

**OXYGEN UPTAKE BY THE LARVAL STAGES  
OF PENAEID SHRIMP**

*P. monodon* (FABRICIUS, 1798)

**MASTER OF SCIENCE  
IN  
INLAND FISHERIES ADMINISTRATION  
AND MANAGEMENT  
1994 - 96 BATCH**

**BY  
ASHOK R. GALPHADE**

**UNDER THE GUIDANCE OF  
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**CENTRAL INSTITUTE OF FISHERIES EDUCATION  
(DEEMED UNIVERSITY)  
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VERSOVA, MUMBAI - 400 061  
(INDIA)**

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**DISSERTATION SUBMITTED TO**

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**TOWARDS PARTIAL FULFILMENT FOR THE**

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**DEDICATED TO**

**MY BELOVED PARENTS, JIJAJI & AUKKA**



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### C E R T I F I C A T E

This is to certify that this dissertation entitled  
"OXYGEN UPTAKE BY THE LARVAL STAGES OF PENAEID SHRIMP P.  
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our guidance and is submitting the same for partial  
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(ASHOK R. GALPHADE)

## D E C L A R A T I O N

I do hereby declare that the dissertation entitled "Oxygen Uptake by larval stages of penaeid Shrimp P. Monodon" is my own work done under the guidance of Mr. M.B. Iftekhar, Scientist (S.S.), Temperate and tropical aquaculture Division, Central Institute of Fisheries Education (Deemed University), Mumbai.

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## A B S T R A C T

Oxygen consumption of P. Monodon mysis I to post larva PL2 were measured. Daily oxygen requirement was found to vary. Even the oxygen requirement during 1st hour and 11nd hour of experimentation was recorded with variations. Comparing the oxygen consumption rate with other decapod larvae the values of oxygen requirement were found to be higher than megalopa larvae or other larval stages of Brachyarean larval stage.

The minimum value was recorded to be  $0.52 \text{ Mjg/O}_2/\text{Ind/hr.}$  and the maximum value being  $11.80 \text{ mg/O}_2/\text{ind/hr.}$

## सारांश

पीनीयस मोनोडोन माइसीस से पोस्ट लावा पी. एल २ के आक्सीजन उपभोग को मापा गया। प्रतिदिन आक्सीजन की मात्रा घटती-बढ़ती हुई पायी गई। प्रयोग के दौरान प्रति पहले एवं दूसरे घंटों में आक्सीजन की मात्रा बदलती हुई पायी गई।

आक्सीजन उपभोग दर की अन्य डेकापोड्स लावा, मेगालाप लावा एवं ब्रेचुरीयन लावा के स्तर से तुलना करने पर पी. मोनोडोन लावा में आक्सीजन की मात्रा अधिक पायी गई।

कम से कम मात्रा ०.५२ मि. ग्रा. / आ. २/ प्रत्येक/ घंटा होगी एवं ज्यादातर मात्रा १.८० मि. ग्रा. / आ. २/ प्रत्येक/ घंटा होगी।

# Introduction

## I N T R O D U C T I O N

In "aerobes" the general term "respiration" may be divided into several unit processes. In terms of oxygen uptake, these are 1) ventilation, or the transport of oxygen from the environment to the respiratory exchange 2) oxygen uptake from the environment across the respiratory exchange area 3) perfusion, or oxygen removal from the respiratory exchange area; oxygen transport to the tissues by the hemolymph and lastly 4) aerobic metabolism or oxygen utilization by the tissues.

The regulation of oxygen consumption and blood oxygen transport have been studied for a number of crustaceans. Redmond, 1968, Johnsen et al; 1970. Van Bruggen, 1971. The physiology of poikilotherms depends, in nature, on a number of factors acting in synergy. Coastal marine organisms are confronted with greater temporal and spatial fluctuations of environmental conditions than pelagic organisms. For most shrimp, the biological cycle includes a marine phase, among the first stages of development, then an estuarine or brackish phase for the postlarvae and juveniles. Following that, the individual continue their development and their adult life in marine waters. It thus appears that the degree of tolerance towards environmental factors differs according to the age of the individuals considered. In aquaculture successful production depends to a large extents on the rate of survival of the younger stages. It is therefore important to determine the most favourable conditions of rearing for each stages. This optimum can be determined directly from the analysis of mortality and growth rates. Another approach, more analytic, consist of evaluating, for each larval stages,

the intensity of respiratory metabolism. This is, in effect, a good indicator of the general physiological activity of organisms, as it takes into account the energy needs necessary for osmotic regulation. In the present dissertation an attempt is made to analyse oxygen uptake and variations in respiratory metabolisms of the larval stages of *penaeus monodon*.

## Review of Literature

## A. SITES OF GAS EXCHANGE.

General Considerations:

In both oxygen uptake and Carbon dioxide elimination movement of gas across the respiratory surface can only occur by diffusion. This may be facilitated by the action of respiratory pigments in the hemolymph, but no active transport process has been demonstrated. Thus, exchange of either gas across the surface may be simply described by a form of the Fick diffusion equation.

$$M = \frac{K - A}{E} P$$

where M is the quantity of gas in  $\text{mmol-min}^{-1}$  moved across the membrane, K is the diffusion constant  $\text{mmol-min}^{-1}$ , A is the area of the gas exchange surface, E is the average thickness of the gas exchange surface, and P is the partial pressure gradient for that gas across the respiratory surface.

The diffusion constant (Krogh's constant) K takes into account not only the physical diffusion through the membrane (D) but also the solubility coefficient of the adjacent medium i.e.  $K = D \cdot B$ . Thus in aquatic solutions, where  $\text{CO}_2$  is much more soluble,  $K_{\text{CO}_2}$  exceeds  $K_{\text{O}_2}$  by approximately 25 - fold. Therefore, in aquatic animals diffusion of oxygen rather than carbon dioxide is generally considered to be the limiting factor in gas exchangers, and the attainment of oxygen supply the major modifying factor in the evolutionary design, of and major controlling factor in the operation of, respiratory systems.



In the smallest and simplest crustaceans, and in smaller larval stages, sufficient gas exchange may occur by diffusion of oxygen across the body surface and through the tissues, unaided by specialized structures or movements. However, the oxygen capacity of even pure water is rather low ( $0.46 \text{ mmol-liter}^{-1}$  at  $0^{\circ}\text{C}$ ) and is further reduced by increase in temperature or salinity. This coupled with the reduced diffusibility of oxygen across the chitin layers covering all crustacean respiratory surfaces (Krogh, 1919) indicates that, in the majority of active crustaceans, special mechanisms must occur to boost oxygen uptake. these include: increase in surface area available for gas exchange, usually by development of specialized respiratory structures such as gills or lungs; ventilation of the external medium past the gas exchange sites; perfusion of the internal medium through the gas exchange site and the presence of respiratory pigments, which, by removing  $\text{O}_2$  from solution in the hemolymph and thus maintaining the diffusion gradient across the gills, facilitate oxygen uptake as well as increase oxygen carrying and delivery capacities of the hemolymph.

Automatically, the scaphognathite is the flattened exopodite of the second maxilla. The blade of the scaphognathite oscillates complexly within a narrow channel. Pressure recordings from the branchial cavities of a number of aquatic crab species/lobsters and shrimps, demonstrate as typical biphasic wave form. Both upward and downward strokes of the scaphognathite generate force and are equally involved in movement of water.

The scaphognathite is not a unidirectional pump but can, in some crustaceans, be reversed, and within a single beat it can reverse the pressure gradient and direction of branchial water flow through the branchial cavity and, potentially, across the gills.

- a) Forward Pumping: In this mode, pumping of the scaphognathite propels water out of the scaphognathite channel anteriorly. Above a certain minimum beat frequency this forward pumping of the scaphognathite is sufficient to maintain branchial pressure below ambient, and thus allows continuous flow of water into the branchial cavity and across the gills. The actual pressure maintained in the branchial chamber is generally dependent both on the rate of scaphognathite pumping and animal size.

In the majority of decapods, forward pumping apparently predominates. In all least brachyuran decapodes, this pumping mode allows countercurrent gas exchange between hemolymph and branchial water and may thus enhance gas exchange.

- b) Reversed Pumping: In this mode, the scaphognathite attack angle changes so that water is forced posteriorly into the branchial chambers. The incidence of reversed pumping is variable within the decapods: it is restricted to single reversed beats seen rarely in crayfish and more frequently in lobsters and it is present as bursts of reversed pumping of varying incidence and duration in several brachyuran crabs.

- c) Ventilatory water flow is less well known in non-brachyuran types, having been described only for the lobster, crayfish, and shrimp. In both the lobster and crayfish, water enters equally through spaces between the limb bases and is channeled immediately upward, circulating through the filamentous gills before being pumped out anteriorly.
- d) Assessment of Ventilation Volume. Two methods are in vogue to quantify the flow of water through the branchial chambers (ventilation volume  $V_w$ ). Both involve covering the animal's mouthparts with a loose fitting mask, which isolates the respiratory exhalent apertures. In one case the animal is restrained and the outflow collected in a separate chamber, while in the second an electromagnetic flow meter is incorporated into the mask allowing the outflow to be sensed without restraint. An advantage of the flowmeter technique is that it allows separation and quantification of both forward and reversed flows, while the collection method shows only net forward flow. The presence of the mask has been shown to affect ventilatory and cardiac pumping patterns and may affect the animal's performance in reversed flow situations. Ventilation volume can also be estimated indirectly during respirometry using the Fick principle, if oxygen tensions of inspired ( $P_m$ ) and expired ( $P_{ta}$ ) branchial water are measured by means of chronically implanted catheters.

Ventilation may be quantified in more functional terms as the amount of water (in liters) necessary to allow the acquisition of 1

mmol.  $O_2$ . This quantity of water, termed the convection requirement ( $V_w/M_{O_2}$ ) by Dejours (1975), not only must provide sufficient oxygen, but must also maintain an effective gradient for carbon dioxide elimination from the body by removal of this substance from the respiratory site. There is, of course, a simultaneous requirement for perfusion of the respiratory surface. Thus we may also define a second convection requirement ( $V_1/M_o$ ) as the amount of hemolymph (in liters) required to move 1 mmol.  $O_2$  from the respiratory surface. Sufficient hemolymphs must perfuses the gills to ensure elimination of  $CO_2$  as well as to maintain an adequate gradient to ensure gas exchange. In many crustaceans at least the latter process is facilitated by the presence, in hemolymph, of oxygen carrier molecules such as hemoglobin and hemocyanin. These molecules combine with oxygen in the gills, facilitating oxygen uptake and increasing oxygen carrying capacity, thus reducing the hemolymph convection requirement. Some water and hemolymph convection requirements documented by earlier worker are completed for Crustacean species are presented in Table.1 Available information suggests that the ventilatory and cardiac pumping systems are closely interrelated and need complex integration by the nervous system.

#### Circulation and Perfusion of the Gill System:

The circulatory system in crustaceans is generally regarded as an "open" system i.e. one in which the circulating body fluid is not totally confined with out tubular distribution system. Clearly, however, within the phylum, many variations on this theme occur, ranging from the minimal system seen in some copepods and ostracodes,

which lack both heart and vessels, to the complexly organised systems in certain malacostracans, which involve not only muscular hearts but "arterial" systems that divide repeatedly, eventually to form very small tubules of a diameter (2-10  $\mu$ m) Sandeman (1967) similar to the capillaries of many "closed" systems. Full anatomical, and many functional, details of Crustacean Circulatory systems are provided by Maynard's (1960) (Belman, 1975, 1976 and, Burnett et al. 1979).

#### PRESSURE AND FLOW CAPABILITIES OF THE MALACOSTRACAN OPEN SYSTEM

- a) The Heart and General Circulatory System. The introduction of high sensitivity, low-volume displacement pressure transducers has allowed measurement of pressures throughout the circulatory systems of a range of crustacean types. These are presented together with comparative data from other aquatic species in Table 2. These more recent results show the hearts capable of producing systolic pressures of similar magnitude to those found in other aquatic invertebrates and in fishes. Diastolic pressures fall toward, but rarely reach, zero (= ambient external) pressure. In the initial part of systole, contraction is isometric, raising pressure to a level sufficient to open the valves at the origin of the major arterial outlets. Arterial (anterior abdominal artery) pressure then rises to virtually equals with intercardiac pressure during cardiac ejection. during cardiac ejection (Table 2) Arterial diastolic pressures, however, decline slowly and are

maintained substantially above intracardiac pressures during diastole. Reflux of hemolymph is improved by the arterial valves. There is an apparent absence of smooth muscle in the arterial walls of crustaceans, but elastic fibres are present and no doubt contribute to maintenance of arterial hemolymph pressure. After passing through the smaller vessels, hemolymph enters the general body cavity (hemocoel) through which it passes by discrete channels (Burger and Smythe, 1953) to collect in the infrabranial sinus. Infrabranial sinus pressures are pulsatile, but the pressure pulse is rarely more than 1 Torr. Mean infrabranial pressures are substantially (50-70%) lower than arterial pressures (Table II), indicating that the resistance of the tissue vessels accounts for a major part of the "peripheral resistance", at least in the larger decapod crustaceans, Belman (1975) has recorded the velocity of hemolymph flow in both arterial (8-10 cm/sec) and infrabranial sinus (1.3 - 1.6 cm. sec.) systems of the lobster *Panulirus*.

From the infrabranial sinus, hemolymph passes through the limb bases and the different branchial channels before perfusing the filaments and lamellae of the gills. Despite the pressure drop in the tissues, infrabranial pressure must be maintained at a sufficiently high level to power flow through the complex perfusion channels in the gills, which, unlike those of fishes, occur on "Venous" return to the heart. Simultaneous measurements of pressure on either side of the gills of crustaceans, however, suggest that a pressure drop of 1-2 mm

Hg is sufficient to power flow through even the most complex gill systems. This pressure drop is very low compared with the 7 (dogfish: Piiper et al. 1977) to 11 mm Hg (trout: Stevens and Randall, 1967) required for perfusion of the gills of fishes. Elaborate accessory flow systems and muscular control systems ~~such as have~~ been described for fish have not been described in crustaceans, and this may explain the very much lower resistance exhibited by crustacean gills.

## B) OXYGEN UPTAKE

### QUANTIFICATION AND METHODS OF MEASUREMENT

Oxygen uptake (consumption) is the most frequently used (and perhaps misused) parameter in crustacean respiration physiology levels of oxygen uptake in different crustaceans differ based on their size, stage of development and physiological state of the individual animals.

One major difficulty in comparing results between groups is that we rarely know the limits or range of oxygen uptake exhibited by these animals. Clearly each species has its own level of basal metabolism - that level of O<sub>2</sub> uptake necessary for bodily maintenance under a particular set of environmental conditions that approximate the seasonal norm. In addition, each species has a maximal oxygen consumption - active metabolism - resulting from sustained maximal activity. The range, which will be different for all animals, may be labeled the 'Scope for activity' or more accurately the 'aerobic metabolic scope'. Knowledge of these limits, and their variability with environmental

exposure acclimation, and adaptation should be the goal of the investigators in this field, thereby providing the framework into which a particular set of data can be incorporated, and a basis for quantitative comparison between crustacean groups and with other animal forms, these same, or similar, animals under similar conditions (e.g. Homarus vulgaris, measured value = 17 mol. O<sub>2</sub> Kg<sup>-1</sup> at 15°C (Butler et al. 1978) as compared with the "standard" value = 30 mol. O<sub>2</sub> JKg<sup>-1</sup> min<sup>-1</sup>, and Orconectes virilis, measured value = 7.5 mol. O<sub>2</sub> Kg<sup>-1</sup> min<sup>-1</sup> compared with the standard value = 94 mol. O<sub>2</sub> Kg<sup>-1</sup> min<sup>-1</sup> given in prosser. 1973).

Thus, in some cases, extrapolation to standard metabolism may yield erroneously high values.

The lower values quoted above result from studies in which animals were allowed to acclimate to experimental conditions which were adjusted to resemble, so far as practicable, their natural habitat. For instance, Butler et al (1978) used respirometers which were shaded to yield normal light intensities yet allowed for normal conditions of photoperiod, i.e. flowing natural seawater and shelter for the normally cryptobiotic lobsters. These and other considerations, such as placing animals that are normally benthic on a natural substratum into which they may dig or burrow, all serve to reduce oxygen consumption markedly. In this regard, choice of a respirometry system may also be important. Static systems should perhaps be avoided for most animals, as both the oxygen depletion and hypercapnia inherent in this



design may affect the oxygen uptake (as well as other parameters) of the animals under study. While superior in this regards, constant flow systems also must be adjusted so that their flow rates and conditions are not themselves disturbing to the animals. Automatic respirometers of the type described by Sutcliffe et al (1975) probably involve a significant advantage in simulating natural conditions.

Accolimation to the experimental conditions is also important. Many recent reports (McMahon et al 1974, McMahon and Wilkens 1974, 1972, Butler et al 1978; Taylor and Butler 1978) show that oxygen uptake of apparently inactive animals declines significantly for 24-48 hr. following introduction into the experimental chambers McDonald (1977) and McMahon et al (1978, 1979) have shown that lactic acid levels and acid base status also do not stabilize until 24-48 hr following activity or disturbance. Hormones released during disturbance of activity may also have protracted effects and both factors could be responsible for the extended acclimation period necessary. Protected periods of inactivity such as are imposed in these long running experiments may not be found in the natural environment. Nonetheless, these minimal levels must approach basal metabolism, and they do provide a basis for comparison with results from other aquatic animals. Such comparisons show that, at equivalent temperature, basal levels of metabolism for crustaceans are similar to those recorded for fishes under similar conditions (Brett 1972, McMahon et al 1979).

#### OXYGEN UPTAKE AND EFFECTS OF ACTIVITY

Much less is known of the oxygen uptake rates of crustaceans exposed to strenuous activity. Both active and quiescent (basal) rates are available for relatively few species (See Table II); however, these

data allow calculation of the aerobic metabolic scope. At 8°C, Cancer magister (McMahon et al 1979) can increase oxygen consumption from a low of 16+5 mol. O<sub>2</sub> Kg<sup>-1</sup> min<sup>-1</sup> to a maximum of 61 + 20 mol. O<sub>2</sub> Kg<sup>-1</sup> min<sup>-1</sup>, representing an aerobic metabolic scope of 45 mol. O<sub>2</sub> Kg<sup>-1</sup> min<sup>-1</sup> or an increase of approximately four fold over quiescent rates. At similar temperatures a fresh water crayfish, pacifastacus leniusculus (Rutledge and Pritchard, 1981) shows similar aerobic metabolic scope ( 61 mol O<sub>2</sub> Kg<sup>-1</sup> min<sup>-1</sup>), but this increases to a maximum (117 mol. O<sub>2</sub> Kg<sup>-1</sup> min<sup>-1</sup>) at 20°C. Maximum rate of oxygen consumption of the air breathing brachyuran Cardisoma guanhumi exercised on a treadmill was 120 mol. O<sub>2</sub>. Kg<sup>-1</sup> Min<sup>-1</sup>, equivalent to an aerobic metabolic scope of 97 mol O<sub>2</sub> Kg<sup>-1</sup> min<sup>-1</sup>, an increase of approximately fivefold over routine levels (Herreid et al 1979). Active rates of the pelagic mysid Gnathophausia ingens could be increased ninefold over standard level (Belman and Childress, 1976). Maximal rates of oxygen consumption and aerobic metabolic capacities exhibited by these crustacean species are nevertheless five to ten times lower when compared with most results for active fish species such as the sockeye salmon (540 mol. O<sub>2</sub> Kg<sup>-1</sup> min<sup>-1</sup> Brett 1972). However the crustacean data compare favourably with levels reported for more sluggish fish species, such as the range of amblyopsid cave fishes (39 - 100 mol. O<sub>2</sub> Kg<sup>-1</sup> min<sup>-1</sup>; Poulson, 1963) and for the dogfish, Squalus acanthias (30 mol. O<sub>2</sub> Kg<sup>-1</sup> min<sup>-1</sup> Brett and Blackburn 1978). These data suggest that both minimal oxygen uptake levels and aerobic metabolic scopes of the crustaceans studied may be similar to those of fish species with comparable activity patterns.

Oxygen uptake is not only affected by locomotor activity but also by many physiological activities, including egg production, disturbance, and by change in many environmental parameters. Responses to environmental change are often biphasic with an initial 'Startle' response, followed by a protracted response. Compensatory mechanisms to the environmental change involve increased metabolic effort and hence oxygen demand.

### REGULATION OF OXYGEN UPTAKE

In Activity, Elevation of oxygen uptake over basal rates may theoretically be effected in several ways. Increase in ventilation, and hence oxygen supply to the respiratory surface may be a natural consequence of activity in crustaceans with exposed gills. In species with enclosed gills, however, specific ventilatory responses, such as increased frequency of scaphognathite pumping, must occur. Such increases have been observed in response to activity in Cancer (McMahon et al 1979) Cardisoma ganhumi (Herreid et al 1979) Pacifastacus leniusculus (Rutledge, 1981) and Gnathophausia ingens (Belman and Childress 1976) increased ventilation also occurs in response to a decrease in environmental salinity (Carcinus maenas: A.C. Taylor, 1977) and in response to temperature increase in Carcinus maenas (Taylor et al: 1973) and in Cancer magister (McMahon et al: 1978b).

Increase in Oxygen uptake could also be facilitated by increase in gill perfusion which by removing oxygen from the inside of the gas

exchange surface, could ensure a favourable pressure gradient for oxygen diffusion. Although data are available for only a few species, some evidence suggests that this may be important in crustaceans. Fick estimates suggest that cardiac output doubles following strenuous activity in Cancer magister (McMahon et al 1979) and more than doubles in the crayfish Pacifastacus (Rutledge, 1981). In both cases the ventilation perfusion ratio is maintained, i.e. perfusion increases to remove the extra oxygen supplied by increased ventilation, a situation essentially similar to that observed during exercise in fish. Regulation of cardiac output to adjust uptake in response to environmental changes is also discussed by Mangum and Towle (1977).

Perhaps the most potent modifier of oxygen uptakes is oxygen utilization by tissues. This acts to increase oxygen uptake at the gills by reduction of prebranchial oxygen tensions ( $P_{vo2}$ ). Reduction of  $P_{vo2}$  could increase oxygen uptake simply by increasing the pressure gradient for  $O_2$  across the respiratory surface, but clearly other factors can be involved. In activity, as in other situations in which the oxygen demand increases, prebranchial venous oxygen tension is driven down into the steeply descending portion of the dissociation curve and the participation of hemocyanin in tissue oxygen transport is greatly increased. Small changes in prebranchial  $PO_2$  thus may induce major changes in oxygen binding at the gills, explaining the enhanced oxygen uptake observed.

An understanding of these effects allows some interpretation of the very

variable relationship between percent oxygen extraction ( $\text{Extrw} = 100 (\text{P10}_2 - \text{P10}_2)$ ) and branchial water flow observed in the published literature. A general relationship where decrease in extraction accompanies any increase in ventilation volume, has been quantified for the crab Callinectes sapidus by Batterton and Cameron (1978), and apparently occurs during recovery from disturbance in both crayfish (McMahon et al 1974) and lobsters (Butler et al 1978). However, this relationship is by no means universal. No significant decrease in oxygen extraction was associated with a two to three fold increase in ventilation volume following strenuous exercise in Cancer magister (McMahon et al 1979) nor with a ventilatory increase of similar magnitude following exposure to low salinity in Carcinus (A.C. Taylor, 1977). Additionally,  $\text{Extrw}$  and ventilation volume decrease simultaneously during periodic ventilation in Cancer products (McMahon and Wikens 1974). Clearly, factors other than ventilation volume effect oxygen extraction from the branchial water stream. In conditions where increased ventilation is associated with locomotor or other activity, prebranchial oxygen tensions are depressed, resulting in enhanced oxygen uptake with maintenance of percent oxygen extraction rates, even at high ventilation volumes. However increased scaphognathite rate and hence ventilation volume may result from other factors, i.e. disturbance, which are not necessarily associated with increased locomotor activity. Under these conditions oxygen demand may not increase proportionally and  $\text{Pvo}_2$  may remain steady or even rise slightly, resulting in a decrease in percent oxygen extraction from the branchial water circulating oxygen tensions, associated with high ventilation volumes, in recently disturbed animals. McDonald (1977) and McDonald et al (1977), however, reported similar values for recently

stressed animals, but showed that both ventilation volume, and hemolymph oxygen tensions decreased with recovery from disturbance (Fig. 5, Table III). Two respiratory patterns were observed in these quiescent animals. In the first, bilateral ventilation (both scaphognathites continually active) caused a combined ventilatory flow of 288 ml. kg.  $1. \text{ min}^{-1}$ . Under these conditions, mean postbranchial oxygen tensions were  $81 \pm 14$  (SE) torr and the mean prebranchial oxygen tensions were  $15 \pm 5$  (SD) torr ~~Table 4~~. These values are lower than those recorded by Johansen et al. (1970) but, even under these conditions, hemocyanin-bound oxygen still only accounted for 30-40% of the oxygen transported to the tissues. In the second condition, unilateral ventilation (only one scaphognathite active), ventilation volume decreased 50%, and hemolymph oxygen tensions were substantially lower ( $P_{\text{ao}_2} = 32 \pm$  torr). As pointed out by McDonald (1977), these low values are caused by admixture of hemolymph from the ventilated ( $P_{\text{ao}_2} = 77 \pm 5$  torr) and nonventilated  $P_{\text{ao}_2} = 11 \pm 7$  torr) gill sets (Fig. 8).

Perbranchial oxygen tensions decline ( $P_{\text{vo}_2} = 7.9 \pm 2$  torr) and under these conditions hemocyanin conveys 8-90 of the oxygen delivered to the tissues. Simplifying the animal has two ventilatory patterns, "alert" and "quiescent". In the alert State, the animal ventilates both chambers achieving a high degree of oxygenation of both post and prebranchial hemolymph. The actual levels achieved depend on the ratio between ventilatory and locomotor activity (as discussed above). In largely native animals  $P_{\text{vo}_2}$  is high and hemocyanin bound oxygen capacity is kept as "venous reserve". In exercise,  $P_{\text{vo}_2}$  is high and

hemocyanin bound oxygen capacity is kept as "venous reserve". In exercise  $P_{vo}$  falls markedly and this venous reserve is utilized McMohan et al. (1979). In the quiescent state energy is conserved by unilateral pumping (accompanied by a mean 30% fall in oxygen consumption, McDonald 1977) both pre-and postbranchial oxygen tensions are depressed, and again, the hemocyanin works near maximal efficiency, conveying 80-90% of the oxygen delivered to the tissues. Similar utilization of the venous reserve also provides maintenance oxygen supply during pauses, where both heart and scaphognathite cease pumping for extended period McMohan and Wilkens, 1972, 1974; Talor et al. 1973; McDonlad 1977; and it is utilized during temporary air exposure of littoral crabs (Butler and Taylor, 1978, deFur and McMohan, 1978, Taylor and Wheatly 1980). During strenous activity, a decrease in prebranchial hymph PH (combined metabolic and respiratory acidosis) also contributes to efficient tissue oxygenation, as the Bohr effect allows near maximal oxygen release, while protectinig the hemolymph-to-tissued oxygen gradient.

Elevation of Oxygen uptake is thus clearly effected a number of factors including increased oxygen supply (increased  $V_w$ ), increased Oxygen transport away from the gills (increased  $V_b$ ) and by an increase in oxygen binding to hemocyanin, all acting to increase the gradient for  $O_2$  across the gills, at least in the crab, Cancer Magister and presumably in other circumstances, most, or all, of these factors are involved of differential degreee in response to increase in oxygen demand. Other factors such as increases in gill area effectively perfused or ventilated

remain possible but have not yet been demonstrated.

b. In Hypoxia. The extent of an animal's ability to regulate oxygen consumption is also affected by change in the environment, particularly where metabolic compensation to the environmental change is involved. Rutledge (1981) shows that the aerobic metabolic scope of Pacifastacus leniusculus rises with increase in temperature until 20°C. where it equals 117  $\mu\text{mol. O}_2 \text{ Kg}^{-1} \text{ min}^{-1}$ , an increase of tenfold over "standard" metabolism. The scope then decreases with further temperature increase, falling to 77  $\mu\text{mol O}_2 \text{ kg.}^{-1} \text{ min}^{-1}$ , or a threefold increase over "standard" levels at 30°C. Regulation of oxygen uptake in hypoxic water provides a convenient example. Contrary to previous reports (Wolfekamp and Waterman, 1960) the majority of, at least malacostracan, crustaceans have considerable ability to maintain routine or quiescent levels of oxygen consumption, in the face of considerable environmental oxygen depletion (Taylor and Butler, 1978). In hypoxic exposure, the animal responds to reduction in oxygen supply, rather than to an increase in oxygen demand, as in the activity response discussed above, but the responses are essentially similar, involving increased ventilation, perfusion, and reduction in  $P_{\text{vo}_2}$  with concomitant depletion of the venous reserve (Batterton and Cameron, 1978; Butler et al 1978; Burnett 1979, Mangum and Towle 1977; MacMahon and Wilkens, 1974, 1972; McMahon et al. 1978, A.C. Taylor 1976; E.W. Taylor et al, 1973, 1977 young, 1973). Similar constraints also apply, Maximal regulatory ability is exhibited by quiescent animals, well acclimated to their experimental conditions and neither disturbed nor



exposed to environmental stress. Minimal regulatory ability is shown by animals which are active, disturbed, fettered, or exposed to additional physiological or environmental stress. Mangum and van Winkle (1973) detailed the immense variability in regulatory ability among aquatic animals of a wide range of invertebrate groups. Within the Crustacea, some of the variability may be attributed to differing degrees of complexity of the respiratory apparatus and control systems (i.e. compare copepods with decapods); or with the degree of hypoxic exposure normally encountered in the habit (i.e. consider the remarkable abilities of *Gnathophausia ingens* from the oxygen minimum layer (Childress, 1971); or by differences in physiological, psychological, or activity state (i.e. compare *Homarus gammarus* as reported by Thomas, 1954, and by Butler et al. 1978). In experimental conditions, as in the natural environment, the extent of the animal's ability to manipulate oxygen uptake must vary with all of these factors.

Despite the regulatory abilities discussed above, the maximal aerobic capacity is insufficient to met the needs of protracted exercise, at least under experimental conditions. In several species of crayfish (Phillips et al 1977, B.R. McMahon and C.D. Hassall) unpublished results; P.S. 1977; B.R. McMahon and C.D. Hassall, unpublished results; P.S. Rutledge, 1981 and even at low temperatures, in the crab *Cancer magister* (McMahon et al, 1979) the animals resort to anaerobic metabolism, apparently mediated largely via a pathway involving lactic acid production. Whereas it is not possible to accurately quantify the

participation of aerobic and anaerobic systems, over 75% of the total oxygen consumption resulting from a 20 min period of sustained activity. Oxygen debt occurred after the exercise period i.e. in repayment of an oxygen debt (McMahon et al, 1979).

Although oxygen uptake systems are generally unable to supply sufficient oxygen for maximal activity (see Bennett, 1978), it may nonetheless be instructive to consider where the limitations on oxygen uptake occur in crustacean systems. Several theoretical limitations may occur. Scaphognathite pumping frequencies reach maximum levels early in enforced exercise in *Cancer magister* (McMahon et al 1979) and decrease at elevated temperatures in *Pacifastacus* (Rutledge, 1981). As the scaphognathite functions as fixed volume (Fig. 4), limitations in maximum ventilation volume, and hence oxygen supply to the gills, may occur. More likely the efficiency of oxygen uptake may be limited at high ventilation volumes, Randall (1970b) suggests that anatomical, distributional, and diffusion dead space all increase with elevation of ventilation volume in fish. These could also limit oxygen uptake efficiency in crustaceans. Probably limitation in oxygen uptake also occurs in the gills, themselves. Gill area seems adequate, being equal to or greater than that of fishes of equivalent weight, but crustacean gills contain a chitinous layer, which may comprise upto 80% of the diffusion path (Taylor and Butler, 1978). Since oxygen diffusion through chitin is apparently tenfold slower than through most other tissues (Krogh, 1919) this layer could certainly limit oxygen uptakes, especially at high transfer rates, interestingly, *Gnathophausia ingens*,

which must effect oxygen uptake from very low external tensions in the oxygen minimum layer, has gill of greater area, and with a substantially thinner cuticles, then those of most other crustaceans (Belman and Childress, 1976). Finally limitations might occur in the fill perfusion system. This could result from limitation in cardiac output, perhaps especially so in crustaceans where this parameter is already high due to low  $O_2$  capacity, or may arise from the low  $O_2$  capacity directly, by limitation of facilitated oxygen uptake across the gills. Probably a combination of all these factors plays a role, but arterial  $PO_2$  is reduced to some degree following activity in several crabs (Mangum and Weiland, 1975; McMahon et al 1979) and in crayfish species P.S. Rutledge, 1981), a factor that tends to support limitation in the delivery and diffusion, rather than perfusion, systems. Heart rate increases little (McMahon et al. 1979) or may even decrease (Herried et al. 1979) in many exercising crustaceans in interesting fact which might also be construed as arguing against a perfusion-limited system.

Although there is anatomical evidence for counter-current exchange between water and blood in at least brachyuran crustacean gills, physiological evidence for this (i.e. arterial oxygen tensions greater than those of expired water) is rarely observed (Johnsen et al 1970; McDonald, 1977) it is likely that countercurrent exchange is actually occurring throughout normal forward pumping, but is masked by the effects of a large dead space increase in ventilation volume in crustaceans (Johnsen et al. 1970) then this also may constitute a ventilation limitation of aerobic capacity.

## Material & Methods.

## MATERIALS & METHODS

After an equilibration period of 1 hour, Oxygen consumption of larval shrimp was measured by placing 25 individuals in transparent glass bottle containing the desired sea water culture medium. The ambient temperature in experimental containers vary between  $28 \pm 2^{\circ}\text{C}$  and salinity  $29 \pm 2\%$ . The larvae were fed on nauplii of Artemia Salina before being subjected to experimental set up. The observed vitality of the organisms (Experimented animals) suggests that the larvae tolerate confinements quite well. After 1 hour and 2 hours the respiration of the larvae was estimated from the difference in the oxygen content between the experimental bottle and controls. The duration of incubation and the duration (day) of development were taken into account. The Oxygen consumption rate from mysis I to postlarva PL were measured on a daily observation for oxygen consumption for 1 hour & 2 hours respectively. The quantum of total oxygen needed as the larval development cycle continues was monitored each time using 25 individuals in the bottle. The larval stock comprised from single brood. The data on salinity and temperature variation during experimentation on oxygen consumption was also monitored. For the measurement of oxygen consumption, the sample oxygen in glass bottle was fixed after a duration of 1 & 2 hours. Oxygen was determined by winklers methods (Hour & Hickman, 1967).

## 5. Results and Observation

OBSERVATIONS AND RESULTS

Table 1 indicate the individual oxygen demand during growth phase of larva mysis I to Postlarva. The oxygen requirement was analysed daily subjecting the 25 prawns larvae for 1 hour and 2 hours durations. The amount of oxygen consumption during mysis II was recorded to be 0.52. This value is low compared to mysis I and post larval stage (1.80). The requirement was found to be low during Mysis II Phase which increased during later developmental stages. Apart from the fact that the requirement of oxygen depends on the size of the individual animal, the weight, and physiological status of the individual too plays major role as far as the fluctuation in the oxygen requirement is concerned. Variation in oxygen consumption during different days of larval development was noted. The salinity and temperature variation were minimum, as short duration experimental trials were run. The data indicate that on an average the oxygen consumption during mysis I was 1.80 mg/ind. The requirement of oxygen was found to drop 0.52 during mysis II and then increases marginally as development advanced.

While comparing the above data and the oxygen consumption behaviour in other decapod crustaceans it was found that the oxygen consumption rate in penaeid prawn larvae are higher than similar larval stages of other decapod crustaceans. Comparative data on the oxygen consumption during different larval forms as recorded by earlier worker has been complied. Table 2 analysing the data, comprehensive picture emerge that the oxygen requirement of prawn mysis stages are higher than the megalopa larvae of crabs.

Table - NO-1

Oxygen uptake by the mysis stages to Postlarva PL2

Date	Stage	Time of Fixing C.Bottle (C)	After 1 hr. (A)	Two Hrs. (B)	C-A	C-B	A-B	Mean
27.4.96	Mysis(I)	8.80	8.00	6.20	0.80	2.60	1.80	1.80 ± 0.0
28.4.96	Mysis(I)	8.80	8.00	6.20	0.80	2.60	1.80	
29.4.96	Mysis II	7.04	5.44	5.32	1.60	1.72	0.12	0.52 ± 0.00
30.4.96	Mysis II	7.73	6.13	5.2	1.60	2.53	0.93	
01.05.96	Mysis III	8.40	6.86	5.86	1.54	2.54	1.00	1.00 ± 0
02.05.96	Mysis III 2nd day	8.40	6.60	5.60	1.80	2.80	1.00	
03.05.96	PL1	8.20	6.00	5.08	2.20	3.12	0.92	0.94 ± 0.02
04.05.96	PL II 2nd day	7.80	5.82	4.84	1.98	2.96	0.98	

c-A = consumption in 1st hour

C-B = Consumption in 2 hours

A-B = Consumption in next 1 hr.



TABLE - NUMBER - 2

Oxygen consumption of Decapod larvae of similar size larvel stages and present study

Organism	Stage	Temperature	Wet weight (ug)	Oxygen consumption (ui O <sub>2</sub> /mg/hr	Reference
<u>Cancer irroratus</u>	III	25	--	0.3D	2.
<u>Uca Rapax</u>	M	25	326	1.18	1.
<u>U. pugilator N.C.</u>	M	25	360	1.21	1.
<u>U. pugilator Mass</u>	M	25	468	1.16	1.
<u>Euthusa mascorone</u>	Z	15	500	2.32 D *	3.
<u>C. borealis</u>	M	25	-	0.4D	2.
<u>C. irroratus</u>	M	25	-	0.18D	2.
<u>Emerita talpoida</u>	VI	25	2310	0.98	4.
Present study					
P. monodon	Mysis	28	-	1.80 *	
P. monodon	Mysis	29	-	0.52	
P. Monodn	Mysis	28	-	1.00	
P. Mondon	PL	30	-	0.94	

\* Oxygen consumption expressed as mg of oxygen used /ind/hr.

\* Data corrected to 25°C. assuming a 10 of 2.  
M= Megalopa. Z=unidentified zoea

1. Sasthy & McCarthy (1973)
2. Vernberg & Costlow (1966)
3. Nival et al.
4. Frank C. Schjatzlen and John D. Costlow Jr.

TABLE - 10 - 3

## Pressure and Flows Recorded from the Open Circulatory Systems of Several Decapod Crustaceans

	n	Temp (°C)	Wt (g.)	Ventricular Pressure		Arterial pressure		Intrabranchial sinus pressure mean	Brachio- pericardial vein pressure mean	Pericardial cavity pressure mean
				Systolic	Diastolic	Systolic	Diastolic			
<u>Cancer antennation</u>	7	16	516	18 ± 2	3.7 ± 0.7	--	--	7.4 ± 1.0	--	--
<u>Cancer products</u>	6	16	379	10.4 ± 1.3	6 ± 1.0	--	--	7.2 ± 1.0	--	--
<u>Cancer magister</u>	10	12	346	--	--	--	--	--	--	1.5 - 3.0
	8	8	850	--	--	--	--	--	--	--
	8-10	8-10	--	--	--	--	--	--	--	6.3
	5	16	600	20.4 ± 3.5	7.6 ± 2.5	--	--	11.8 ± 2.5	--	--
<u>Loxorhynchus cripatus</u>	5	16	600	20.4 ± 3.5	7.6 ± 2.5	--	--	11.8 ± 2.5	--	--
<u>Pugettia producta</u>	6	16	151	19.2 ± 1.8	7.8 ± 1.1	--	--	10.3 ± 1.0	--	--
<u>Pachygrapsus crassipes</u>	7	17	21	26.3 ± 3	13.5 ± 1.8	--	--	16.3 ± 1.6	--	--
<u>Carcinus maenas</u>	8	20	8	10.3	0	9.2	6.3	3.0	1.08	0
<u>Callinassa californiensis</u>	9	15	50 ± 4	--	--	--	--	--	--	--
	4	15	10	6.1 ± 0.2	3.8 ± 0.2	--	--	--	--	--
	14	16-20	462	14	1.2	--	Mean = 11	4.7	--	--
	6	12-15	500	--	--	--	--	--	--	--
<u>Homarus americanus</u>	6	12-15	500	--	--	--	--	--	--	--
<u>Homarus vulgaris</u>	300	15	300	--	--	--	--	--	--	--
<u>Panulirus interruptus</u>	10	15	501	36 ± 2.1	16.1 ± 1.8	--	--	18.8 ± 1.5	--	17.9
<u>Parasiphaea sulcatitrons</u>	1	--	--	41	15	41	37	28	--	21
	1	--	--	--	--	--	--	12.5	11	--
	2	5	11	15.1	10.4	--	--	--	--	--
	15	5	10-17	18.1 ± 0.5	--	--	--	15.3 ± 0.6	--	--
<u>Cnathophausia ingens</u>	15	5	--	15.7	12.5	15.7	14.8	14.6	--	13.7

TABLE NQ-3

	Arterial flow/velocity	Cardiac output (ml/kg)	Heart frequency (bts/min)	Stroke Volume (ml/beat)	Hemolymph volume (% wet wt.)	Hemolymph convection requirement (liter/minol-O <sub>2</sub> )	H <sub>2</sub> O Convection requirement (liter/minol O <sub>2</sub> )	Source
<u>Cancer antennarius</u>	--	--	114 ± 8	--	--	--	--	Belman (1976)
<u>Cancer productus</u>	--	--	150 ± 10	--	--	--	--	Belman (1976)
<u>Cancer magister</u>	--	103-275	94-100	1.9-2.8	--	5	9-22	McMahon and Wilkens (1977)
	--	92-170	66	1.5-2.6	--	3.7-2.8	13-14	McMohan et al. (1979)
<u>Loxorhynchus crispatus</u>	--	--	--	--	--	--	--	McDonald (1977)
	--	29.5	--	--	--	1.1	20.4	Johansen et al. (1970)
	--	--	--	--	30%	--	--	Alspach (1972)
	--	--	117 ± 8	--	--	--	--	Belman (1976)
	--	--	187 ± 14	--	--	--	--	Belman (1976)
<u>Pugettia producta</u>	--	--	133 ± 8	--	--	--	--	Belman (1976)
<u>Pachygrapsus crassipes</u>	--	--	108	--	--	--	--	Blatchford (1971)
<u>Carcinus maenas</u>	--	118	92 ± 5	1.3	--	--	--	Taylor and Butler (1978)
<u>Callinassa californiensis</u>	--	--	79	--	--	--	--	Belman (1976)
<u>Homarus americanus</u>	--	22-67	90	--	17%	--	--	Burcher and Smythe (1953)
<u>Homarus vulgaris</u>	--	--	92	--	--	--	15-22	McMahon and Wilkens (1975)
	--	43	33 ± 2	1.3	--	8.3	13.7	McMahon et al. (1978a)
	9.7 cm/sec	128 (A)	64 ± 3	1.4	33	--	--	Belman (1976)
<u>Panulirus interruptus</u>	--	148 (F)	60	--	--	--	--	Belman (1975)
<u>Parapapiphea sulcatifrons</u>	--	--	60	--	--	--	--	Belman (1975)
	--	--	83	--	--	--	--	Belman (1976)

TABLE NO-4

Oxygen Uptake, and Hemolymph Oxygen, Carbon Dioxide, and pH Levels in Aquatic Crustaceans, at Several Levels of Activity

Species	Activity State	Temp (°C)	P <sub>at</sub>	V <sub>a</sub> (ml/kg/min)	%Ext <sub>a</sub>	M <sub>12</sub> (umol/kg/min)	f <sub>te</sub> (bts/min)	f <sub>ti</sub> (bts/min)	P <sub>ao2</sub> (torr)	P <sub>co2</sub> (torr)	C <sub>ao2</sub> (mmol/liter)	C <sub>co2</sub> (mmol/liter)	pH <sub>a</sub>	pH <sub>i</sub>	P <sub>co2</sub> (torr) (+ = calc.)	P <sub>co2</sub> (torr)
<b>Brachyura</b>																
<u>Cancer magister</u>	Quiescent	8	141	135 ± 42	50 ± 8	16 ± 4	49 ± 17	50 ± 8	32 ± 6*	7 ± 2	-	-	-	-	-	-
	unilateral															
	Quiescent	8	129-141	288 ± 69	34 ± 7	25 ± 7	52 ± 16	58 ± 9	96 ± 12 (81 ± 14)*	15 ± 5	0.45	0.18	7.969	7.938	1.7 ± 0.3	-
	bilateral															
Strenuous activity	Strenuous	8	129-141	810 ± 40	61 ± 19	61 ± 19	151 ± 5	69 ± 4	45 ± 5	10 ± 5	0.42	0.06	7.512	7.493	3.2 ± 0.9	-
	Distributed	8-10	132	622	16	23	-	-	91	21	1.52	0.8	-	-	-	-
	Quiescent	10	135-140	158 ± 73	-	-	37 ± 2	33 ± 3	51 ± 6	13 ± 4	0.28 ± 0.03	0.05 ± 0.01	7.839 ± 0.02	7.901 ± 0.06	2.4 ± 0.16	21 ± 3
	Macrura															
<u>Homarus americanus</u>	Quiescent	12	100-150	487	23	22	101	92	69	18	-	-	-	-	-	-
	fettered															
	bilateral															
	Quiescent	15	130-135	233 ± 39	41 ± 7	17 ± 1	-	33	49 ± 13	-	0.41	-	7.800	7.704	2.0 ± 0.1 + *	2.5 ± 0.2 + *
<u>Homarus gammarus</u> <u>Procambarus clarkii</u>	bilateral															
	Quiescent	10	140	-	43	-	31 ± 7	21 ± 3	87 ± 3	59 ± 3	0.86 ± 0.09	0.48 ± 0.04	8.10 ± 0.017	8.17 ± 0.03	2.9 ± 0.21	2.3 ± 0.1
	mostly															
	bilateral															
Strenuous activity	Strenuous	10	140	-	22	-	172 ± 17	43 ± 2	62 ± 5	9 ± 2	0.48 ± 0.10	0.31 ± 0.03	7.530 ± 0.033	7.656 ± 0.03	12.3 ± 1.1	5.7 ± 1.1

## 6. Discussion

## DISCUSSION

In penaeid prawns oxygen consumption during early stages of larval development was analysed as a function of larval age, Gonsalves et al (1977), recorded oxygen uptake as a function of body weight (W) and he evaluated oxygen consumption using following equation.

$VO_2 = KW^b$  in its logarithmic form.

$\text{Log } VO_2 = \text{Log } K - b \log W$ . Using the method of least squares it was possible to calculate the parameters K and b. Further the whole oxygen consumption from body, lungs/gills etc. can be evaluated by the equation.

$$VO_2 \text{ (ml/hr)} = 0.120 W^{0.782}$$

The relationship between body size, oxygen consumption, metabolic rate has been an object of remarkable interest, many reviews have tried to explain the nature of the reduced exponent b. (Gonsalves and Sawaya; 1977) have documented that in submerged animals the relationship between  $O_2$  uptake and body weight is a function of surface area.

Schatzlein and Costlow; (1977) have documented decrease in oxygen consumption relative to molting phase in the larval cycle. However their study on oxygen consumption in relation to temperature variation from 15 - 25°C was recorded with relative increase in oxygen consumption volumes.

Metabolic rates are difficult to compare due to the profound influence of size, nutritional state activity, age, habitat, season, and culture conditions. At lower oxygen tensions the respiration of most decapods becomes dependant on the oxygen content of the environment Zenthen, (1955); Winget (1969); Belmen and Childress (1973); Jawed, (1973), The relationship between size and oxygen consumption of invertebrates has been reviewed and summarized by Zenthen 1947, 1955; Newell (1970), Verberg and Vernberg (1973). Even the variation in metabolic rate were recorded to vary in decapod crustaceans. When the animal's neuroendocrine mechanism was affected through eye stalk ablation, Teyan et al, (1959); Passano, (1961); Thornborough and Mengebier, (1967); Kleinholz (1976).

During present experimentation the fluctuation of oxygen consumption rate is prominent. No gradual increase in oxygen consumption was found as larval development progressed, Contrary, a drop in oxygen consumption was recorded. The probable explanation to the fact that, the oxygen consumption rate was dropped during mysis II indicate that the oxygen requirement during transition from mysis I to II decreases because of moult behaviour, or channelization of energy requirement to other target organs. Similar observation were also documented by Marais (1976). The routine oxygen consumption is defined as the oxygen consumption of individual larval whose movements are spontaneous. (Beamish & Mookherji 1964) (Beamish and Mookherji 1964), and Fry and Hochaka (1970) indicated that routine oxygen consumption embraced all values which lie between standard and active metabolism Job (1955) mentioned

that routine oxygen consumption is nearly 50% of active metabolism  
Winberg 1956 regarded twice the routine metabolism level as an  
approximate estimate of metabolic rate of fish under natural conditions.



22 Summary.

## S U M M A R Y

The metabolic rate of an individual measured by oxygen consumption or ammonia excretion, varies directly with temperature and inversely proportional with individual weight. In general the rate of larval oxygen consumption are used as an additional index of the influence of the environment on development. During the course of present dissertation an attempt is made to measure oxygen consumption rate during larval growth phase mysis I to post larva PL 2. The variation recorded during the investigations suggest that the oxygen requirement is  $1.80 \text{ mg/O}_2/\text{ind.hr.}$  in mysis I and the oxygen requirement increases gradually during the development phase. However, once the animal settles for a benthic habitat, the oxygen requirement decreases. The variation in the total oxygen requirement also depend on the environmental factors, larval growth phase and individual length and weight of the animal.

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