THE EFFECT OF TEMPERATURE INCREASE ON THE BEHAVIOR OF ANTARCTIC FISH*

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Abstract: Along the gradual increase in the water temperature from 0° C to 10° C at a rate of 1° C/h, respiratory and behavioral alterations were observed in the Antarctic Notothenidae fish *Trematomus bernacchii*, Notothenia neglecta and Notothenia rossii marmorata. The main reaction of N. neglecta was a gradual increase in the respiratory frequency; N. rossii marmorata and T. bernacchii presented both a manifestive temperature of 4.5° C, N. rossii marmorata being the most affected according to the behavior observed.

1. Introduction

Temperature is an environmental controlling factor (FRY, 1971; LOVE, 1970, 1980) which acts at molecular level influencing the rate of molecular activation and the metabolic rate. There are many effects of temperature on animals. Through their sense organs fish may distinguish not only very small thermal variations (BULL, 1936) but also an increase from a decrease in the environmental temperature. Depending on the previous thermal story of the fish (SULLIVAN, 1954; FRY, 1964), many behavioral and physiological reactions of the individuals can be observed within the zone of resistance as well as the effects of the stress imposed upon them. At the lethal temperature, the animal becomes visibly incapacitated. According to WOHLSCHLAG (1964) death comes at 5°C or a little above for Antarctic fishes.

Temperature is usually correlated to standard metabolism and activity (BRETT, 1964; FRY and HART, 1948; RANDALL, 1970). Since the changes in the temperature impose a certain level of instability, the living system counteracts by the way of energy-yielding reactions measured through the respiratory frequency. This causes continuous behavioral changes along the temperature increase.

Through the analysis of behavioral changes it was possible to detect the impact of evironmental factors upon some subtropical fish species (FANTA-FEOFILOFF, 1983; FANTA-FEOFILOFF *et al.*, 1983, 1985). In this way, changes in locomotion, cleaning, welfare and other kinds of behavior, as responses to the changes in temperature, were

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correlated to the stress developed in different fish species.

Antarctic fish normally live in a very narrow range of thermal changes. The effect of temperature lowering on its physiology and freezing resistance was studied mainly by DEVRIES (1971), DEVRIES and EASTMEN (1981), SOMERO and DEVRIES (1967) and WOHLSCHLAG (1957, 1964). On the other hand, only a few data on the behavior of Antarctic fish (mainly activity) at normal water conditions are available (MONTGOMERY and MCDONALD, 1984; JOHNSTON, 1985; TWELVES, 1972: BURCHETT *et al.*, 1983) and only sparse information is found on the resistance to temperature increase.

In the present paper a study of thermal stress imposed by gradual temperature increase was carried out with the aim to analyze the extent of the evolutionary adaptation of Antarctic fish to cold temperature. It was considered that all fish have evolved to carry out physiological functions with maximal efficiency, even in extreme environmental conditions. Along the evolution, to be more or less stenothermal may signify bigger chances of survival of the species.

2. Materials and Methods

Three species of the Notothenidae (Pisces, Teleostei) were studied: Notothenia neglecta, Notothenia rossii marmorata, and Trematomus bernacchii. The animals were caught off the Admiralty Bay (King George Island, South Shetlands) during the summer 1984/85, with bottom gillnets (ROSMAN, 1980), at 40 m depth and transported alive to the Brazilian Antarctic Station Comandante Ferraz. The standard length of all animals was selected to be around 30 cm.

After being kept in a round tank $(1.20 \text{ m}\phi)$ with continuous water flow at 0°C to 1°C water temperature, the fish were placed individually in an experimental chamber (see LUCCHIARI *et al.*, 1984) with water maintained at constant levels of oxygen (air saturated) and temperature (0°C). Measurements and observations were first made at 0°C. After that, the temperature was raised at a constant rate of 1°C per hour with a circulation heating bath which surrounded the experimental chamber and was controlled by a thermostat. The temperature was measured by a sensor connected to a water monitoring unit which allowed simultaneous measurements of water pH, dissolved oxygen, salinity and temperature. The behavior was observed and described along the whole experiment by direct monitoring, the nomenclature of BAERENDS (1971) being used and adapted for the experimental conditions carried along this paper.

3. Results

All three species of fish remain relatively immotile at 0° C in the experimental chamber. If not disturbed, they produce swimming movements only every 5 or 6 hours, during the day, and every 2 or 3 hours during the night. Their color is usually dark, only becoming pale when the animals are subjected to any stressful conditions. In normal conditions, swimming to the surface and increased frequency of swimming periods were not observed. The eventual occurrence of welfare and cleaning movements are considered as normal behavior of the animals, but an increase in their frequency may be considered as a symptom. Alert and raising fins were observed only

in the presence of other fishes or if the animal is disturbed. Jumping and all behavioral features included in other symptoms (Figs. 1–3), were never observed in normal healthy animals, even when placed in the experimental chamber. The normal mean respiratory frequency value is always shown as the first point in the respiration curves (Figs. 1–3).

In N. neglecta (Fig. 1) a slight increase of the respiratory frequency observed from 0° C to 0.5° C was followed by a slight decrease up to 1.5° C and a continuous increase up to 10° C. Between 0° C and 2.5° C some behavioral aspects as alternation between swimming and resting, yawning and spitting as well as an alert posture can be observed. Above 2.5° C the animal keeps resting with a short interruption between 8 and 8.5° C, changing its color from dark to medium at 5.5° C. N. neglecta seems to be very resistant to temperature increase showing no point in which a signal of special thermal stress is observed, besides weak reactions at 2° , 5° and 8° C.

N. rossii marmorata seems to be much affected by the temperature (Fig. 2). At 4° C, a clear critical point, begins a decrease of the respiratory frequency after reaching a high peak, accompanied by many double respiratory movements, open mouth, body

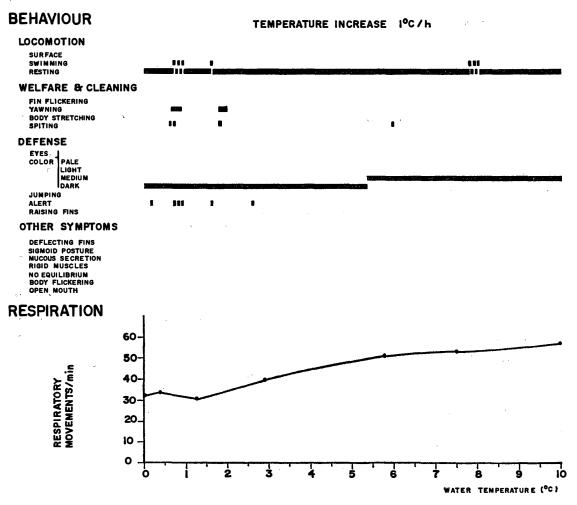


Fig. 1. Effect of the increase of the environmental water temperature at a rate of $1^{\circ}C/h$ from 0° to $10^{\circ}C$ on Notothenia neglecta. The observed behavior and the respiratory frequency were plotted along the whole experiment.

flickering, loss of equilibrium, raising fins, jumping and the increase of swimming activity. A short time after, the animal shows muscle stiffness, a sigmoid posture as well as short periods of body stretching and spitting. At 3.5° and 6.5° C the color changes from dark to medium and to pale respectively, when the respiratory movements increase to a second peak with periods of double respiratory movements. Above 7°C the respiratory frequency decreases to about the same level found at 0°C. For this species, 4.5° C and 7°C seem to be important temperatures for their physiological control mechanisms, a fact which is still under analysis in this laboratory.

In *T. bernacchii* (Fig. 3) exposed to a temperature increase the first symptom is a slight decrease in the respiratory frequency observed from 0° to 1° C, followed by a gradual increase up to 3.5° C, maintaining a constant level from this point up to 7° C. A continuous slow decrease was then observed from 7° to 10° C. From 0° to 10° C the color was constantly medium. Around 4.5° C body flickering and, later, open mouth and loss of equilibrium were observed. At 7.5° C the three symptoms are present again, accompanied by a decrease in the respiratory frequency. From 2.5° to 7° C, longer resting periods can be observed. For this species 4.5° and 8° C seem to be temperatures of physiological significance. At 4.5° C there is the occurrence of several symptoms, which are intensified at 8° C.

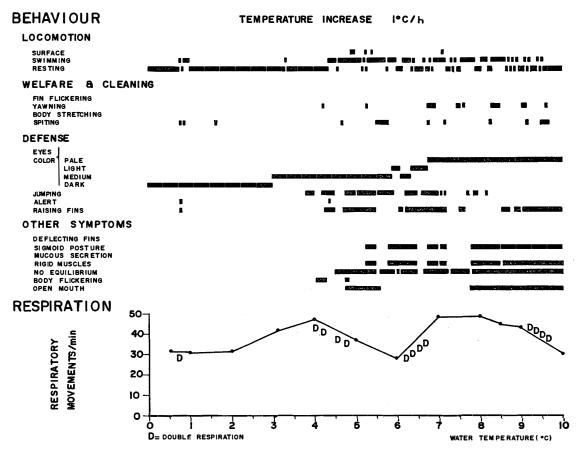


Fig. 2. Effect of the increase of the environmental water temperature at a rate of $1^{\circ}C/h$ from 0° to $10^{\circ}C$ on Notothenia rossii marmorata. The observed behavior and the respiratory frequency were plotted along the whole experiment.

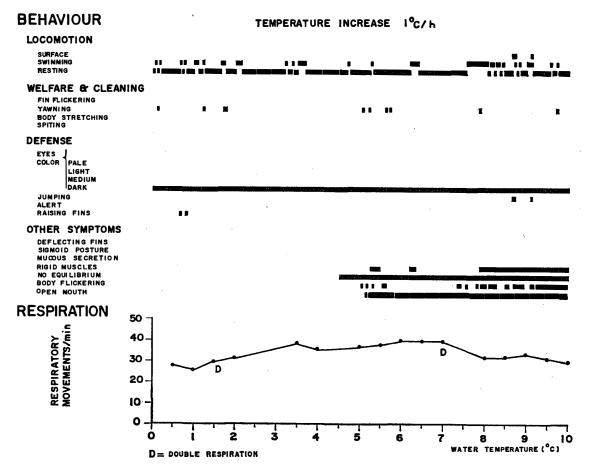


Fig. 3. Effect of the increase of the environmental water temperature at a rate of $1^{\circ}C/h$ from 0° to $10^{\circ}C$ on Trematomus bernacchii. The observed behavior and the respiratory frequency were plotted along the whole experiment.

The behavior observed in these acute tests allows to detect the first change in behavior caused by temperature increase (T_E) as 0.5° C for *N. neglecta*, 0.7° C for *N. rossi marmorata* and 1.0° C for *T. bernacchii*. The manifestive point with an accumulation of symptoms (T_M) lies at 4.5°C for *N. rossii marmorata* and *T. bernacchii*, but not so clear for *N. neglecta*. The temperature of death was not reached in these experiments. Furthermore, it is important to state that all animals recovered perfectly were when returned to the original temperature of 0° C.

4. Discussion

Consistent low temperatures are typical of the polar marine environment, so that the organisms endemic to the region must be physiologically adapted to such conditions, showing specific evolutionary trends.

N. neglecta and *N. rossii marmorata* are endemic species to the antarctic and subantarctic regions and *T. bernacchii* is a typical Antarctic fish (DeVRIES, 1971). They are adapted to temperatures from -1.98° C to $+1.5^{\circ}$ C. Antarctic species are considered as those which die between 10 and 20°C.

The central nervous system integrates incoming thermal information, compares them and activates restorative (behavioral) and anticipatory (respiratory) responses (CRAWSHAW, 1977). Increases in metabolic rate, thermaly induced, lead to decreases in dorsal aortic P_{0_2} , rapidly sensed by the fish, and to a compensatory increase in respiratory activity (SHELTON, 1970; BAMFORD, 1974). Changes in gill ventilation are related to the absolute temperature and not to the rate of change.

The mean values of the respiratory frequency at 0°C for *N. neglecta, N. rossii* marmorata and *T. bernacchii* are almost the same. After a small increase of the respiratory frequency at the beginning of the experiment (fish may sense an increase as small as 0.03° C, according to BULL, 1936) and a drop at 1.5° C to the original level, *N. neglecta* shows a gradual increase along the thermal gradient with a gain of 62% at 10°C over the initial frequency. According to FRY (1971), the previous thermal story explains the first reactions when the temperature goes from 0° to 1°C and the continuous appearing of new behavioral expressions along the uninterrupted temperature increase. *T. bernacchii* shows a similar kind of respiratory curve but, at the end, after a slow increase, the frequency falls to values close to the initial ones. However, *N. rossii marmorata* displays a completely different curve, showing two peaks after being unreactive up to 2°C. This kind of curve is also obtained for activity along a thermal gradient for temperate species (FISHER and SULLIVAN, 1958).

In N. neglecta, other behavioral factors were observed such as alert around 1 to 1.5° C, together with spitting and yawning, the last normally used in situations of oxygen depletion. In the same range of temperature the resting of the animal is interrupted by a few swimming periods. Thus, in N. neglecta most of the symptoms occur during the first 2°C of the thermal gradient increase. Later on, only a discrete lightening of the color (from dark to medium) at 5.8°C and a new short swimming periods at 8°C were observed. The opposite occurs in N. rossii marmorata which shows all kinds of behavioral symptoms starting at 4 to 4.5°C and being intensified at 7.5°C. At 5.2°C, periods with muscular stiffness and sigmoidal posture can be observed. Furthermore, the animal undergoes a stronger thermal stress accompanied by loss of equilibrium. In this way, N. rossii marmorata may have an activation of escape response, described by CRAWSHAW and HAMMEL (1971) for N. corriceps, as a result of temperature selection behavior.

The movements associated with thermoreception may be a gross response of activity (RUBIN, 1935) whereby quiet resting fish show activity in warming waters when lethal temperatures are reached. This was observed for *T. bernacchii* at 8°C, for a few minutes, for *N. neglecta* at 8 to 8.5° C, and for *N. rossii marmorata* from 4.8 up to 10° C.

In general, the fish body temperature is slightly above the environmental temperature, the difference being in the order of 0.5° C to 2.6° C (NICHOLLS, 1931; LINDSEY, 1968). The body temperatures in which biological reactions occur are probably higher than that of each point from 0° to 10°C. Comparing the amount of muscle available oxygen during temperature increase (LUCCHIARI *et al.*, 1989) *N. neglecta* and *T. bernacchii* have both bimodal curves while *N. rossii marmorata* displays an incapacity to maintain the muscle oxygen level along with the temperature increase.

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References

- BAERENDS, G. P. (1971): The ethological analysis of fish behavior. Environmental Relations and Behavior, ed. by W. S. HOAR and D. J. RANDALL. New York, Academic Press, 279–370 (Fish Physiology, Vol. 6).
- BAMFORD, O. S. (1974): Oxygen reception in the rainbow trout (Salmo gairdneri). Comp. Biochem. Physiol., 48A, 69-76.
- BRETT, J. R. (1964): The respiratory metabolism and swimming performance of young sockeye salmon. J. Fish. Res. Board Can., 21, 1183-1226.
- BULL, H. O. (1936): Studies on conditioned responses in fishes VII; Temperature perception in Teleosts.
 J. Mar. Biol. Assoc. U. K., 21, 1-27.
- BURCHETT, M. S., SAYERS, P. J., NORTH, A. E. and WHITT, M. G. (1983): Some biological aspects of the nearshore fish population at South Georgia. Br. Antarct. Surv. Bull., 59, 63-74.
- CRAWSHAW, L. I. (1977): Physiological and behavioral reactions of fishes to temperature change. J. Fish. Res. Board Can., 34, 730-739.
- CRAWSHAW, L. I. and HAMMEL, H. T. (1971): Behavioral thermoregulation in two species of Antarctic fish. Life Sci., 10(1), 1009–1020.
- DEVRIES, A. L. (1971): Freezing resistance in fishes. Environmental Relations and Behavior, ed. by W. S. HOAR and D. J. RANDALL. New York, Academic Press, 157–190 (Fish Physiology, Vol. 6).
- DEVRIES, A. L. and EASTMEN, J. T. (1981): Physiology and ecology of Notothenioid fishes of the Ross Sea. J. Roy. Soc. N. Z., 11(4), 329-340.
- FANTA-FEOFILOFF, E. (1983): Temperature and low oxygen tolerance in three species of fresh water Pimelodidae (Teleostei, Siluriformes). Arq. Biol. Tecnol. 26(4), 495-507.
- FANTA-FEOFILOFF, E., TAKAHASHI, N. S. and BOSCARDIM, A. T. (1983): Behavioral changes with temperature increase in the Ariidae Genidens genidens (Teleostei, Siluriformes). Arq. Biol. Tecnol. 26(4), 535-544.
- FANTA-FEOFILOFF, E., EIRAS, D. R. de B., BOSCARDIM, A. T. and LACERDA-KRAMBECK, M. (1985): Effect of salinity on the behavior and oxygen consumption of *Muqil curema* (Pisces, Mugilidae). Physiol. Behav., 36(6), 1029–1034.
- FISHER, K. C. and SULLIVAN, C. M. (1958): The effect of temperature on the spontaneous activity of speckled trout before and after various lesions of the brain. Can. J. Zool., 36, 49-63.
- FRY, F.E.J. (1964): Animals in aquatic environment; Fishes. Handbook of Physiology, ed. by Am. Physiol. Soc. and J. FIELD. Baltimore, Williams and Wilkins, 715-728.
- FRY, F. E. J. (1971): The effect of environmental factors on the physiology of fish. Environmental Relations and Behavior, ed. by W. S. HOAR and D. J. RANDALL. New York, Academic Press, 1–98 (Fish Physiology, Vol. 6).
- FRY, F. E. J. and HART, J. S. (1948): The relation of temperature to oxygen consumption in goldfish. Biol. Bull., 94, 66-77.
- JOHNSTON, I. A. (1985): Temperature, muscle energetics and locomotion in inshore Antarctic fish. Oceanics, 11(2), 125-142.
- LINDSEY, C. C. (1968): Temperature of red and white muscle in recently caught merlin and other large tropical fish. J. Fish. Res. Board Can., 25, 19-52.
- Love, R. M. (1970): The Chemical Biology of Fishes. London, Academic Press, 209-221.
- Love, R. M. (1980): The Chemical Biology of Fishes, Vol. 2. London, Academic Press, 318-349.
- LUCCHIARI, P. H., FANTA-FEOFILOFF, E., BOSCARDIM, A. T. and BACILA, M. (1984): A technique for the determination of the available oxygen in living carp (*Cyprinus carpio*) muscle. Comp. Biochem.

Physiol., 78A(4), 675-679.

- LUCCHIARI, P. H., FANTA, E. and BACILA, M. (1989): The effect of temperature on the muscle oxygen levels in Antarctic fish. Proc. NIPR Symp. Polar Biol., 2, 117-122.
- MONTGOMERY, J. C. and McDONALD, J. A. (1984): Performance of motor systems in Antarctic fishes. J. Comp. Physiol., 154A, 241-248.
- NICHOLLS, J. V. V. (1931): The influence of temperature on digestion in *Fundulus heteroclitus*. Contrib. Can. Biol. Fish., 7, 47–55.
- RANDALL, D. J. (1970): Gas exchange in fish. The Nervous System, Circulation and Respiration, ed. by W. S. HOAR and D. J. RANDALL. New York, Academic Press, 253–292 (Fish Physiology, Vol. 4).
- ROSMAN, I. (1980): Fishing with Bottom Gillnets. Rome, FAO Training Series, 3, 30 p.
- RUBIN, M. A. (1935): Thermal reception in fishes. J. Gen. Physiol., 18, 643-647.
- SHELTON, G. (1970): The regulation of breathing. The Nervous System, Circulation and Respiration, ed. by W. S. HOAR and D. J. RANDALL. New York, Academic Press, 293–359 (Fish Physiology, Vol. 4).
- SOMERO, G. N. and DEVRIES, A. L. (1967): Temperature tolerance of some Antarctic fishes. Science, 156, 257–268.
- SULLIVAN, C. M. (1954): Temperature reception and response in fish. J. Fish. Res. Board Can., 11, 153–170.
- TWELVES, E. L. (1972): Blood volume of two Antarctic fishes. Br. Antarct. Surv. Bull., 31, 85–92.
- WOHLSCHLAG, D. E. (1957): Differences in metabolic rates of migratory and resident freshwater forms of an arctic whitefish. Ecology, 38, 502–515.
- WOHLSCHLAG, D. E. (1964): Respiratory metabolism and ecological characteristics of some fishes in McMurdo Sound, Antarctica. Biology of the Antarctic Seas, ed. by M.O. LEE. Washington, D.C., Am. Geophys. Union, 33-62 (Antarct. Res. Ser., Vol. 2).

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