Daan, N. and Ringelberg, J. (1969). Further studies of the positive and negative phototactic reactions of *Daphnia magna* Straus. *Neth. J. Zool.* **19**: 525—540.

Dartnall. H. J. A. (1974). Assessing the fitness of visual pigments for their photic environments. In: Ali, M. A. (ed.) *Vision in Fish.* Plenum Press, New York, p. 543—563.

Douglass, J. K. (1986). The ontogeny of light and dark adaptation in the compound eyes of grass shrimp, *Palaemonetes pugio* Holthuis. Ph.D. thesis, Duke University.

Ewald, W. F. (1910). Uber Orientierung Lokomotion und Licht-reaktionen einiger Cladoceren und deren Bedeutung fur die Theorie der Tropismen. *Biol. Zbl.* **30**: 1—16; 49—63; 379—384; 385—399.

Forward, R. B., Jr. (1976). Light and diurnal vertical migration: photobehavior and photophysiology of plankton. In: Smith, K. (ed.), *Photochemical and Photobiological Review*, Vol. 1. Plenum Press, New York, p. 157—209.

Forward, R. B., Jr. (1986). A comparative study of crustacean larval photoresponses (in press).

Forward, R. B., Jr., Cronin, T. W. (1979). Spectral sensitivity of larvae from intertidal crustaceans. *J. Comp. Physiol.* **133A**: 311—315.

Forward, R. B., Jr., Cronin, T. W., Stearns, D. E. (1984). Control of diel vertical migration: Photoresponses of a larval crustacean. *Limnol. Oceanogr.* **29**: 146—154.

Jerlov, N. G. (1968). *Optical Oceanography.* Elsevier, Amsterdam, p. 1—194.

Lang, W. H., Forward, R. B., Jr., Miller, D. C. (1979). Behavioral responses of *Balanus improvisus* nauplii to light intensity and spectrum. *Biol. Bull.* **157**: 166—181.

Lythgoe, J. N. (1966). Visual pigments and underwater vision. In: Bainbridge, R. Evans, G. C. Rackham, O. (eds.) *Light as an Ecological Factor.* Oxford: Blackwell, p. 375—391.

Lythgoe, J. N. 1968. Visual pigments and visual range underwater. *Vision Res.* **8**: 997—1012.

McFarland, W. N., Munz, F. W. (1975). The evolution of photopic visual pigments in fish. *Vision Res.* **15**: 1071—1080.

Munz, F. W. (1958). The photosensitive retinal pigments of fish from relatively turbid coastal waters. *J. gen. Physiol.* **42**: 445—459.

Munz, F. W., McFarland, W. N. (1973). The significance of spectral position in the rhodopsins of tropical marine fishes. *Vision Res.* **13**: 1829—1874.

Ringelberg, J. (1964). The positively phototactic reaction of *Daphnia magna* Straus: a contribution to the understanding of diurnal vertical migration. *Neth. J. Sea. Res.* **2**: 319—406.

Ritz, D. A. (1972). Behavioral response to light of the newly hatched Phyllosoma larvae of *Panulirus longipes cygnus* George (Crustacea: Decapoda: Palinuridae). *J. exp. mar. Biol. Ecol.* **10**: 105—114.

Rose, M. (1925). Contribution à l'étude de la biologie du plankton: le problème des migrations verticales journalières. *Arch. Zool. exp. Gen.* **64**: 387—542.

Rozenberg, G. V. (1966). *Twilight — A study in atmospheric optics.* Plenum Press, New York.

Russell, F. S. (1927). The vertical distribution of plankton in the sea. *Biol. Revs. Biol. Proc. Cambridge Phil. Soc.* **2**: 213—262.

Shanks, A. L. (1986). Vertical migration and cross-shelf dispersal of larval *Cancer* spp. and *Randallia ornata* (Crustacea, Brachyura) off the coast of southern California. *Mar. Biol.* (in press).

Visscher, J. P., Luce, R. H. (1928). Reactions of cyprid larvae of barnacles to light with special reference to spectral color. *Biol. Bull.* **54**: 336—350.

White, G. M. (1924). Reactions of larvae of the shrimp *Palaemonetes vulgaris* and the squid *Loligo pealii* to monochromatic light. *Biol. Bull.* **47**: 265—272.

Vlaams Instituut voor de Zee
Flanders Marine Institute

RESPIRATION DURING HYPOXIA OF THE SHRIMPS CRANGON CRANGON AND PALAEMON ADSPERSUS FROM BRACKISH WATER

L. Hagerman[1], A. Szaniawska[2]

[1] Marine Biological Laboratory, Strandpromenaden. DK-3000 Helsingor, Denmark
[2] Instytut Oceanografii, Uniwersytet Gdański, al. Czołgistów 46, 81-378 Gdynia, Poland

ABSTRACT

The respiration of *Crangon crangon* and *Palaemon adspersus* was measured under normoxic and hypoxic conditions. All experiments were run for at least 24 hours (S, 20‰; T, 20°C).

In normoxia *Crangon* shows a clear diel respiratory pattern: highest respiration during early night and early morning, lowest in daytime. This respiratory rhythm can be correlated to the diel activity pattern. The respiratory rhythmicity disappears when oxygen tension decreases below ca 100 torr due to an increase in the average activity of *Crangon* (a response to avoid the hypoxic conditions). *Crangon* can maintain its routine respiration independent of oxygen tension in the medium (P_wO_2) down to a P_wO_2 of 30 torr, the so-called P_c. The typical diel mean routine respiratory level for intermoult *Crangon* (w.w. 0.25 and 1.1 g) are 0.9 and 0.2 ml $O_2 g^{-1} h^{-1}$ respectively when sand is supplied as substrate and 1.6 and 0.65 ml $O_2 g^{-1} h^{-1}$ when no substrate is supplied. Moulting has not been noted during the hypoxia respiration experiments.

Palaemon adspersus shows no diel respiratory rhythmicity under the given experimental conditions, possibly a result of a "wrong" substrate in the experimental chamber. *Palaemon* can maintain its respiratory independency down to a P_wO_2 of 45 torr. Typically *Palaemon* with a wet weight of for instance 0.7; 1.0 and 2.1 g has a respiration of 0.65; 0.41 and 0.13 ml $O_2 g^{-1} h^{-1}$ respectively.

The results are discussed in relation to the ecology of the species and specially in relation to hypoxic conditions increasingly occurring in shallow eutrophicated waters.

INTRODUCTION

The increasingly eutrophicated brackish water areas are the habitat of a shrimp stock, which is important from both an ecological as well as an economic viewpoint. In Danish waters both *Crangon crangon* and *Palaemon adspersus* are locally subject to an intense fishery. One consequence of eutrophication is impaired oxygen conditions in the shallow water, resulting in shorter or longer periods of low oxygen concentrations. Most of these periods occur in the summertime (Miljøstyrelsen, 1984) when due to high water temperature the solubility of oxygen is already lowered and the metabolic rate of

most organisms is higher. Since the metabolic rate of the animals is influenced and because species show different degrees of tolerance to changed oxygen conditions, such periods of lower oxygen conditions may change the balance of the whole ecosystem.

Our knowledge of the respiratory rate (MO_2) of brackish water animals is now reasonably good due to improved techniques and better understanding of the physiological processes in the organisms. However, most results published deal with short time experiments, i.e. von Oertzen (1984), Hagerman and Weber (1981), van Donk and de Wilde (1981) and only few e.g. Butler et al. (1978) record the MO_2 for extended periods. As the respiration is likely to vary with time it is important (i) to record MO_2 after the animal has recovered from handling and acclimated to the new environment and (ii) to record MO_2 long enough to reveal any rhythmicity. These precautions make it necessary to use a flow-through system for recording the MO_2. Such a system is, however, always better than a closed one (von Oertzen, 1984).

The purpose of the present paper is thus to record the MO_2 of *Crangon crangon* and *Palaemon adspersus* under normoxic and hypoxic conditions for at least diel periods.

MATERIAL AND METHODS

Crangon crangon and *Palaemon adspersus* were collected in August—September in the Rockilde–and Isefjord area, Northern Sealand, (S, 20‰; T, 15—20°C) on sandy *Zostera* covered bottoms at depths of 0.5—1.5 m by means of a small handoperated trawl. In the laboratory the shrimps were stored (S, 20‰; T, 20°C) for at least 3—4 days before experimentation. Mysids were provided as food.

Oxygen consumption measurements (MO_2) were performed in a flow through system. The shrimp was placed in a respiration chamber (8 cm long, 2.5 cm inner diam.) and sand or a piece of net was added as substrate. The oxygen tension of the water entering and leaving the chamber was monitored continuously by two Radiometer E 5047 electrodes connected to two Radiometer PHM 71b acid-base analysers and a Goerz Servogor 220 recorder. The thermostatted water was pumped via a Cole-Palmer peristaltic pump and tygon tubing was used. The flow through the chamber was adjusted to give a MO_2 of around 15% of the available oxygen, what normally meant a flow of 1.2—3.2 $ml \cdot min^{-1}$, depending on the size of the shrimp. Controls were run before and after each experiment with substrate in the chamber but without the animal. The shrimp was allowed to recover from handling and to get used to the respiration chamber for a couple of hours before the actual experiment started. A plastic sheet prevented the shrimp from receiving any visual stimuli from the surrounding. Each experiment was run, unless otherwise stated, for at least 24 hours. Lower, stable, P_wO_2 were obtained by blowing N_2 through the reservoir water.

RESULTS

Respiration (MO_2) and wet weight

The relations between routine MO_2 and wet weight for *Palaemon adspersus* (n = 16) and for *Crangon crangon* (n = 12) during day-time are shown in Fig. 1.
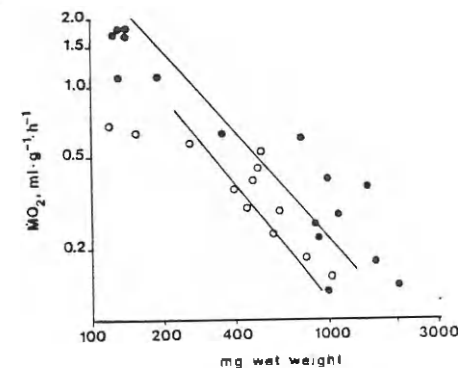

Fig. 1. *Crangon crangon* (o) and *Palaemon adspersus* (●). Routine oxygen consumption rate as a function of wet weight ($MO_2 = aW^b$) (log—log scale). S, 20‰; T, 20°C.

The general expression $MO_2 = aW^b$ relating respiration and weight was for *Crangon* $MO_2 = 0.19 \ W^{0.78}$ (r = 0.80) and for *Palaemon* $MO_2 = 0.28 \ W^{0.85}$ (r = 0.84). The coefficient b is well within the range of the general coefficient for all crustaceans (b = 0.81; Winberg, 1950). The constant a gives a species difference of 0.09 and this difference and the difference in b are responsible for the higher weight specific MO_2 for *Palaemon*. As is seen from Fig. 1 *Palaemon* had a MO_2 0.15—0.3 ml $O_2 g^{-1} h^{-1}$ higher than for *Crangon* of similar weight.

Diel normoxic MO_2

Palaemon showed very small diel deviations from the 24-hour mean MO_2 (Fig. 2) and thus no clear diel respiratory pattern was evident for this species. *Crangon*, on the other hand, (Fig. 2; 4 individual 24-h cycles chosen for each species, the rest showed the same pattern, n = 12 for *Palaemon*, n = 12 for *Crangon*) showed a clear diel respiratory rhytmicity where lowest MO_2 occurred during the day (September—October: 8 to 17 o'clock). This MO_2 was generally ca. 15% lower, in extreme cases 40% lower, than the 24 hour mean. The highest MO_2 was consequently found during night-time with values up to 30% higher than the corresponding 24 hour mean. The shrimps did moult occasionally during the normoxic experiments, increasing the MO_2 during the ecdysis with around 16%.
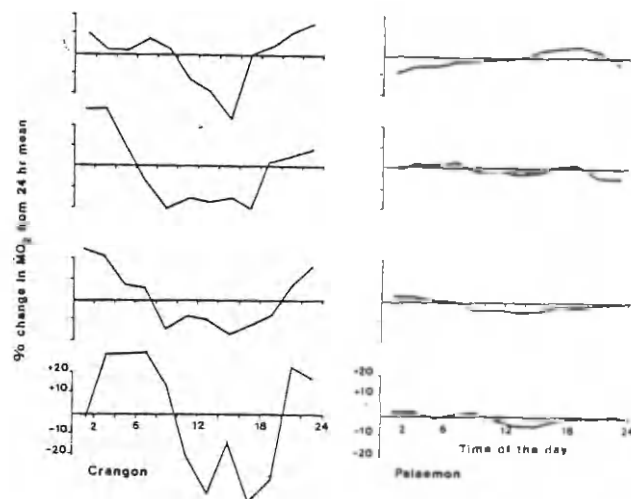
Fig. 2. *Crangon crangon* and *Palaemon adspersus*. Diel variations in MO_2 for four specimens of each species under normoxic conditions. MO_2 expressed as integrated percentage hourly deviations from the 24 hour mean. S, 20‰; T, 20°C.

Diel hypoxic MO_2

At a water oxygen saturation (P_wO_2) of less than 70%, the diel respiratory pattern of *Crangon* was disturbed and only minor deviations from the 24 hour mean occurred (Fig. 3). A covariance analysis also showed that the 24 hour mean in P_2O_2 70, 50, and 35% saturation was higher than the corresponding normoxic 24 hour mean MO_2 (p < 0.01). In P_wO_2 70% MO_2 increase was 10 to 50% (from for instance 0.25 to 0.37 ml $O_2g^{-1}h^{-1}$ for a *Crangon* of 0.56 g w.w.). In P_wO_2 50% the increase was between 20 to 90% (from for instance 0.26 to 0.49 ml $O_2g^{-1}h^{-1}$ for a *Crangon* of 0.47 g w.w.) and in P_wO_2 30 to 35% it was 16 to 50% of the 24 hour mean normoxic MO_2. This MO_2 change corresponds to the change found earlier when *Crangon* changes its activity level from routine to swimming (Hagerman and Szaniawska, 1986). Under hypoxic conditions longer than 24 hours (up to 72 hours) MO_2 remained at the same level as during the first diel period. Moulting did not occur during the hypoxia experiments.

MO_2 under hypoxia (definition of the P_c)

The possibility to maintain MO_2 independent of P_wO_2 was tested in a series of short-term experiments where the P_wO_2 was lowered 5—10% per hour. The percentage change from the normoxic MO_2 for the two shrimp species are shown in Fig. 4. Both *Crangon* and *Palaemon* showed a considerable ability to control their respiration irrespective of the P_wO_2, *Crangon* down to a P_wO_2 of
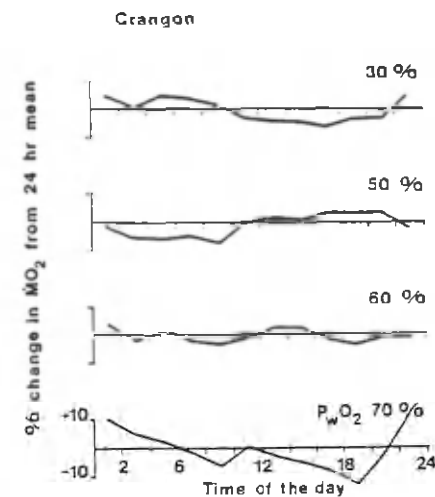
Fig. 3. *Crangon crangon*. Examples of diel variations in MO_2 under hypoxic conditions (% saturation). MO_2 expressed as integrated percentage hourly deviations from the 24 hour mean. S, 20‰; T, 20°C.
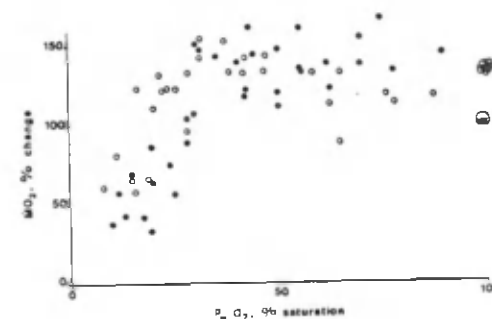

Fig. 4. *Crangon crangon* (o) and *Palaemon adspersus* (●). Relative changes in routine MO_2 with decreasing oxygen tension of the water. The big half-filled dot at P_wO_2 100% indicates the relative MO_2 for settled animals. S, 20‰; T, 20°C.

20%, *Palaemon* down to a P_wO_2 of 30%. This ability seemed independent of size, even if, of course, the MO_2 varied according to the size of the individual. Both *Crangon* and *Palaemon* showed an increase in MO_2 when P_wO_2 decreased from normoxia.

In Fig. 4 this increase is not so evident, because in these short-term experiments the specimens were not allowed to settle down long enough in the respiration chamber. Settled animals have a respiration ca. 25—30% lower than non-settled animals (Hagerman and Szaniawska, 1986). Thus the starting point in Fig. 4 at P_wO_2 100% should be placed lower for settled animals which would make the hypoxia MO_2 increase evident.

This increase occurred for Palaemon in the P_wO_2 80—30%, for *Crangon* in the P_wO_2 50—30%. For *Crangon* this P_wO_2 corresponds to the emersion response (Hagerman and Szaniawska, 1986) and for *Palaemon* to the range where an increased locomotory activity has been noted (Hagerman and Weber, 1981; von Oertzen, 1979).

DISCUSSION

In the present work it was found that *Palaemon adspersus* always had a higher MO_2 than similar sized *Crangon crangon*. In nature both species are subjected to roughly similar variations in the environmental conditions (S, T, O), but inhabit different biotopes. The burying *Crangon* always is associated with sandy bottoms while *Palaemon* inhabits algae and plants and thus does not have the ability to bury in a substrate. Bridges and Brand (1980) noted generally lower MO_2 in burrowing crustaceans compared to non-burrowing species. This is probably also valid for other groups, for instance de Wilde (1973) found reduced MO_2 in the buried bivalve *Macoma* compared to epifaunal bivalves. Reduction in MO_2 has also been noted intraspecific in buried compared to non-buried horseshoe crabs (Johansen and Petersen, 1975) and in buried/non-buried *Nephrops norvegicus* (Hagerman and Uglow, 1985) and recently in *Mesidothea entomon* (Hagerman and Szaniawska, in prep.).

A typical routine respiratory level for intermoult *Crangon* (w.w. 0.25 and 1.1 g) under normoxic conditions are 0.9 and 0.2 ml $O_2g^{-1}h^{-1}$ in the present investigation. Earlier work on the respiratory rates of *Crangon* has shown values slightly higher than those found here (Hagerman, 1970) or in the same range (van Donk and de Wilde, 1981). The differences are often caused by the different techniques used, for instance Hagerman (1970) used a closed respiratory system and the experiments were short-term (a couple of hours) where handling and other types of stress caused a respiration higher than that showed by an animal adapted to a long term experiment, preferably not less than 24 hours. It has been shown also by von Oertzen (1975) and by Kristensen (1983) that the MO_2 for *Gammarus* and and for *Nereis* were much higher in short--term than in long-term experiments. In this connection the necessity of a correct substratum must be stressed if a reliable value of MO_2 is to be obtained. If *Crangon* has no suitable substrate, in nature corresponding to displacement to a rocky or hard substrate, the diel locomotory rhythmicity breaks down (Hagerman, 1970) and the respiratory rate increases to 1.6 and 0.65 ml O_2 $g^{-1}h^{-1}$ for the specimens mentioned above. Regnault and Lagardère (1983) observed that an increased noise level (compared to the background noise always prevailing at sea) increased the metabolic rate in *Crangon* when measured both as ammonia excretion and as oxygen consumption. A common response to all kinds of disturbancies is certainly a modification of the activity level and rhythmicity resulting in an increased MO_2.

Typical routine MO_2 for *Palaemon adspersus* in the present investigation were (wet weight 0.7, 1.0 and 2.1 g) 0.65, 0.41 and 0.13 ml $O_2g^{-1}h^{-1}$ under normoxic conditions. These values can be compared to earlier findings of MO_2 of 0.15 for an individual of 2.5 g wet weight (Hagerman and Weber, 1981) and 1.35 µl $O_2gDW^{-1}h^{-1}$ as found by von Oertzen (1984) under similar environmental conditions.

In *Crangon* the diel normoxic MO_2 can be correlated to the diel locomotory pattern (Hagerman, 1970), i.e. MO_2 shows peaks during the same diel periods as *Crangon* is active. *Crangon* is a voracious predator, feeding mainly just after dawn and before dusk (Pihl and Rosenberg, 1984). The locomotory activity of *Crangon* is mainly influenced by exogenous factors (Hagerman, 1970) and as the metabolic cost of swimming is low (Hagerman and Szaniawska, 1986) the noted respiratory rhythmicity is probably endogenous in origin, reflecting digestive and endocrine processes in the animal.

For *Palaemon adspersus* the absence of a pronounced diel rhythmicity will, despite a nocturnal locomotory activity (Hagerman and Østrup, 1980) reflect endogenous processes at, however, a higher rate that in *Crangon*. The latter can in the respiration chamber bury in the sand, while *Palaemon* always will be more exposed to external stimuli and thus keeps its metabolic state at a more vigilant level. Smit (1965) noted in goldfish an increased MO_2 that was not reflected in activity changes and Halcrow and Boyd (1967) showed that excited, but not moving, *Gammarus* had a higher MO_2. In addition measurements of heart rate has shown a large excitement dependent variability (Dyer and Uglow, 1978) in shrimps and crabs and these authors also showed that heart and ventilatory rates, and thus MO_2, decreased when specimens buried.

It is now generally accepted that most crustaceans that in nature might be exposed to variation in external P_wO_2 have developed an ability to maintain respiratory independence during hypoxia. Such an ability is also found in some molluscs where Taylor and Brand (1975) found an increase in the ability of bivalves to maintain oxygen independence with increasing size during hypoxia. Famme and Kofoed (1980) noted that the MO_2 of *Mytilus* to a certain extent was independent of the P_wO_2.

The P_wO_2 where oxygen consumption independence no longer can be maintained is usually defined as the so-called P_c (Newell, 1979; Herreid, 1980). In the present investigation the MO_2 of *Palaemon* and *Crangon* rose during progressive hypoxia, specially when a P_wO_2 of ca 45—60 torr was reached. This is interpreted as an increase in the activity when the animal perceives and/or reacts to the decreasing P_wO_2 around 75—60 torr. Below this the MO_2 is still high due to the stress caused by the still decreasing P_wO_2. The P_c, as defined above, is for *Crangon* obviously at a very low P_wO_2 (ca 30 torr). However, this point reflects only the P_wO_2 where oxygen independence can no longer be maintained, i.e. where the active MO_2 is decreasing. Oxygen supply to the tissues for routine/basal metabolism is still adequate and the P_c is in this sense thus not critical as the animal can sustain these conditions for extended pe-

riods. However, when the oxygen supply for the basic metabolic needs is distur-bed, i.e. when anaerobic metabolism is initiated, a real critical point ($,,P_{lactate}$") is reached. This level is ca 15 torr in *Crangon* (Hagerman and Szaniawska, 1986) where, as a result of anaerobiosis, lactate is beginning to accumulate. In *Crangon*, a species shown to be tolerant to hypoxia, the traditional P_c and the point where anaerobic metabolism accelerates, are very close to each other but there is an evident difference in the level of $\dot{M}O_2$. However, under inappropria-te experimental conditions or with disturbed animals the traditional P_c will certainly move upwards (Herreid, 1979; Butler et al., 1978; Dall, 1986). Analo-gically to this the P_wO_2 for the traditional P_c in *Palaemon* was ca.45 torr while the level where an anaerobic metabolism was found to increase was 30 torr. Both values are higher than for *Crangon* but well in agreement with the ecology of the species.

REFERENCES

Bridges, C. R., Brand, A. R. (1980). The effect of hypoxia on oxygen consumption and blood lactate levels of some marine crustacea. *Comp. Biochem. Physiol.* **65A**: 399—409.

Butler, P. J., Taylor, E. W., McMahon, B. R. (1978). Respiratory and circulatory changes in the lobster (*Homarus vulgaris*) during long term exposure to moderate hypoxia. *J. exp. Biol.* **73**: 131—146.

Dall, W. (1986). Estimation of routine metabolic rate in a penaeid prawn, *Penaeus esculentus* Haswell. *J. exp. mar. Biol. Ecol.* **86**: 57—74.

Donk, E. van, Wilde, P. A. W. J., de (1981). Oxygen consumption and motile activity of the brown shrimp *Crangon crangon* related to temperature and body size. *Neth. J. Sea Res.* **15**: 54—64.

Dyer, M. F., Uglow, R. F. (1978). Heart and scaphognathite beat behaviour in laboratory-held *Crangon crangon* (L.). *J. exp. mar. Biol. Ecol.* **32**: 209—218.

Famme, P., Kofoed, L. H. (1980). The ventilatory current and ctenidial function related to oxygen uptake in declining oxygen tension by the mussel *Mytilus edulis*. L. *Comp. Biochem. Physiol.* **66A**: 161—171.

Hagerman, L. (1970). Locomotory activity patterns of *Crangon vulgaris* (Fabr.) (Crustacea, Nata-ntia). *Ophelia* **8**: 255—266.

Hagerman, L., Østrup, J. (1980). Seasonal and diel activity variations in the shrimp *Palaemon adspersus* Rathke from a brackish, non-tidal area. *Mar. Ecol. Prog. Ser.* **2**: 329—335.

Hagerman, L., Weber, R. (1981). Respiratory rate, hemolymph oxygen tension and hemocyanin levels in the shrimp *Palaemon adspersus* Rathke. *J. exp. mar. Biol. Ecol.* **54**: 13—20.

Hagerman, L., Uglow, R. F. (1985). Effects of hypoxia on the respiratory and circulatory regula-tion of *Nephrops norvegicus*. *Mar. Biol.* **87**: 273—278.

Hagerman, L., Szaniawska, A. (1986). Behaviour, tolerance and anaerobic metabolism under hypoxia in the brackish water shrimp *Crangon crangon* L. *Mar. Ecol. Prog. Ser.*, **34**: 125—132.

Halcrow, K. R., Boyd, C. M. (1967). The oxygen consumption and swimming activity of the amphi-pod *Gammarus oceanicus* at different temperatures. *Comp. Biochem. Physiol.* **23A**: 233—242.

Herreid, C. F. (1980). Hypoxia in invertebrates. *Comp. Biochem. Physiol.* **67A**: 311—320.

Johansen, K., Petersen, J. A. (1975). Respiratory adaptations in *Limulus polyphemus*. In: Vern-berg (ed.). *Ecophysiology of estuarine organisms*. Univ. South Carolina Press, Columbia. p. 129—145.

Kristensen, E. (1983). Ventilation and oxygen uptake by three species of *Nereis* (Annelida: Poly-chaeta). I. Effect of hypoxia. *Mar. Ecol. Prog. Ser.* **12**: 289—297.

Miljøstyrelsen, (1984). *Iltsvind og fiskedød i 1981. Omfang og årsager*. Copenhagen, Ministry of Environmental Protection.

Newell, R. C. (1979). Biology of intertidal animals. *Marine Ecological Surveys* Ltd, Faversham.

Oertzen, J.-A. von (1975). Long-term continous respiration measurements as a precaution for the assessment of secondary production. *Merentutk. Julk. Havsf. Skr.* **239**: 213—221.

Oertzen, J.-A. von (1979). *Versuch einer kausalökologischen Leistungsanalyse an brackwasserleben-den Tieren. Thesis*, 188 pp., Wilhelm-Pieck-Universität Rostock.

Oertzen, J.-A. von (1984a). Influence of steady-state and fluctuating salinities on the oxygen consumption and activity of some brackish water shrimps and fishes. *J. exp. mar. Biol. Ecol.* **80**: 29—46.

Oertzen, J.-A. von (1984b). Open and closed system — their suitability for functional respiration measurements. *Limnologica* (Berlin) **15**: 541—545.

Pihl, L., Rosenberg, R. (1984). Food selection and consumption of the shrimp *Crangon crangon* in some shallow marine areas in western Sweden. *Mar. Ecol. Prog. Ser.* **15**: 159—168.

Regnault, M., Lagardière, J.-P. (1983). Effects of ambient noise on the metabolic level of *Crangon crangon*. *Mar. Ecol. Prog. Ser.* **15**: 159—168.

Smit, H. (1965). Some experiments on the oxygen consumption of goldfish (*Carassius* L.) in relation to swimming speed. *Can. J. Zool.* **43**: 623—633.

Taylor, A. C., Brand, A. R. (1975). Effects of hypoxia and body size on the oxygen consumption of the bivalve *Arctica islandica* L. *J. exp. mar. Biol. Ecol.* **19**: 187—196.

Wilde, P. A. W. J. de (1973). A continuous flow apparatus for long term recording of oxygen uptake in burrowing invertebrates. with some remarks on the uptake in *Macoma balthica*. *Neth. J. Sea Res.* **6**: 157—162.

Winberg, G. G. (1950). Metabolic intensity and crustacean size. *Z. Obshch. Biol.* **11**: 367—380.