100 mg, 110 mg, 120 mg, 200 mg, 300 mg and 400 mg weight groups of N. hedleyi in the acclimation salinity of 5 ‰ at 140 mm Hg pO₂ (Values taken from Figs.16-17)

Body weight mg	O ₂ uptake rate μlO ₂ /h	Metabolic rate μlO ₂ /g/h
80	39.90	498.75
90	41.69	463.22
100	44.41	444.10
110	46.99	426.36
120	49.55	412.92
200	67.13	335.65
300	85.47	284.90
400	101.50	253.75

Table 37. Oxygen uptake rate and metabolic rate for 80 mg, 90 mg, 100 mg, 110 mg, 120 mg, 200 mg, 300 mg and 400 mg weight groups of N. hedleyi in the acclimation salinity of 20 ‰ at 140 mm Hg pO₂ (Values taken from Figs.18-19)

Body weight mg	O ₂ uptake rate μlO ₂ /h	Metabolic rate μlO ₂ /g/h
80	40.46	505.75
90	43.45	482.78
100	46.28	462.80
110	48.98	445.27
120	51.64	430.33
200	70.34	351.70
300	89.86	299.53
400	106.40	266.00

Table 38. Oxygen uptake rate and metabolic rate for 80 mg, 90 mg, 100 mg, 110 mg and 120 mg weight groups of T. furcifera in the acclimation salinity of 30 ‰ at 140 mm Hg pO₂ (Values taken from Figs.20-21)

Body weight mg	O ₂ uptake rate μlO ₂ /h	Metabolic rate μlO ₂ /g/h
80	13.70	171.25
90	14.62	162.44
100	15.47	154.70
110	16.29	148.09
120	17.10	142.50

of T. furcifera reveals that the rates are lower in the latter. As already mentioned, N. hedleyi occurs throughout the year in the Cochin Harbour region and is subjected to wide variations in salinity. This will naturally result in much stress and strain on the animals to withstand the variations requiring higher energy consumption. Further, they grow to comparatively larger size and bore deep into the wood. These two factors probably demand higher energy expenditure compared to the smaller sized stenohaline T. furcifera which is found only during the high saline period and boring more in the peripheral region of the wooden structures.

B. Oxygen consumption in relation to variations in salinity at 140 mm Hg pO₂

The 'b' values obtained for N. hedleyi acclimated in 5 ‰S and experimented in 0.60 ‰, 3 ‰, 5 ‰, 10 ‰, 15 ‰, 20 ‰ and 25 ‰ salinities at 140 mm Hg pO₂ are 0.6923, 0.6195, 0.5959, 0.5999, 0.6195, 0.5342 and 0.9798, respectively. Comparison of the 'b' values obtained in the acclimation salinity (5 ‰) with those in the test salinities shows that significant difference exists only in 25 ‰S. When the 'b' values in all the test salinities are statistically compared, significant differences are observed between the regression coefficients in 0.60 ‰ and 25 ‰, 3 ‰ and 25 ‰, 10 ‰ and 25 ‰, 15 ‰ and 25 ‰ and 20 ‰ and 25 ‰ salinities (Table 39).

The oxygen uptake rate and metabolic rate at 140 mm Hg pO₂ for 100 mg, 200 mg, 300 mg and 400 mg weight groups of N. hedleyi acclimated in 5 ‰S and experimented in different salinities are given in Tables 18-24. The interrelationships of the above four weight groups in their rate of

Table 39. Comparison of the regression coefficients obtained for N. hedleyi acclimated in 5 ‰ salinity and experimented in different salinities at 140 mm Hg pO₂

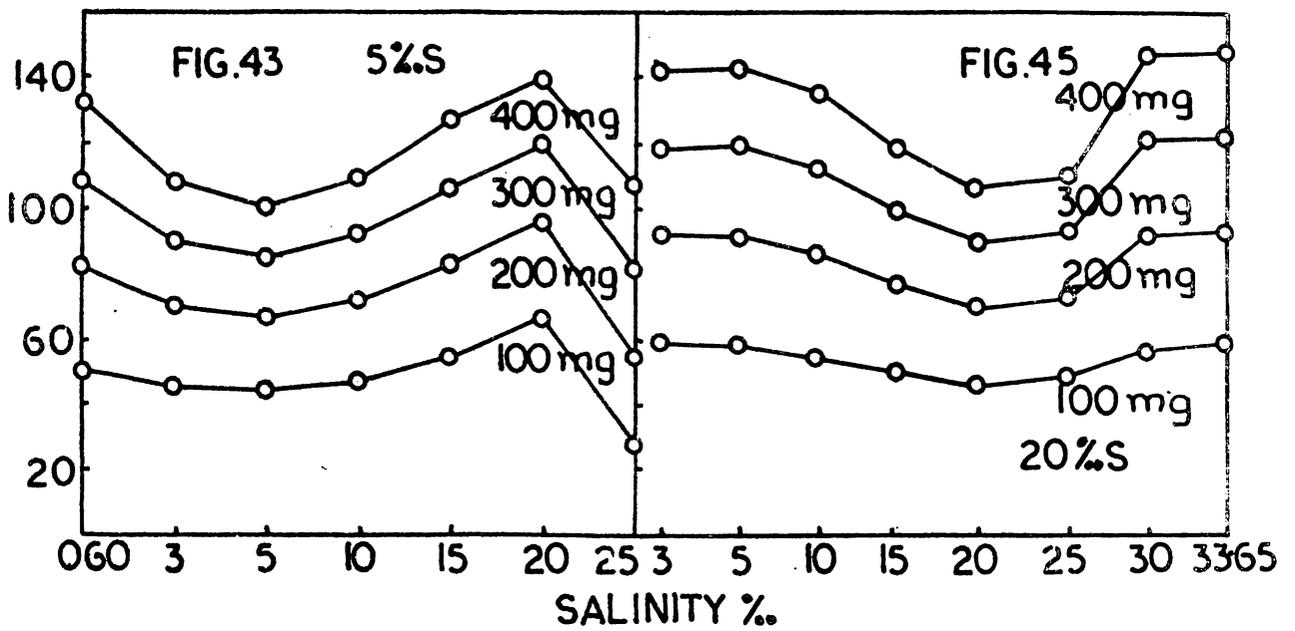
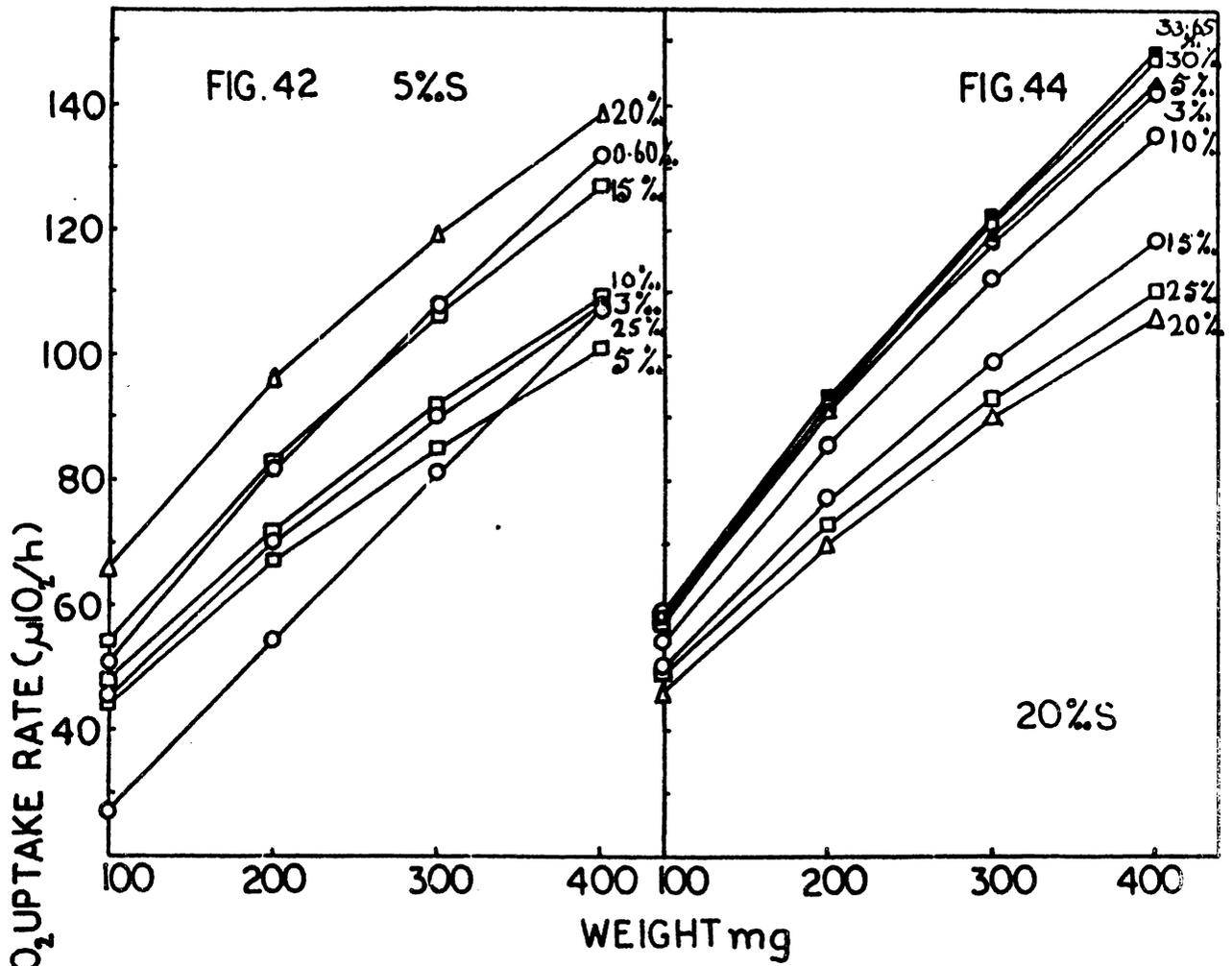
Comparing media ‰	Probability
0.60 and 3	N.S. *
0.60 and 5	N.S.
0.60 and 10	N.S.
0.60 and 15	N.S.
0.60 and 20	N.S.
0.60 and 25	0.02 - 0.05
3 and 5	N.S.
3 and 10	N.S.
3 and 15	N.S.
3 and 20	N.S.
3 and 25	0.002 - 0.005
5 and 10	N.S.
5 and 15	N.S.
5 and 20	N.S.
5 and 25	< 0.001
10 and 15	N.S.
10 and 20	N.S.
10 and 25	0.002 - 0.005
15 and 20	N.S.
15 and 25	< 0.001
20 and 25	< 0.001

* N.S. - Not significant.

oxygen uptake are shown in Fig.42. It can be observed from the above tables that oxygen uptake rate increases with increase in body size in all the experimental media. A closer examination of the figure reveals the existence of similar rates for certain weight groups of animals in different salinities. Thus 260 mg size animals show the same rate in 0.60 ‰ and 15 ‰ salinities and 340 mg animals, in 5 ‰ and 25 ‰ salinities. Similar rates are observed for a particular weight group in a sub- and supranormal salinity and not in two consecutive sub- or supranormal media. Since the oxygen consumption of N. hedleyi increases in sub- and supranormal

Figs. 42 and 44 Interrelationship in the oxygen uptake rate ($\mu\text{lO}_2/\text{h}$) of the four size groups (100, 200, 300 and 400 mg) of Nausitora hedleyi acclimated in 5 ‰S and 20 ‰S and experimented in different salinities at 140 mm Hg pO_2

Figs. 43 and 45 Trend of variation in the oxygen uptake rate ($\mu\text{lO}_2/\text{h}$) of the four size groups (100, 200, 300 and 400 mg) of Nausitora hedleyi acclimated in 5 ‰S and 20 ‰S when experimented in different salinity media at 140 mm Hg pO_2



salinities, there is chance for getting the same rate of oxygen uptake in a lower and a higher salinity for a definite weight group of animal.

The variations in the oxygen uptake rate in different salinities for the various size groups of N. hedleyi acclimated in 5 ‰S are shown in Fig.43. It can be observed from that figure that the oxygen uptake rate is minimum in the acclimation salinity and that it increases with increase or decrease in salinity, except in 25 ‰S where the oxygen uptake rate of 100 mg, 200 mg and 300 mg animals is lower than that in the acclimation salinity (5 ‰) and in 400 mg animal is slightly higher. From the salinity tolerance studies (Ref. Chapter V) it is found that 25 ‰S is the lethal level and this probably explains the exceptionally lower rate in the same.

The regression coefficients obtained for N. hedleyi acclimated in 20 ‰S and experimented in 3 ‰, 5 ‰, 10 ‰, 15 ‰, 20 ‰, 25 ‰, 30 ‰ and 33.65 ‰ salinities at 140 mm Hg pO_2 are 0.6269, 0.6440, 0.6533, 0.6117, 0.6043, 0.5840, 0.6813 and 0.6581, respectively. A comparison of the above 'b' values with that obtained in the acclimation medium (20 ‰S) shows that they are statistically the same. A comparison between the regression coefficients also reveals that in all the salinities the values are not statistically different (Table 40). Hence, the average of the 'b' values, 0.6333, can be taken as the common regression coefficient in all the media (Zar, 1974).

The oxygen uptake rate and metabolic rate at 140 mm Hg pO_2 for 100 mg, 200 mg, 300 mg and 400 mg weight groups of N. hedleyi acclimated

Table 40. Comparison of the regression coefficients obtained for N. hedleyi acclimated in 20 ‰ salinity and experimented in different salinities at 140 mm Hg pO₂

Comparing media ‰	Probability
3 and 5	N.S. *
3 and 10	N.S.
3 and 15	N.S.
3 and 20	N.S.
3 and 25	N.S.
3 and 30	N.S.
3 and 33.65	N.S.
5 and 10	N.S.
5 and 15	N.S.
5 and 20	N.S.
5 and 25	N.S.
5 and 30	N.S.
5 and 33.65	N.S.
10 and 15	N.S.
10 and 20	N.S.
10 and 25	N.S.
10 and 30	N.S.
10 and 33.65	N.S.
15 and 20	N.S.
15 and 25	N.S.
15 and 30	N.S.
15 and 33.65	N.S.
20 and 25	N.S.
20 and 30	N.S.
20 and 33.65	N.S.
25 and 30	N.S.
25 and 33.65	N.S.
30 and 33.65	N.S.

* N.S. - Not significant

in 20 ‰S and experimented in different media are presented in Tables 25-32. The interrelationships of the different body weights in their oxygen uptake rate in different salinities are shown in Fig.44. It will be seen from that figure that in all the salinities, the oxygen uptake rate increases with size. Further, it is observed that in 218 mg animals, the rate of

respiration is the same in 5 ‰S and 3 ‰S. The reason attributed for a similar phenomenon noticed for N. hedleyi acclimated in 5 ‰S seems to be applicable here also.

The variation of oxygen uptake rate in different salinities for the various size groups of N. hedleyi acclimated in 20 ‰S is shown in Fig.45. It can be seen from the figure that for all the size groups the rate of respiration is minimum in the acclimation salinity and it increases in both sub- and supranormal salinities.

A comparison of the oxygen uptake rate of N. hedleyi in the acclimation salinity of 5 ‰ with those obtained when experimented in 20 ‰S shows that the rate is higher in the latter. A vice-versa comparison between the rates of oxygen uptake of animals in the acclimation salinity of 20 ‰ with the values obtained when experimented in 5 ‰S shows higher rates of oxygen consumption in the latter. It can be seen that as the salinity changes from the acclimation medium, rate of oxygen uptake increases. But due to prolonged acclimation the rate declines to almost the original level as evidenced by the comparable rates in the two acclimation salinities (5 ‰ and 20 ‰). Kinne (1971) has stated that many aquatic invertebrates respire at most economic rates in salinities to which they have been acclimated over prolonged periods of time and to which they have been genetically adjusted. The present observation is in agreement with the generalization given by Kinne (1971).

Potts and Parry (1964) have objected the hypothesis of Schlieper (Remane and Schlieper, 1958) that increased respiratory rate in subnormal



salinities is due to increased energy demands for active ion transport. The reasons they pointed out against are that (1) Changes in metabolic rate are in most cases too large to be attributable to energy expenditure for ion and osmoregulation alone. (2) In several cases increase in metabolic rate caused by reduced salinities is not confined to tissues which are expected to perform osmotic work. (3) The large change in the respiratory rate imply very low efficiencies of ion transport system, whereas experiments with isolated tissues reveal high efficiencies. (4) Respiratory rates of some aquatic animals are lower in sub-normal salinities, increase in supra-normal salinities or are not measurably affected by salinity stress. Kinne (1971) has stated that the effect of salinity on metabolic rate may be in different ways, via stimulation or diminution of locomotory activity, increase in internal ion ratios and interference with neuromuscular, hormonal or enzymatic mechanism. He also pointed out that the immediate increase in respiratory rate following a variation in salinity may be due to peripheral osmotic stimulation and increased overall alertness to counteract the physiological stress. In N. hedleyi the rate of oxygen uptake is observed to increase in sub- and supranormal salinities. Since the present study is confined only to determine the oxygen consumption in varying salinities, which of the above discussed methods the animal employ to counteract the osmotic stress in a changed salinity cannot be specified.

There is only a few works on the oxygen consumption of bivalves in different salinities comparable to the present study. A decrease in oxygen uptake with decrease in salinity has been observed by Nagabhushanam (1962) in Martesia striata. In Mytilus edulis, the rate of respiration is lower

in sub- and supranormal salinities (cited by Kinne, 1971). Mytilus viridis shows a fall in the respiratory rate as the salinity decreases (Shafee, 1976), Kinne (1971) and Vernberg and Vernberg (1972) have observed that the increase in oxygen uptake rate in sub- and supranormal salinities is characteristic of euryhaline animals. In N. hedleyi acclimated in 5 ‰S and 20 ‰S, the rate increases in sub- and supranormal salinities. Further, N. hedleyi has considerable capacity to tolerate wide ranges of salinity as evidenced by the seasonal intensity studies (Chapter III) and laboratory studies on salinity tolerance (Chapter V). Hence, the results of the present study fully agree with the findings of Kinne (1971) and Vernberg and Vernberg (1972) that in euryhaline animals the rate of respiration increases in sub- and supranormal salinities.

C. Oxygen consumption in relation to oxygen tension.

The 'b' values and their standard errors obtained under different partial pressures of oxygen for N. hedleyi acclimated in 5 ‰S and experimented in different media are presented in Table 41. A comparison of the above 'b' values obtained in the same medium under declining pO_2 is given in Table 42. A perusal of the same will show that the 'b' values under different pressures of oxygen in each salinity are statistically the same with exceptions in 15 ‰S and 20 ‰S. In 15 ‰ and 20 ‰ media, the 'b' values from 140 to 40 mm Hg pO_2 are not statistically different while the values obtained at 20 mm Hg pO_2 are higher. From the salinity tolerance studies it can be seen that for animals acclimated in 5 ‰S, the percentage of survival is comparatively less in 15 ‰S and 20 ‰S (Ref. Chapter V).

Table 41. Regression coefficients and their standard errors obtained under different pO_2 in different salinities for N. hedleyi acclimated in 5 ‰ salinity

pO_2 mm Hg		Salinity ‰						
		0.60	3	5	10	15	20	25
140	b	0.6923	0.6195	0.5959	0.5999	0.6195	0.5342	0.9798
	S_b	0.0919	0.0826	0.0603	0.0804	0.0479	0.0671	0.0838
120	b	0.6923	0.6195	0.5959	0.5999	0.6195	0.5493	1.1170
	S_b	0.0919	0.0826	0.0603	0.0804	0.0479	0.0694	0.0774
100	b	0.6923	0.6195	0.5959	0.5999	0.6195	0.5727	---
	S_b	0.0919	0.0826	0.0603	0.0804	0.0479	0.0690	---
80	b	0.6727	0.6195	0.5959	0.5999	0.6195	0.6137	---
	S_b	0.0945	0.0826	0.0606	0.0804	0.0479	0.0682	---
60	b	0.7100	0.6195	0.5959	0.5999	0.5540	0.6394	---
	S_b	0.0938	0.0820	0.0603	0.0804	0.0316	0.0715	---
40	b	0.7325	0.5936	0.5702	0.5537	0.6927	0.7424	---
	S_b	0.0946	0.0797	0.0599	0.0798	0.0480	0.0859	---
20	b	0.7803	0.6580	0.6049	0.7331	0.8598	0.8615	---
	S_b	0.0888	0.0769	0.0575	0.0769	0.0563	0.0739	---

Though at higher pO_2 the animals are able to keep the same oxygen uptake rate body weight relationship, as the pO_2 declines to 20 mm Hg, the relationship changes evidently due to the combined effect of salinity variation and very low oxygen tension.

The regression coefficients and their standard errors obtained under different oxygen concentrations for N. hedleyi acclimated in 20 ‰S and experimented in different salinities are given in Table 43. Comparison

Table 42. Significance of difference between the regression coefficients obtained in different media under various pO₂ for N. hedleyi acclimated in 5 ‰ salinity

Comparing pO ₂ mm Hg	Experimental media ‰						
	0.60	3	5	10	15	20	25
140 and 120	N.S.*	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
140 and 100	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	---
140 and 80	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	---
140 and 60	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	---
140 and 40	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	---
140 and 20	N.S.	N.S.	N.S.	N.S.	0.002 - 0.005	0.002 - 0.005	---
120 and 100	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	---
120 and 80	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	---
120 and 60	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	---
120 and 40	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	---
120 and 20	N.S.	N.S.	N.S.	N.S.	0.002 - 0.005	0.002 - 0.005	---
100 and 80	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	---
100 and 60	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	---
100 and 40	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	---
100 and 20	N.S.	N.S.	N.S.	N.S.	0.002 - 0.005	0.005 - 0.01	---
80 and 60	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	---
80 and 40	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	---
80 and 20	N.S.	N.S.	N.S.	N.S.	0.002 - 0.005	0.01 - 0.02	---
60 and 40	N.S.	N.S.	N.S.	N.S.	0.02 - 0.05	N.S.	---
60 and 20	N.S.	N.S.	N.S.	N.S.	< 0.001	0.02 - 0.05	---
40 and 20	N.S.	N.S.	N.S.	N.S.	0.02 - 0.05	N.S.	---

* N.S. - Not significant.

Table 43. Regression coefficients and their standard errors obtained under different pO_2 in different salinities for N. hedleyi acclimated in 20 ‰ salinity

pO_2		Salinity ‰							
		3	5	10	15	20	25	30	33.65
140	b	0.6269	0.6440	0.6533	0.6117	0.6043	0.5840	0.6813	0.6581
	S_b	0.0699	0.0733	0.0715	0.0943	0.0688	0.0601	0.1179	0.0867
120	b	0.6492	0.6600	0.6533	0.6117	0.6043	0.5840	0.6813	0.6581
	S_b	0.0686	0.0757	0.0715	0.0943	0.0688	0.0601	0.1179	0.0867
100	b	0.8695	0.6396	0.6533	0.6117	0.6043	0.5840	0.6813	0.6519
	S_b	0.0699	0.0719	0.0715	0.0943	0.0688	0.0601	0.1179	0.0869
80	b	—	0.6901	0.6362	0.6117	0.6043	0.5840	0.6449	0.6695
	S_b	—	0.0734	0.0739	0.0943	0.0688	0.0601	0.1152	0.0833
60	b	—	0.7106	0.6838	0.6554	0.6043	0.5709	0.6678	0.7419
	S_b	—	0.0707	0.0819	0.0946	0.0688	0.0559	0.1185	0.0926
40	b	—	0.8188	0.6474	0.5997	0.5706	0.5934	0.6984	0.8034
	S_b	—	0.0738	0.0927	0.0945	0.0749	0.0552	0.1189	0.0933
20	b	—	0.9356	0.7261	0.7239	0.5786	0.6440	0.7489	0.8975
	S_b	—	0.0786	0.0683	0.0940	0.0755	0.0590	0.1159	0.0968

of the above 'b' values obtained in the same medium under declining pO_2 is given in Table 44. It will be seen from the above table that the decline in pO_2 does not affect the oxygen uptake rate - body weight relationship in each medium, except in 3 ‰ S and 5 ‰ S. As already mentioned, in 3 ‰ S, the measurement could be continued only upto 100 mm Hg pO_2 and the 'b'

Table 44. Significance of difference between the regression coefficients obtained in different media under various pO₂ for N. hedleyi acclimated in 20 ‰ salinity

Comparing pO ₂ mm Hg	Experimental salinity ‰							
	3	5	10	15	20	25	30	33.65
140 and 120	0.01 - 0.02	N.S.*	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
140 and 100	-	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
140 and 80	-	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
140 and 60	-	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
140 and 40	-	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
140 and 20	-	0.01 - 0.02	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
120 and 100	0.02 - 0.05	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
120 and 80	-	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
120 and 60	-	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
120 and 40	-	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
120 and 20	-	0.01 - 0.02	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
100 and 80	-	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
100 and 60	-	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
100 and 40	-	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
100 and 20	-	0.005 - 0.01	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
80 and 60	-	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
80 and 40	-	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
80 and 20	-	0.02 - 0.05	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
60 and 40	-	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
60 and 20	-	0.02 - 0.05	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
40 and 20	-	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.

* N.S. - Not significant

value at 100 mm Hg pO_2 is found to be statistically different from those at 140 and 120 mm Hg pO_2 . In 5 ‰S, the same oxygen uptake rate - body weight relationship is found to be maintained from 140 to 40 mm Hg pO_2 . But at 20 mm Hg pO_2 the 'b' value is observed to be statistically higher. It will be seen from the salinity tolerance studies on the animals acclimated in 20 ‰S that the percentage of survival in 3 ‰S and 5 ‰S is comparatively less (Ref. Chapter V). Hence as in the case of animals acclimated in 5 ‰S, the combined effect of the variation in salinity and reduced oxygen tension may have altered the basic oxygen uptake - body weight relationship.

The 'b' values and their standard errors under different oxygen tension for T. furcifera are given in Table 45. The difference between the 'b' values under various oxygen pressures is analysed statistically and presented in Table 46. It will be seen from the same that in the acclimation medium of 30 ‰S, the same relationship between oxygen uptake rate and body weight is maintained under various partial pressures of oxygen by the species.

Intra- and inter specific comparison of the 'b' values of N. hedleyi acclimated in 5 ‰S, 20 ‰S and T. furcifera acclimated in 30 ‰S under various oxygen tensions is presented in Table 47. It can be observed from this table that for N. hedleyi at various partial pressures of oxygen, the oxygen uptake rate - body weight relationship is statistically the same in the two acclimation salinities. Comparison of the 'b' values for N. hedleyi with those of T. furcifera also shows that they are not statistically different.

Table 45. Regression coefficients and their standard errors obtained under various pO_2 for T. furcifera acclimated in 30 ‰ salinity

pO_2 mm Hg	b	S_b
140	0.5461	0.0650
120	0.5461	0.0650
100	0.5461	0.0650
80	0.5461	0.0650
60	0.5461	0.0650
40	0.6141	0.0668
20	0.4758	0.0598

Table 46. Comparison of regression coefficients obtained at various pO_2 for T. furcifera acclimated in 30 ‰ salinity

Comparing pO_2 mm Hg	Probability
140 and 120	N.S.*
140 and 100	N.S.
140 and 80	N.S.
140 and 60	N.S.
140 and 40	N.S.
140 and 20	N.S.
120 and 100	N.S.
120 and 80	N.S.
120 and 60	N.S.
120 and 40	N.S.
120 and 20	N.S.
100 and 80	N.S.
100 and 60	N.S.
100 and 40	N.S.
100 and 20	N.S.
80 and 60	N.S.
80 and 40	N.S.
80 and 20	N.S.
60 and 40	N.S.
60 and 20	N.S.
40 and 20	N.S.

* N.S. - Not significant

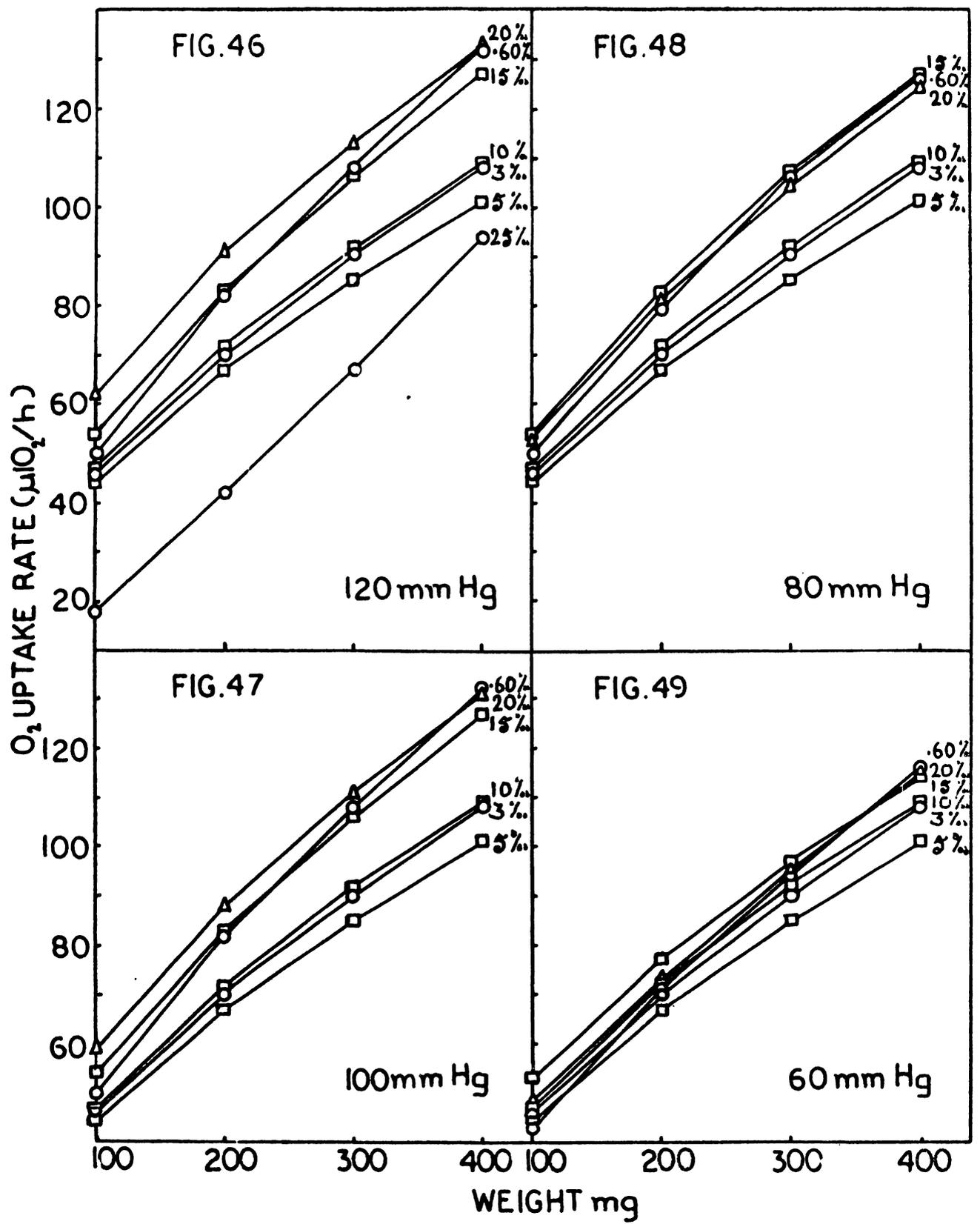
Table 47. Intra-and interspecific comparison of regression coefficients obtained for N. hedleyi acclimated in 5 ‰ and 20 ‰ salinities and T. furcifer in 30 ‰ salinity at various pO₂

pO ₂ mm Hg	Comparing media ‰ (For <u>N. hedleyi</u>) 5 and 20	Comparison of <u>T. furcifer</u> with <u>N. hedleyi</u> accli- mated in 5 ‰ S	Comparison of <u>T. furcifer</u> with <u>N. hedleyi</u> acclimated in 20 ‰ S
140	* N.S.	N.S.	N.S.
120	N.S.	N.S.	N.S.
100	N.S.	N.S.	N.S.
80	N.S.	N.S.	N.S.
60	N.S.	N.S.	N.S.
40	N.S.	N.S.	N.S.
20	N.S.	N.S.	N.S.

* N.S. - Not significant

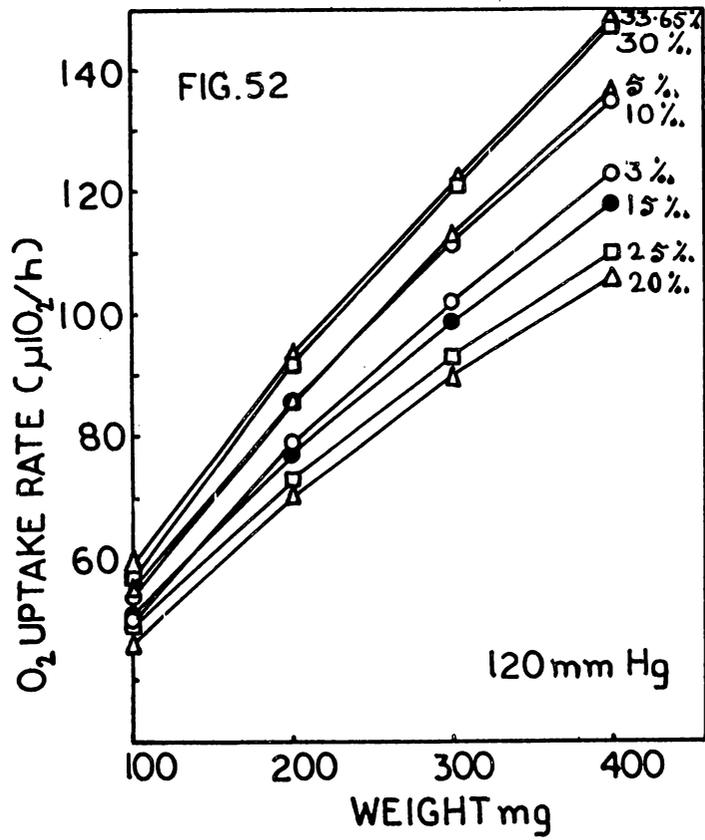
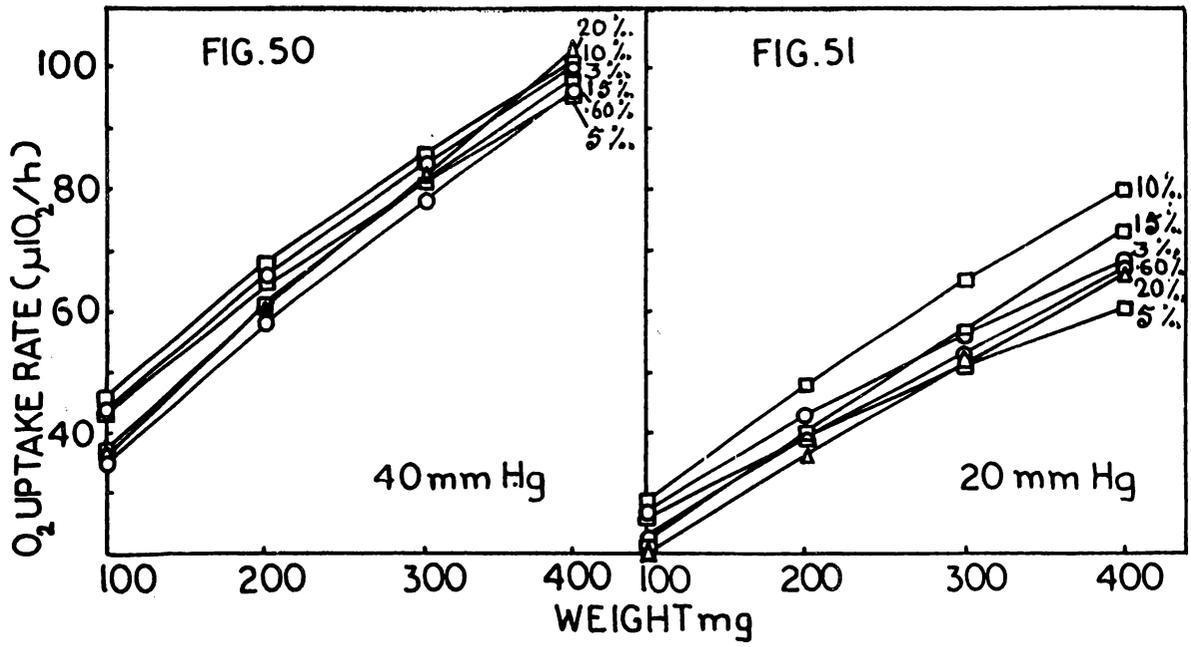
The interrelationship in the oxygen uptake rate of the various weight groups of N. hedleyi acclimated in 5 ‰S and experimented in different salinities at various oxygen concentrations is shown in Figs.42, 46-51. It can be observed from these figures that the oxygen uptake rate increases with body size in all the cases. A closer examination of the figures reveals that at a particular pO₂, certain weight groups of animals have the same rate of oxygen uptake in different salinities, which may probably be due to three reasons. Firstly, as mentioned earlier, as the oxygen consumption in N. hedleyi increases in sub- and supranormal salinities, a definite weight group of animal may show the same rate in a lower and a higher salinity, eg. at 140 mm Hg pO₂ 260 mg animal shows the same rate in 0.60 ‰S and 15 ‰S (Fig.42). Secondly, N. hedleyi is a regulator whose oxygen uptake rate decreases below the critical tension (Pc). The Pc is

Figs. 46-49 Interrelationship in the oxygen uptake rate ($\mu\text{lO}_2/\text{h}$) of the four size groups (100, 200, 300 and 400 mg) of Nausitora hedleyi acclimated in 5 ‰S and experimented in different salinities at 120, 100, 80 and 60 mm Hg pO_2



Figs. 50 and 51 Interrelationship in the oxygen uptake rate ($\mu\text{lO}_2/\text{h}$) of the four size groups (100, 200, 300 and 400 mg) of Nausitora hedleyi acclimated in 5 ‰ S and experimented in different salinities at 40 and 20 mm Hg pO_2

Fig. 52 Interrelationship in the oxygen uptake rate ($\mu\text{lO}_2/\text{h}$) of the four size groups (100, 200, 300 and 400 mg) of Nausitora hedleyi acclimated in 20 ‰ and experimented in different salinities at 120 mm Hg pO_2



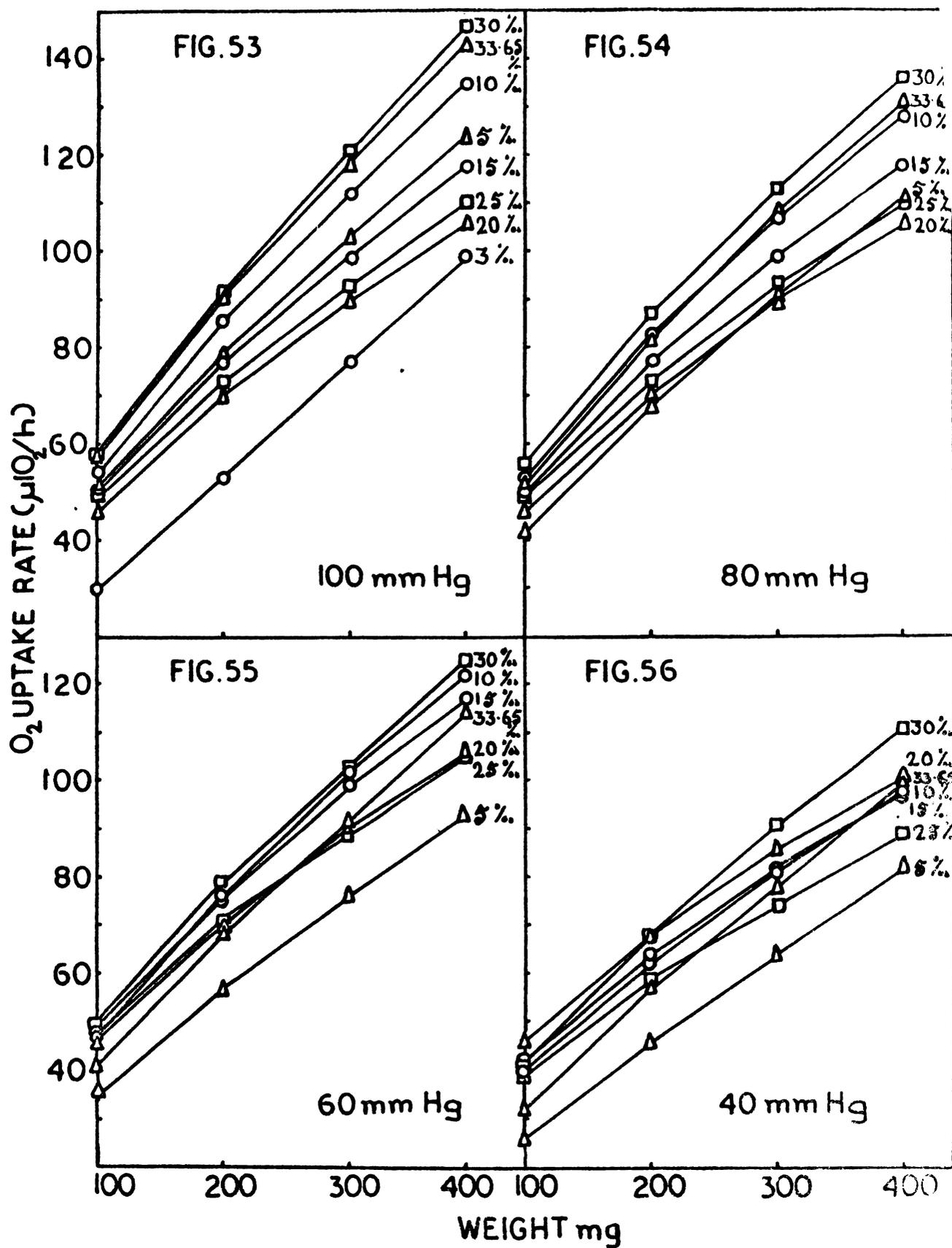
attained at a higher pO_2 if the experimental salinity is farther from the acclimation level. The fall in oxygen uptake rate below a higher P_c may result in the same rate for a particular weight group of animal in different salinities, e.g. at 100 mm Hg pO_2 376 mg animal has the same rate in 0.60 ‰S and 20 ‰S (Fig.47). Thirdly, it may also be due to the disproportionate fall in the oxygen uptake rate of different weight groups of animals in a particular salinity at the same pO_2 . This is especially true at very low pO_2 , eg. at 20 mm Hg pO_2 284 mg animal shows the same rate in 5 ‰S and 20 ‰S (Fig.51).

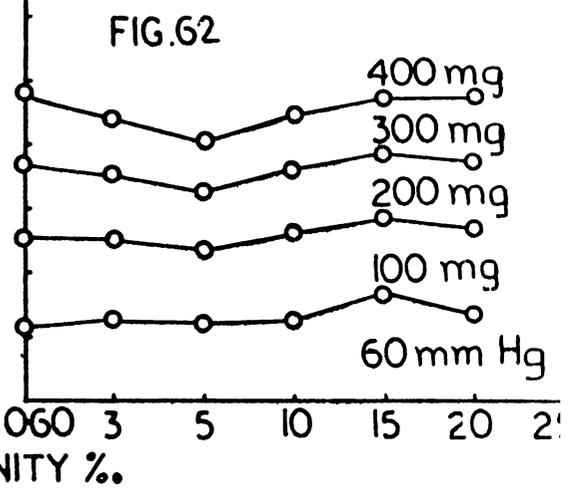
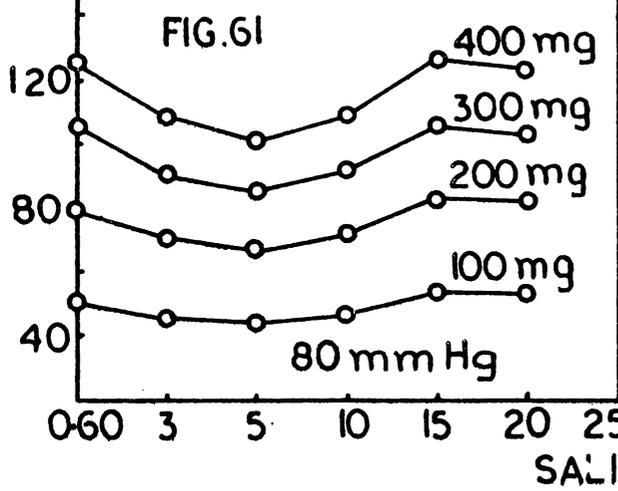
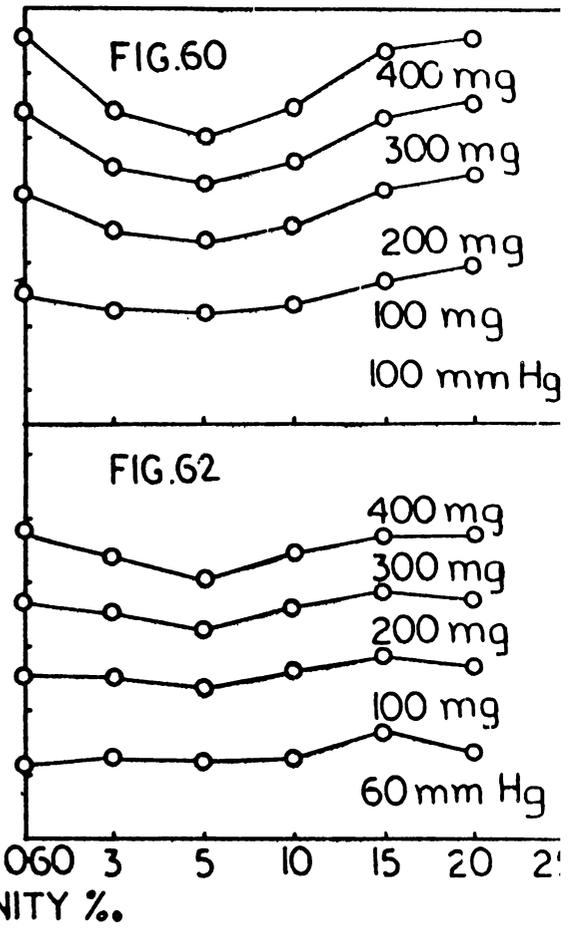
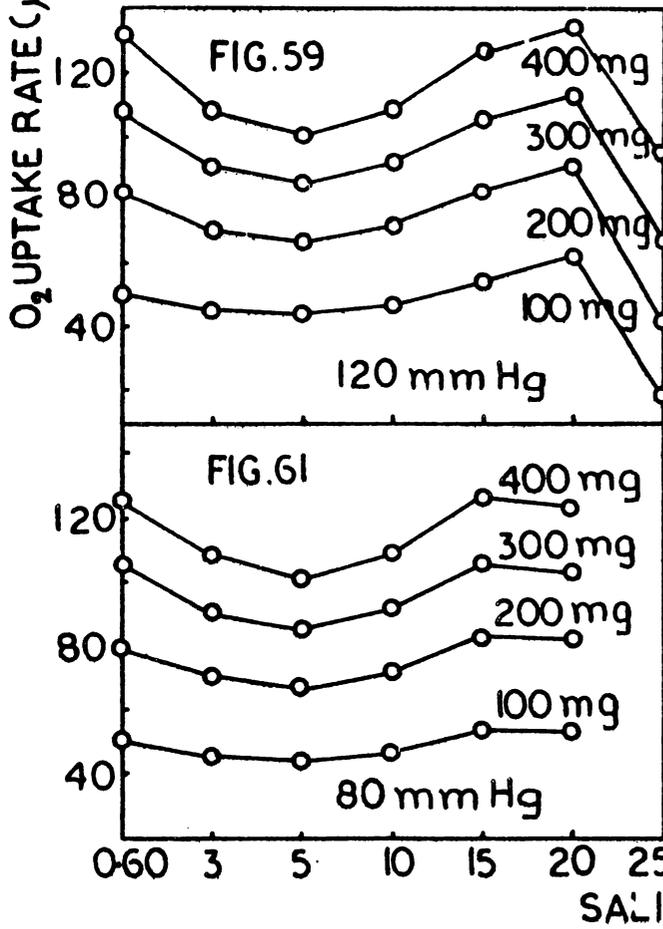
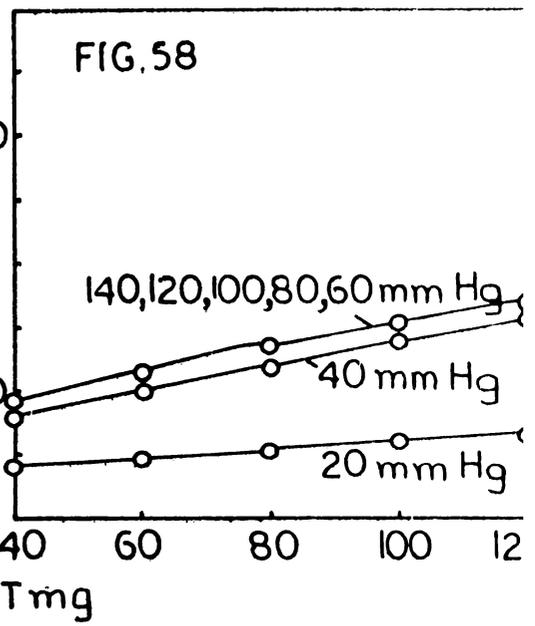
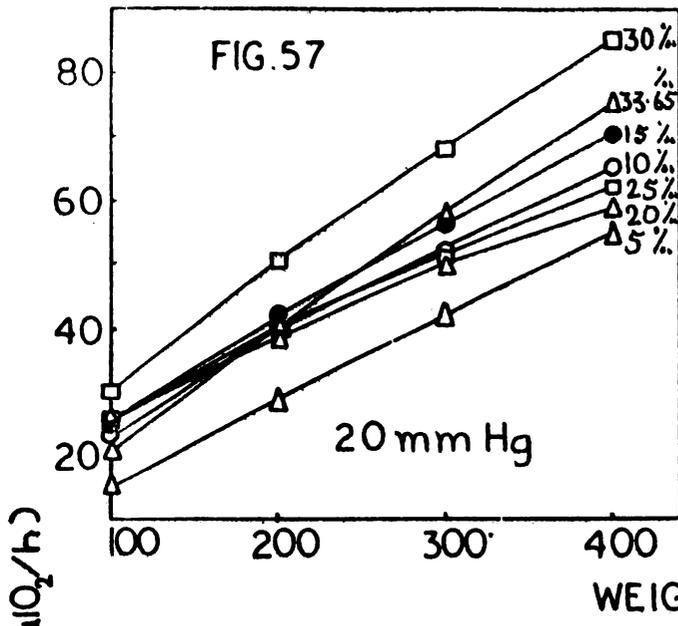
The interrelationships in the oxygen uptake rate of the various weight groups of N. hedleyi acclimated in 20 ‰S and experimented in different salinities under various pressures of oxygen are shown in Figs. 44, 52-57. In all the cases, the oxygen uptake rate increases with body size. A closer scrutiny of the figures reveals that there are instances where a particular weight group of animal shows the same rate in different salinities at a particular pO_2 . The explanations attributed for similar phenomena in the case of N. hedleyi acclimated in 5 ‰S seem to be applicable here.

The interrelationships in the oxygen uptake rate of the various weight groups of T. furcifera acclimated in 30 ‰S under various pressures of oxygen are shown in Fig. 58. As in the case of N. hedleyi the oxygen uptake rate increases with body size in all oxygen concentrations.

The variation of oxygen uptake rate in different salinities under various pressures of oxygen for different weight groups of N. hedleyi

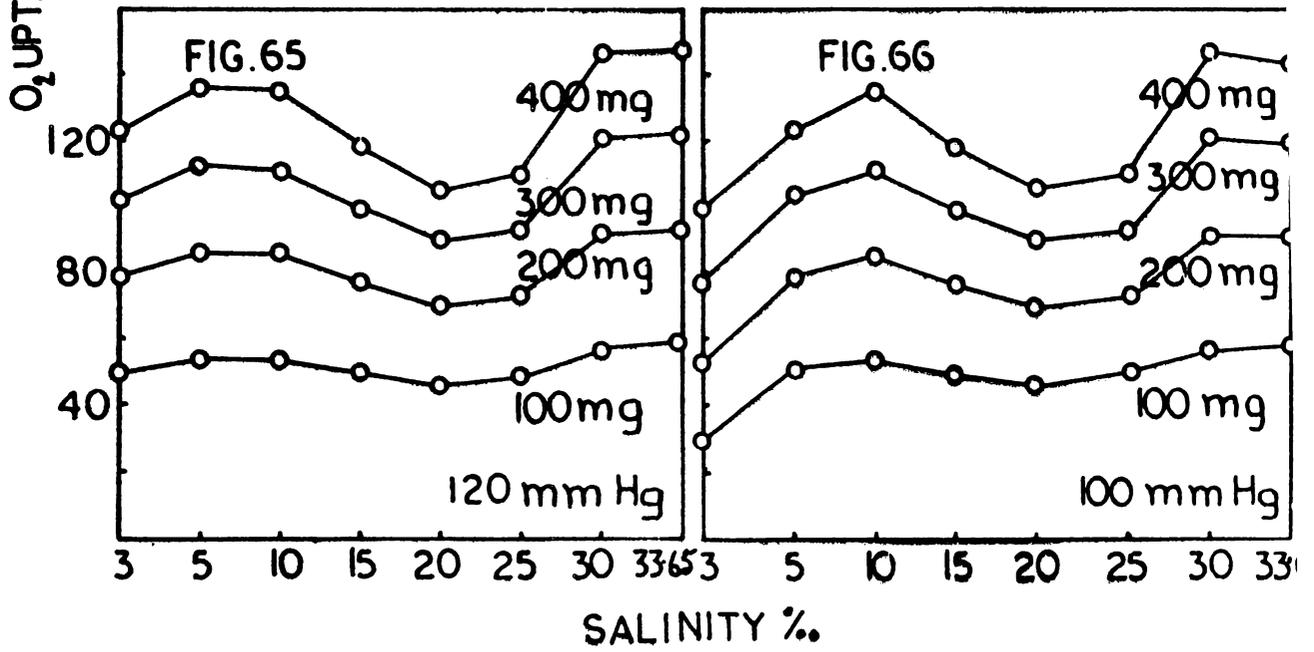
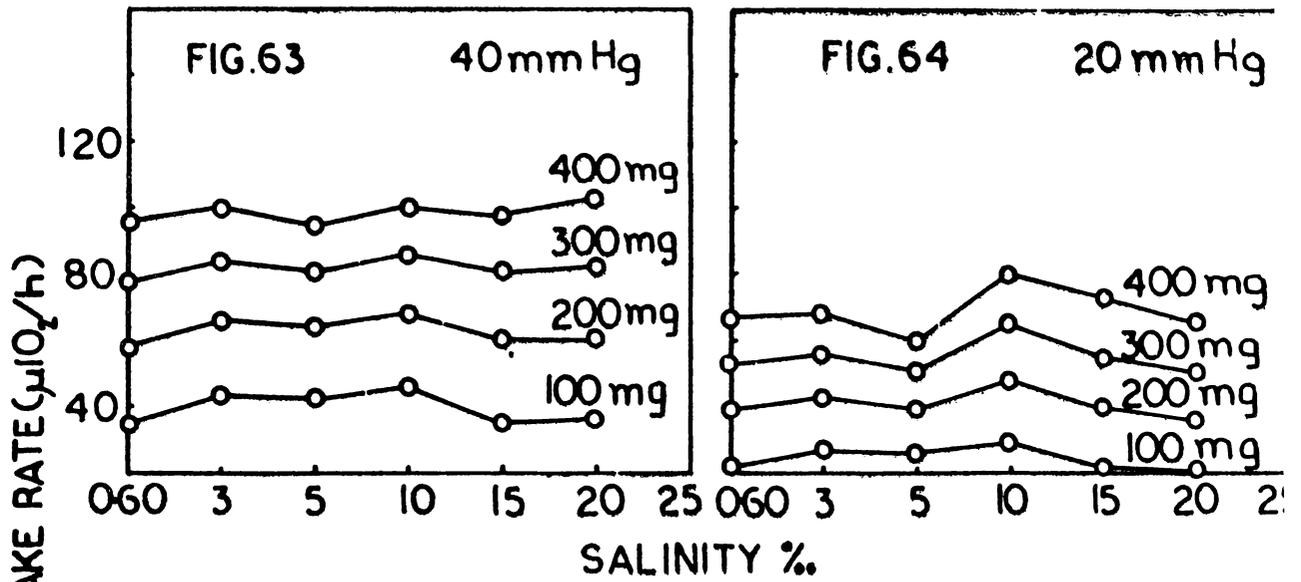
Figs. 53-56 Interrelationship in the oxygen uptake rate ($\mu\text{lO}_2/\text{h}$) of the four size groups (100, 200, 300 and 400 mg) of Nausitora hedleyi acclimated in 20 ‰S and experimented in different salinities at 100, 80, 60 and 40 mm Hg pO_2



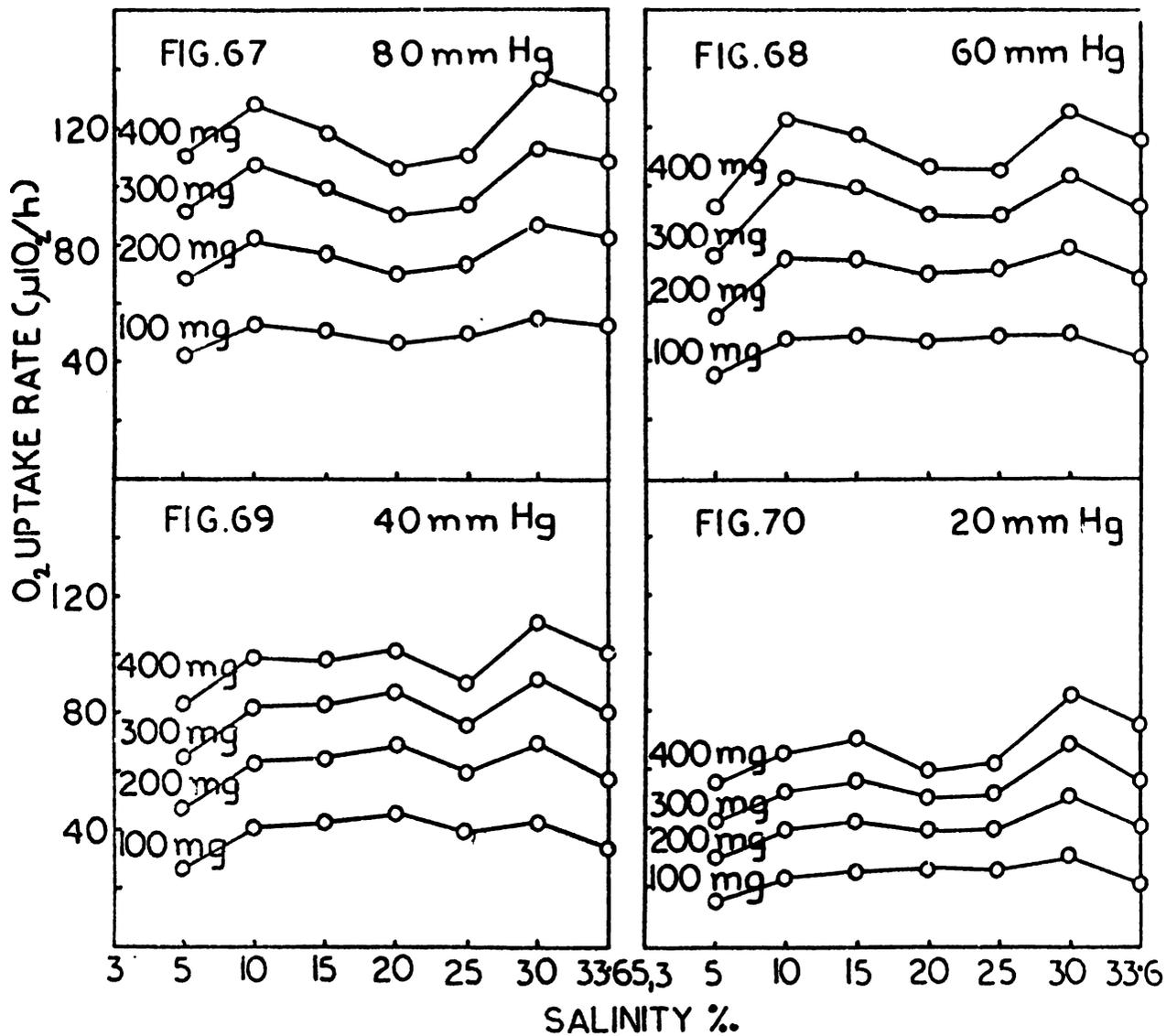


Figs. 63 and 64 Trend of variation in the oxygen uptake rate ($\mu\text{lO}_2/\text{h}$) of the four size groups (100, 200, 300 and 400 mg) of Nausitora hedleyi acclimated in 5 ‰S when experimented in different salinity media at 40 and 20 mm Hg pO_2

Figs. 65 and 66 Trend of variation in the oxygen uptake rate ($\mu\text{lO}_2/\text{h}$) of the four size groups (100, 200, 300 and 400 mg) of Nausitora hedleyi acclimated in 20 ‰S when experimented in different salinity media at 120 and 100 mm Hg pO_2



Figs. 67-70 Trend of variation in the oxygen uptake rate ($\mu\text{lO}_2/\text{h}$) of the four size groups (100, 200, 300 and 400 mg) of Nausitora hedleyi acclimated in 20 ‰ S when experimented in different salinity media at 80, 60, 40 and 20 mm Hg pO_2



acclimated in 5 ‰S is illustrated in Figs.43, 59-64. From 140 to 60 mm Hg pO_2 the oxygen uptake rate is minimum for all the weight groups in the acclimation salinity and it increases with increase or decrease in salinity with exceptions in 20 ‰S and 25 ‰S. Though the rate in 20 ‰S at 80 and 60 mm Hg pO_2 is higher than that in the acclimation salinity, it is lower than that in the preceding salinity (15 ‰). In 25 ‰S, the rate is lower at 140 mm Hg pO_2 compared to that in salinities other than the acclimation medium and at 120 mm Hg pO_2 , it is even lower than that in the acclimation salinity (5 ‰S) below which (120 mm Hg) the animals died. It may be recalled here that 25 ‰S is the higher lethal level for N. hedleyi acclimated in 5 ‰S (Ref. Chapter V). At 40 and 20 mm Hg pO_2 , the initial pattern of oxygen consumption i.e. increase of oxygen uptake rate with increase or decrease in salinity is observed only in salinities immediately near to the acclimation salinity (in 3 ‰ and 10 ‰) beyond which the rate declines, in general.

The variation in oxygen uptake rate in different salinities under various pressures of oxygen for different weight groups of N. hedleyi acclimated in 20 ‰S is shown in Figs.45, 65-70. At 140 mm Hg pO_2 , the rate is minimum in the acclimation salinity and it increases in all the test media as the salinity increases or decreases. But in 3 ‰S, the rate of oxygen uptake decreases as the pO_2 falls below 140 mm Hg and at 100 mm Hg pO_2 it even falls below that in the acclimation salinity. In 3 ‰S, the oxygen consumption could be determined only upto 100 mm Hg pO_2 , below which the animals died. A change in the trend of oxygen consumption of animals in different salinities is noticed below 120 mm Hg pO_2 and is more

conspicuously manifested in the extreme salinities. As the pO_2 reaches 80 mm Hg in the extreme salinities i.e. 5 ‰ and 33.65 ‰, all the weight groups of animals show a definite decline of the oxygen uptake rate. As the pO_2 declines further the original pattern of oxygen consumption is found highly altered and this is evidently due to the individual or combined action of the variation in salinity and the falling oxygen tension.

The trend of change in oxygen uptake rate at various pressures of oxygen for different weight groups of N. hedleyi acclimated in 5 ‰S and experimented in different salinities is shown in Figs.71-77. The oxygen uptake rate of animals in the acclimation salinity is found to be constant over a wide range of pO_2 , 140-55 mm Hg. Below the critical tension (P_c) which is between 40 and 55 mm Hg pO_2 , the oxygen uptake becomes dependent on the external oxygen tension. It can be noticed from the figures that as the salinity decreases or increases, the P_c shifts to higher pressures of oxygen. Thus in 3 ‰ P_c is between 40-60 mm Hg, in 0.60 ‰S 75-105 mm Hg, in 10 ‰S 40-60 mm Hg and in 15 ‰S 60-85 mm Hg. In the supranormal salinity of 20 ‰ and 25 ‰, the animals behave like conformers i.e. oxygen uptake decreases with decline in oxygen tension and in 25 ‰S the animals died below 120 mm Hg pO_2 .

The trend of change in the oxygen uptake rate at various pressures of oxygen for different weight groups of N. hedleyi acclimated in 20 ‰S and experimented in different salinities is illustrated in Figs.78-85. As in the former case the P_c is found to be between 40 and 55 mm Hg pO_2 below which the rate declines. Here also the P_c increases with increase or decrease in salinity. Thus in 25 ‰ S P_c is between 60-80 mm Hg; in 30 ‰S

Figs. 71-76 Trend of variation in the oxygen uptake rate ($\mu\text{lO}_2/\text{h}$) of the four size groups (100, 200, 300 and 400 mg) of Nausitora hedleyi acclimated in 5 ‰S and experimented in 0.60 ‰S, 3 ‰S, 5 ‰S, 10 ‰S, 15 ‰S and 20 ‰S at various partial pressures of oxygen ($p\text{O}_2$)

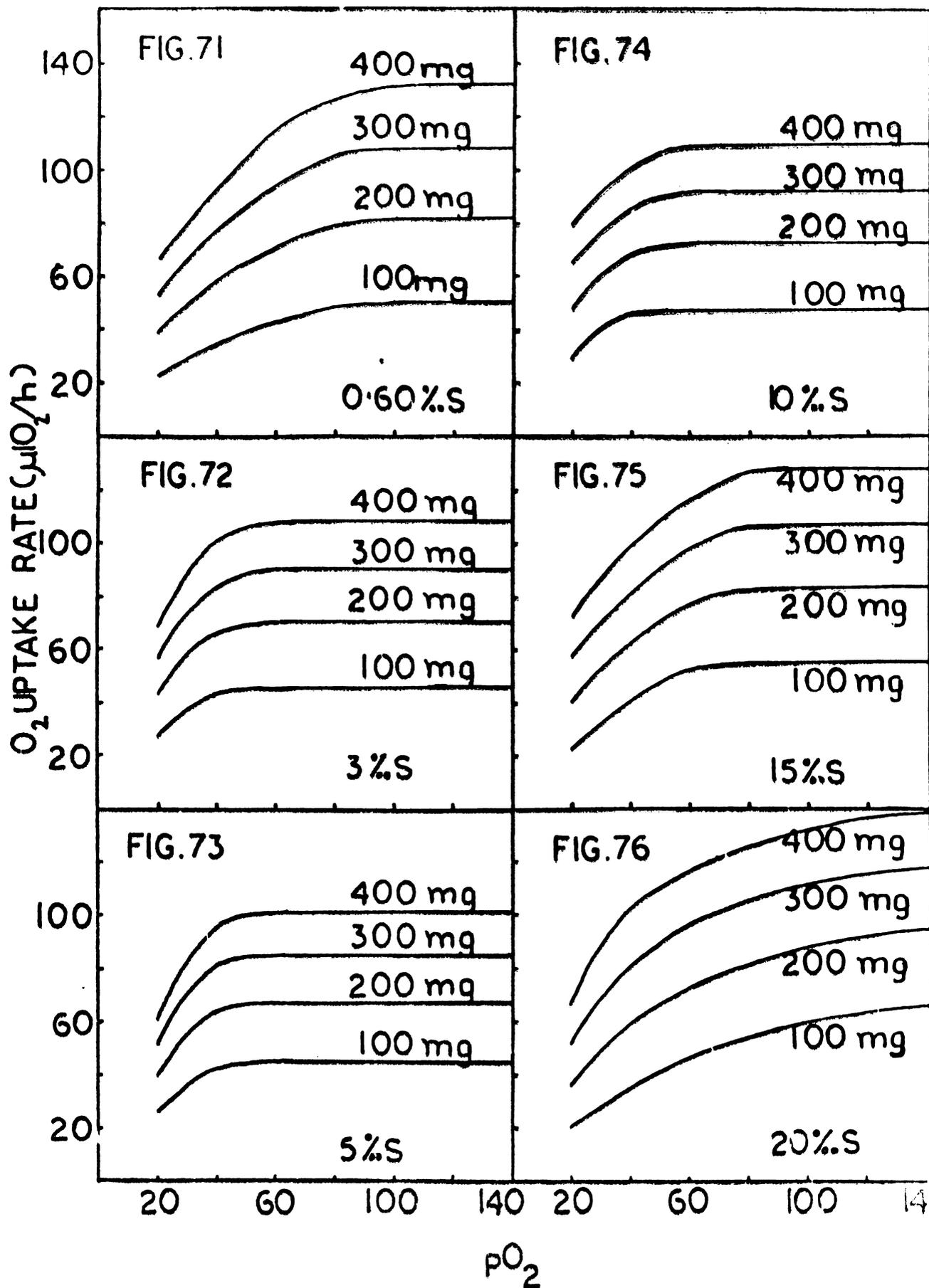
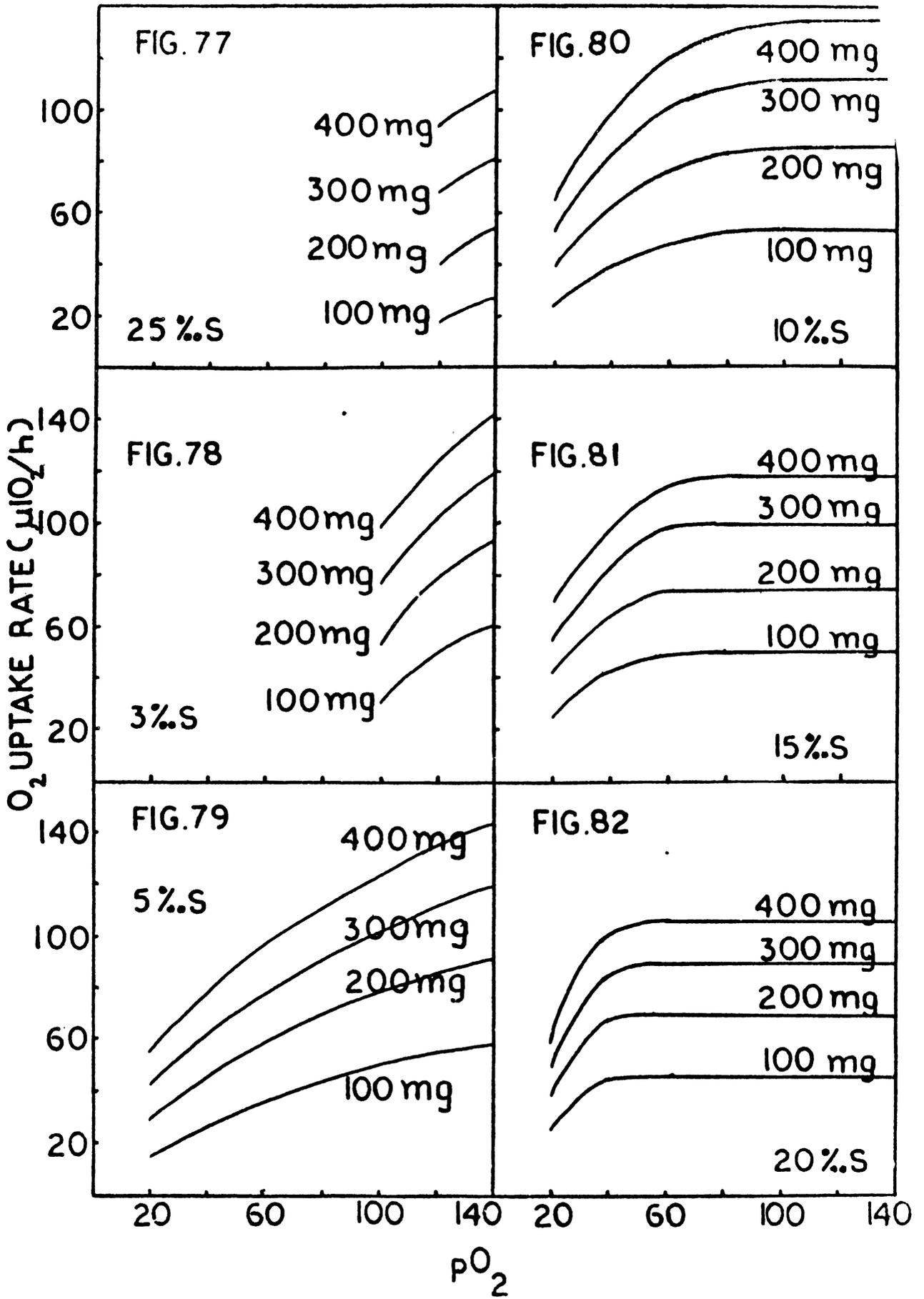


Fig. 77 Trend of variation in the oxygen uptake rate ($\mu\text{lO}_2/\text{h}$) of the four size groups (100, 200, 300 and 400 mg) of Nausitora hedleyi acclimated in 5 ‰S and experimented in 25 ‰S at various partial pressures of oxygen ($p\text{O}_2$)

Figs. 78-82 Trend of variation in the oxygen uptake rate ($\mu\text{lO}_2/\text{h}$) of the four size groups (100, 200, 300 and 400 mg) of Nausitora hedleyi acclimated in 20 ‰S and experimented in 3 ‰S, 5 ‰S, 10 ‰S, 15 ‰S and 20 ‰S at various partial pressures of oxygen ($p\text{O}_2$)

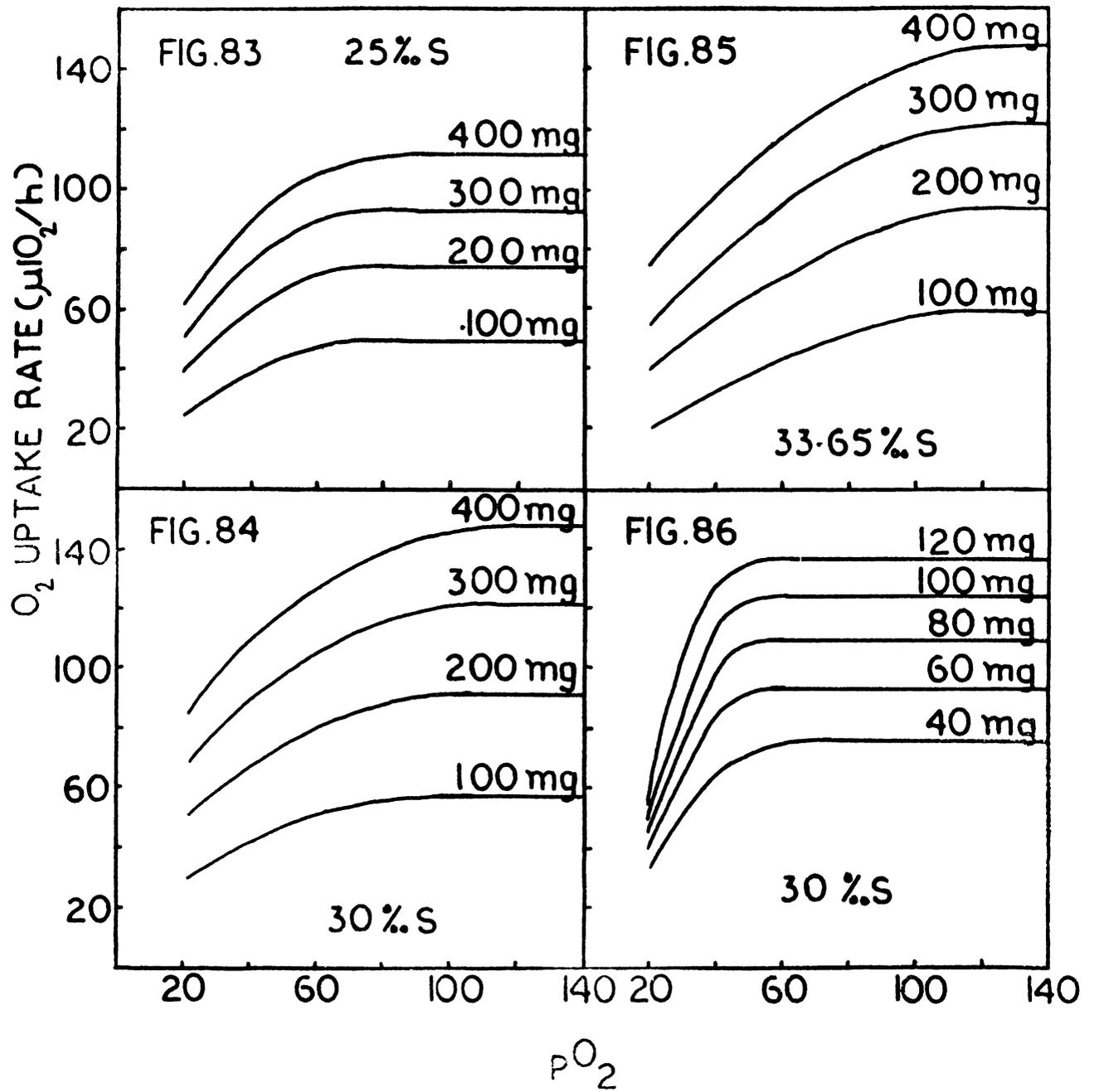


($\mu\text{O}_2/\text{h}$)

Figs. 83-85 Trend of variation in the oxygen uptake rate, of the four size groups (100, 200, 300 and 400 mg) of Nausitora hedleyi acclimated in 20 ‰S and experimented in 25 ‰S, 30 ‰S and 33.65 ‰S at various partial pressures of oxygen ($p\text{O}_2$)

($\mu\text{O}_2/\text{h}$)

Fig. 86 Trend of variation in the oxygen uptake rate, of the five size groups (40, 60, 80, 100 and 120 mg) of Teredo furcifera in the acclimation salinity of 30 ‰ at various partial pressures of oxygen ($p\text{O}_2$)



80-105 mm Hg; in 33.65 ‰S 100-120 mm Hg; in 15 ‰S 60-75 mm Hg and in 10 ‰S 80-100 mm Hg. In the subnormal salinities of 3 ‰ and 5 ‰ the animals are not able to regulate and the oxygen uptake rate declines as the pO_2 falls. In 3 ‰S, the animals died below 100 mm Hg pO_2 .

The trend of change in oxygen uptake at various pressures of oxygen for different weight groups of T. furcifera acclimated in 30 ‰S is shown in Fig.86. As in the case of N. hedleyi, T. furcifera has an independent zone, critical zone between 40 and 55 mm Hg pO_2 and a dependent zone in which the rate of oxygen uptake becomes proportional to the ambient oxygen tension.

The response of animals to varying oxygen tension is grouped in two categories (1) Oxygen dependent response where the oxygen uptake by the animals is proportional to the ambient oxygen tension (2) Oxygen independent response, where the oxygen uptake is relatively constant over a wide range of oxygen tension until a critical tension is reached and below which the rate is dependent on the oxygen concentration in the medium. The present investigation on the oxygen consumption of the shipworms, N. hedleyi and T. furcifera have shown that they come under the above mentioned second category - regulators.

The respiration of most bivalves are independent of external oxygen tension down to a wide range below which the oxygen consumption falls to very low levels. In Ostrea circumpicta the rate is constant up to $1 \text{ CM}^3 O_2 / \text{L}$ (Nozawa, 1929), in O. edulis upto $2.5 \text{ CM}^3 O_2 / \text{L}$ (Galstoff and Whipple, 1930), in O. gigas upto $1.5 \text{ CM}^3 O_2 / \text{L}$ (Ishida, 1935), in Pecten grandis and P. irradians

upto 1.0 to 0.5 mlO₂/L (Van Dam, 1954) and in Martesia striata upto 1 to 1.05 mlO₂/L (Nagabhushanam, 1962). Whedon and Sommer (1937) have stated that in Mytilus californianus, the respiratory rate is unaffected by external oxygen tension until a low level is reached. Moon and Pritchard (1970) have observed for the same species that the P_c is 24 to 34 mm Hg pO₂ for high (tide) level forms and 38 to 53 mm Hg pO₂ for low (tide) level forms. Bayne (1973) has observed that M. edulis regulated oxygen consumption over a wide range of pO₂ with P_c in the range 40-70 mm Hg pO₂.

Bivalves have the capacity to shut themselves off from the environment to escape from the adverse conditions. But in such an adaptation, the problem of oxygen availability and its utilization becomes a matter of utmost significance for the survival of the animal. It is known that many bivalves can withstand even anaerobic conditions for prolonged periods of time. The capacity of many marine bivalves to control their rates of oxygen uptake to very low levels of oxygen tension is pertinent in this connection.. Both N. hedleyi and T. furcifera close their burrows to tide over unfavourable conditions and they too have to depend upon the oxygen that is available in the water engulfed in the mantle cavity. The present investigations have shown that these shipworms also have an independent zone where the oxygen uptake is regulated to a considerably low level of pO₂, which is followed by a dependent zone where the oxygen consumption becomes proportional to the external oxygen concentration with a critical zone in between. This physiological adaptation is of considerable significance for their survival in oxygen deficient conditions.

S U M M A R Y

Teredinids (shipworms), a group of wood boring bivalves occurring in the Cochin Harbour region have been taken up for the eco-physiological studies. On the ecological part, the occurrence, abundance and seasonal intensity of the teredinids in relation to hydrographic conditions have been studied. On the physiological part, salinity tolerance and oxygen consumption of the most commonly occurring shipworms, Nausitora hedleyi and Teredo furcifera have been investigated.

The hydrographic factors studied are temperature, salinity, dissolved oxygen, phosphate, nitrite, silicate and pH. The variation in temperature is found to be comparatively narrow. But seasonal variation in salinity, dissolved oxygen, phosphate, nitrite and silicate has been observed, with the highest values during the monsoon period. In the case of pH, the minimum value has been obtained during the low saline period and the maximum value, during the high saline period. Of the various hydrographic factors studied, salinity has been found to be the most important fluctuating environmental parameter influencing the life of organisms in the habitat.

Ecological studies, conducted by a system of short term and long term panel experiments have shown that T. furcifera and N. hedleyi are the most destructive shipworms in this region. The settlement of T. furcifera is strictly restricted to the high saline pre-monsoon months. The onset of the South West monsoon and the ensued sudden fall in salinity exterminate this stenohaline species. The settlement of N. hedleyi is confined mainly to the low saline period and it starts a short period after the commencement

of the South West monsoon. The intensity of the settlement which goes on increasing throughout the low saline period declines and ultimately stops as marine conditions are established in the region. Almost at this time, the settlement of T. furcifera starts and the cycle of events is repeated.

Long term panel experiments reveal that the monthly pattern of settlement of shipworms is changed as the period of exposure of the test panel is increased. The number of T. furcifera and N. hedleyi in the test panel increases with increase in the duration of submergence. This is mainly due to the repeated settlement of waves of shipworm larvae and also due to the conditioning of the wood. But in certain periods, the intensity of teredinid attack does not increase with duration of exposure of the test panels for various reasons discussed in the text. Long term panel experiments also reveal that T. furcifera is a stenohaline species restricted to the period when marine conditions prevail whereas N. hedleyi is a euryhaline form which can withstand even the pre-monsoon high saline conditions as well as almost fresh water conditions of the monsoon period.

In addition to T. furcifera and N. hedleyi, three more species of shipworms, Lyrodus pedicellatus, Bankia companellata and Nausitora dunlopei have been collected, of which N. dunlopei is a new record from the West Coast of India.

The salinity tolerance studies have shown that N. hedleyi of small and large size groups acclimated in 5 ‰S can be transferred abruptly to 20 ‰S and that the higher lethal salinity is 25 ‰. However, smaller

animals have shown comparatively better tolerance than larger ones. Small and large size groups of N. hedleyi acclimated in 20 ‰ S can be transferred to 5 ‰ S and the lower lethal salinity is 3 ‰. As in the former case, the smaller animals are found to be less sensitive to variations in salinity.

Gradual transfer of small and large size groups of N. hedleyi to lower and higher salinities extended the tolerance limit. Thus animals acclimated in 5 ‰ or 20 ‰ S are found to tolerate the entire salinity range tested (0.60 - 33.65 ‰ S). Here also, smaller animals exhibited better tolerance.

The studies, in general, have shown that ⁱⁿ N. hedleyi, acclimation to lower and higher salinities shifts the lower lethal limit downwards and upper lethal limit upwards, respectively and that smaller animals are observed to tolerate variations in salinity better than larger ones. The investigations have also revealed that N. hedleyi is capable of tolerating a sudden salinity variation of 15 ‰ and if the change is gradual, it can tolerate a wide range of salinities. This gives a fair explanation for the observation that N. hedleyi occurs throughout the year in the Cochin Harbour region.

The 'b' values for N. hedleyi in 5 ‰ S and 20 ‰ S are 0.5959 and 0.6043, respectively and that for T. furcifera in 30 ‰ S is 0.5461. Comparison of the above values have shown that they are not statistically different, revealing the existence of similar metabolic types in the euryhaline N. hedleyi occurring mainly during the low saline period and in the stenohaline T. furcifera which is found only during the high

saline period.

The rate of oxygen uptake for N. hedleyi in the two acclimation media is found to be comparable which suggests the capacity of the euryhaline species to adjust itself gradually to variations in salinity and carry on normal activities without making any appreciable change in the oxygen consumption rate. Comparison of the oxygen consumption rates of N. hedleyi with those of T. furcifera shows that the rates of the former are higher.

The 'b' values obtained for N. hedleyi acclimated in 5 ‰S and experimented in different media varied from 0.5342 (in 20 ‰S) to 0.9798 (in 25 ‰S). Comparison of the regression coefficients shows that statistically significant differences exist between the 'b' values in salinities 0.60 ‰ and 25 ‰, 3 ‰ and 25 ‰, 5 ‰ and 25 ‰, 10 ‰ and 25 ‰, 15 ‰ and 25 ‰ and 20 ‰ and 25 ‰.

The regression coefficients observed for N. hedleyi acclimated in 20 ‰S and experimented in various salinities varied from 0.5840 (in 25 ‰S) to 0.6813 (in 30 ‰S). Comparison of the 'b' values shows that in all the salinities the values are not statistically different.

The oxygen uptake rate of N. hedleyi acclimated in 5 ‰S is found to be minimum in the acclimation salinity and increasing with increase or decrease in salinity, except in 25 ‰S. In the case of animals acclimated in 20 ‰S the oxygen uptake rate is minimum in the acclimation salinity and it increases in sub- and supranormal salinities. The above

findings fully agree with the observations of other workers that in euryhaline animals the rate of respiration increases in sub- and supra-normal salinities. The study also reveals that the increased rate in sub- and supranormal salinities falls to the original level due to acclimation.

The fall in oxygen tension does not affect the oxygen uptake rate - body weight relationship of 5 ‰S acclimated N. hedleyi in different test media, except in 15 ‰S and 20 ‰S where statistically different relationship has been observed at 20 mm Hg pO_2 .

The decline in the oxygen tension does not influence the oxygen uptake rate - body weight relationship of 20 ‰S acclimated N. hedleyi in different experimental media, except in 3 ‰S and 5 ‰S where the 'b' values in lower partial pressures of oxygen show statistically significant difference.

In T. furcifera acclimated in 30 ‰S, the regression coefficients remained statistically the same under declining oxygen tension upto 20 mm Hg pO_2 .

Intra- and interspecific comparisons of the 'b' values of N. hedleyi acclimated in 5 ‰S and 20 ‰S and T. furcifera acclimated in 30 ‰S under various oxygen tension show that the regression coefficients are not statistically different.

The variation in oxygen uptake rate in different salinities under various partial pressures of oxygen of N. hedleyi acclimated in 5 ‰ and

20 ‰ salinities shows that at higher oxygen tensions, the oxygen uptake rate is minimum in the acclimation salinity and it increases with increase or decrease in salinity, in general. But as the pO_2 declines this pattern is highly altered.

For N. hedleyi in the acclimation media of 5 ‰S and 20 ‰S and for T. furcifera in 30 ‰S, the rate of oxygen uptake under falling oxygen tension is found to be constant over a wide range of oxygen tension. The critical level is found to be between 40-55 mm Hg pO_2 below which the rate declines. In the case of N. hedleyi in which metabolic studies have been conducted in different media, it is observed that the critical tension increases with decrease or increase in salinity and in extreme salinities the rate of oxygen uptake becomes dependent on the ambient oxygen tension. Thus in the case of N. hedleyi acclimated in 5 ‰S the critical tension (P_c) is between 40-60 mm Hg in 3 ‰S, 75-105 mm Hg in 0.60 ‰S, 40-60 mm Hg in 10 ‰S and 60-85 mm Hg in 15 ‰S. In 20 ‰S and 25 ‰S the animals behaved like conformers. In the case of animals acclimated in 20 ‰S P_c is between 60-80 mm Hg in 25 ‰S, 80-105 mm Hg in 30 ‰S, 100-120 mm Hg in 33.65 ‰S, 60-75 mm Hg in 15 ‰S and 80-100 mm Hg in 10 ‰S. In 5 ‰ and 3 ‰ salinities the oxygen uptake rate falls as the pO_2 declines.

Thus N. hedleyi and T. furcifera are 'regulators' and they have an independent zone, a dependent zone and a critical zone in between. The capacity of these shipworms to regulate their oxygen uptake rate upto a very low pO_2 is of considerable significance for survival in oxygen deficient conditions.

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