# Behavioral thermoregulation in the intertidal fish Girella laevifrons (kyphosidae): The effect of starvation

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# BEHAVIORAL THERMOREGULATION IN THE INTERTIDAL FISH *GIRELLA LAEVIFRONS* (KYPHOSIDAE): THE EFFECT OF STARVATION

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One of the key factors that determine an animal's distribution and abundance is environmental temperature. This factor affects all the components of an organism's energy budget and fitness. In this study, we tested the effect of water temperature and starvation on patterns of space use in the intertidal fish *Girella laevifrons*. We postulated that starved animals would select cold temperatures as a mechanism of energy conservation while fed animals would prefer higher temperatures as a mechanism to facilitate digestive processes. In a thermal gradient tank, fishes, irrespective of treatment (fed and starved), actively selected temperatures between 15 and 18°C. Starvation did not affect temperature selection, although it did alter the time and number of visits to thermal gradient extremes. Starved fishes stayed longer in, and visited the warmer temperatures of the gradient more frequently. In contrast, fed fishes stayed longer in, and visited cold temperatures more frequently. We discuss the ecological consequences of temperature selection and the possible relationship between water temperature, food selection and digestive processes.

*Keywords:* Intertidal fish; temperature selection; thermal gradient; *Girella laevifrons*

## INTRODUCTION

To understand the dynamics of species assemblages and their association to a particular environment, a thorough knowledge of the effects of environmental factors on the individual is needed. Variations in environmental

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conditions can be biotic (e.g., predators and conspecific density) or abiotic (e.g., physical variables such as temperature). Among abiotic factors, temperature is crucial in determining the distribution patterns of marine organisms (Norris, 1963): it also affects all the biological processes and life history parameters of the individuals, from metabolic rate to clutch size (Cossins and Bowler, 1987; Weiser, 1991; Lenski and Bennett, 1993; Parsons, 1993; Stephen and Porter, 1993); hence it can be considered as one of the most important niche axes in ectotherms (Tracy and Christian, 1986).

Marine intertidal studies mainly refer to sessile invertebrate species occurring on rock platforms and vertical walls of the intertidal (see Moore and Seed, 1986; Raffaelli and Hawkins, 1996). These studies have shown clear zonation patterns, mainly attributed to the influence of biotic and abiotic factors such as predation, competition, and desiccation (Paine, 1977; Connell 1983; Schoener, 1983; Wootton, 1994). In contrast, the effects of abiotic factors on the distribution and abundance patterns of other non-sessile intertidal organisms such as fishes are scarcely documented (Gibson, 1982; Metaxas and Scheibling, 1993).

The distribution of fishes in the intertidal zone has been rarely discussed, and only incidental reports suggest that zonation would be similar to that of sessile individuals (Gibson, 1982; Horn and Gibson, 1988). Metaxas and Scheibling (1993) showed that abundance of intertidal fishes changes seasonally, usually in an inverse relationship to water temperature and specific microhabitats (Gibson, 1982). Temperature has been shown to have a very important role in determining both the vertical distribution and survival of intertidal fishes (Bridges, 1993). Bull (1936) showed that a number of intertidal fish species are able to detect slight changes in water temperature (less than 0.1°C), which suggest that they can react to temperature gradients. Thus, temperature selection by intertidal fishes inhabiting environments with wide variations in physical conditions, particularly temperature, may reveal differential habitat occupation at the individual level which, in turn, may explain the distribution of fishes in the intertidal zone.

On the other hand, starvation has been claimed to be an important factor that affects the fitness of fishes of high intertidal rockpools, which are exposed to periodical stress and food limitation during water renewal (Horn and Gibson, 1988; Metaxas and Scheibling, 1993). Kleiber (1975) pointed out that, irrespective of temperature, starved animals decreased their metabolic rate. In turn, Magunson et al. (1979) and Kubb et al. (1980) reported that fishes entered waters of lethal temperatures for short periods of time during feeding. Further, Weiser (1991) indicated that when food is

scarce, small poikilotherms like young fishes tended to increase their locomotor activity. If the lack of food reached beyond a critical time limit, they would reduce locomotor and metabolic activities as much as possible. All this evidence strongly suggests a trade-off between foraging behavior and environmental temperature.

*Girella laevifrons* is one of the most abundant fish species inhabiting high intertidal rock pools of the Chilean central zone. Juveniles of this species are year round residents, but as adults they live in subtidal habitats (Stepien, 1990; Varas and Ojeda, 1990; Muñoz and Ojeda, 1997). The main goals of this paper were (1) to determine the water temperatures selected by the intertidal fish *G. laevifrons*, by means of an experimental protocol in the laboratory and through field evidence; (2) to evaluate in these fishes the effect of starvation on their temperature selection. Since temperature directly affects energy expenditure, food requirements, and digestive processes in ectothermic vertebrates, we postulated that starved animals would select cold temperatures as a mechanism of energy conservation while fed animals would prefer higher temperatures to facilitate digestive processes.

## MATERIALS AND METHODS

Fishes were collected in October 1997 from eight low intertidal rockpools at Isla Negra in central Chile (33° 26'S, 71° 41'W). Seawater temperature was registered on the surface, bottom, and under boulders of each tidepool using a digital thermocouple. Depths of tidepools ranged from 20 to 50 cm. All these measurements were taken during low tide around noon time. Specimens were captured using the anesthetic MS-222 and handnets. All individuals used in the assays were juveniles (4–6 cm SL).

All *G. laevifrons* individuals collected were placed in 20 l coolers with seawater and aeration, and transported to the laboratory. They were acclimated at 15°C for 14–20 days and fed *ad-libitum* with fresh bivalves. Prior to the experiments, the fishes were separated into two groups, of which one was fed *ad-libitum* and the other starved for three days.

Experiments on temperature selection were performed in a vertical aquarium (30 × 30 × 60 cm) with a thermal gradient. The aquarium was split into six 20 cm cells, separated by a perforated acrylic sheet. The bottom of the aquarium was immersed in a thermoregulated bath at 7.5°C. A heater was placed on the top to maintain the water at 33.0°C. The temperature of each cell was monitored for 2 days by means of a digital thermocouple to record the stability of the temperature gradient.

Ten *G. laevifrons* of each group were placed, one per trial, on the top of the thermal gradient. After 30 min (time needed by the fish to explore the system), the number of visits as well as the total time spent by each fish in each cell were recorded for 20 min. Control experiments were run at a constant temperature of 18.5°C. The temperature of each cell in the gradient was adjusted after each assay. Dissolved oxygen concentration was measured in each cell using a CHEMets colorimetric kit K-7510, which ranged from 7 mg/l in cell 6 to 8 mg/l in cell 1. Differences in the times that fed and starved fishes spent in each cell of the gradient, as well as differences between control and treated fishes as to the times spent in each cell, were tested using one-way ANOVA based on ranks (Conover and Iman, 1981; Potvin and Roff, 1993). The number of visits to each cell was compared between treatments and controls using a Chi-square ($\chi^2$) and Kolmogorov–Smirnov test (Siegel and Castellan, 1988).

## RESULTS

Mean seawater temperature in tidepools varied from 18.5°C ($\pm 0.6$ SD) under boulders to 20.5°C ($\pm 0.6$ SD) at the surface and to 22.0°C ($\pm 0.3$ SD) on the bottom.

The temperature of each cell in the thermal gradient is shown in Table I. The greatest variability in temperature was found in the fourth cell due to its intermediate position. The most stable cell was the lowest one (cell 1). Due to methodological problems related to the physical arrangements of the equipment, it was not possible to arrange a cell with a 20–25°C temperature in the thermal gradient. Fishes visited the fourth cell of the experimental aquarium (18.3°C) more often than the rest of the cells; hence this was considered to be the preferred temperature for *G. laevifrons* juveniles (Kolmogorov–Smirnov $\chi^2 = 1873.12$; df $= 5$; $P < 0.001$; ANOVA $F_{5,257} = 18.48$, $P = 0.0001$, Figs. 1 and 2).

TABLE I  Average temperature (°C) registered at each cell in the thermal gradient. Cells are shown from uppermost (cell 6) to lowermost (cell 1). $\pm 1$ standard deviation

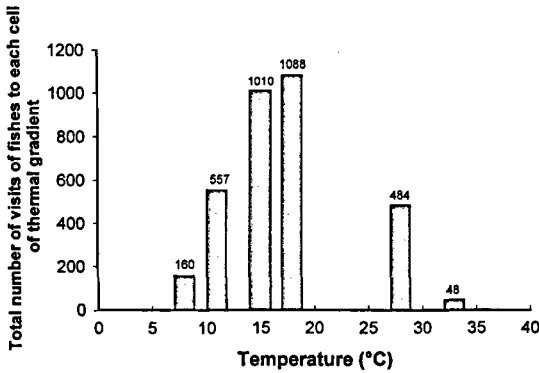|          | Average temperature (°C)    |
|----------|-----------------------------|
| Cell 6   | 33.63 $\pm$ 1.22 (Top)      |
| Cell 5   | 28.71 $\pm$ 1.11            |
| Cell 4   | 18.27 $\pm$ 2.56            |
| Cell 3   | 15.11 $\pm$ 1.76            |
| Cell 2   | 11.30 $\pm$ 1.30            |
| Cell 1   | 5.50 $\pm$ 0.3 (Bottom)     |

FIGURE 1    Total number of fishes that visited each cell in the thermal gradient.
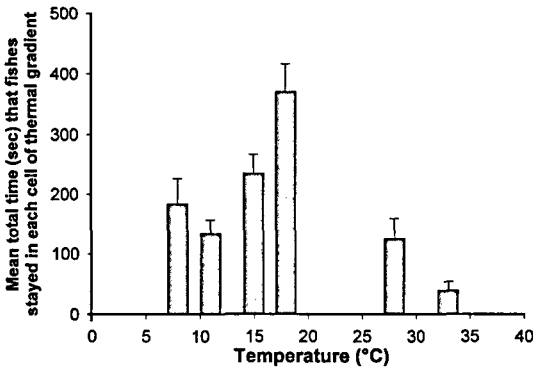


FIGURE 2    Mean total time that fishes stayed in each cell of the thermal gradient. Bars indicate 1 S.E.

Contrary to our hypothesis, fed fishes stayed longer at low water temperatures (cells 1 and 2) than starved ones (cell 1, ANOVA $F_{1,42} = 4.64$, $P = 0.037$; cell 2, $F_{1,42} = 6.90$, $P = 0.012$, Fig. 3). At intermediate temperatures (cells 3 and 4) no differences were found between treatments. At the highest temperatures, (cells 5 and 6) starved fishes stayed longer than fed fishes (cell 5, ANOVA $F_{1,42} = 14.95$, $P = 0.0004$; cell 6, $F_{1,42} = 5.32$, $P = 0.021$, Fig. 3). A comparison of the total amount of time that fishes spent in cells 1 and 2 (coldest), 3 and 4 (intermediate), and 5 and 6 (hottest), showed that fed fishes stayed longer at the colder temperatures (ANOVA $F_{1,85} = 4.8$, $P = 0.031$), while starved fishes stayed longer at the higher temperatures (ANOVA $F_{1,87} = 10.18$, $P = 0.0020$, Fig. 4).
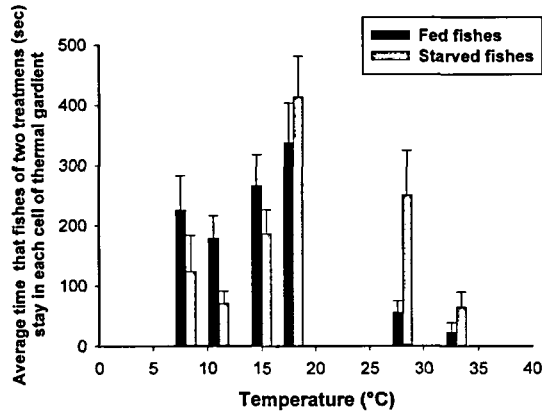
FIGURE 3    Mean total time that fishes under each treatment (fed vs starved) spent in each cell of the thermal gradient. Bars indicate 1 S.E.
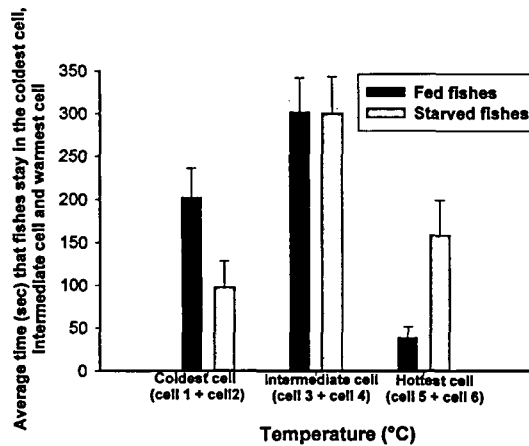


FIGURE 4    Mean time that fishes under the two treatments stayed in the coldest (cells 1 and 2), intermediate (cells 3 and 4) and hottest (cells 5 and 6) temperatures. Bars indicate 1 S.E.

The number of visits to each cell in the gradient by fed and starved fishes showed that 70% of all the fishes that visited the warmest cell (cell 6) were starved, and 70% of the total number that visited the cold cell (cell 1) were fed fishes ($\chi^2 = 73.04$, df $= 5$, $P < 0.001$, Fig. 5). In short, our results indicate that fed fishes selected cold and intermediate temperatures and starved fishes preferred intermediate and warmer temperatures. Moreover, the control fishes of both groups stayed longer in the lowest cell of the system
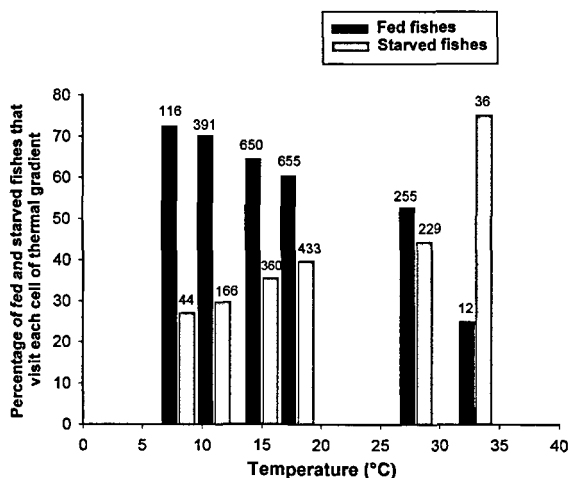
FIGURE 5  Percentage of fed and starved fishes that visited each cell in the thermal gradient. Numbers over bars indicate number of visits.

(fed fishes, ANOVA $F_{1,30} = 7.34$, $P = 0.011$; starved fishes, ANOVA $F_{1,22} = 18.85$, $P = 0.0003$, Fig. 6A and B). The number of total visits of control fishes to each cell was homogeneous among cells (Fig. 7A and B).

## DISCUSSION

The experimental evaluation of temperature selection in *G. laevifrons* indicated that this fish, irrespective of the treatment, selects temperatures between 15°C and 18°C (Figs. 1 and 2; Table I), which are close to those recorded under boulders in intertidal pools. This suggests that fishes exposed to fluctuating temperature regimes in the field, are able to discern specific temperatures in tandem with particular environmental attributes, such as food availability, shelter, and predation risk. The different periods of time and instances when each temperature was visited in our thermal gradient strongly supports these observations (Figs. 1–3). Contrary to our predictions, fed fishes preferred intermediate to colder temperatures, and starved fishes preferred intermediate to highest temperature (Figs. 3–5). We postulate that this temperature selection in *G. laevifrons* might be associated with a higher encounter rate with food (Magunson *et al.*, 1979; Moyle and Cech, 1982; Weiser, 1991).

Temperature selection, the effect of temperature over digestive processes, and other responses of organisms are highly developed in ectotherms
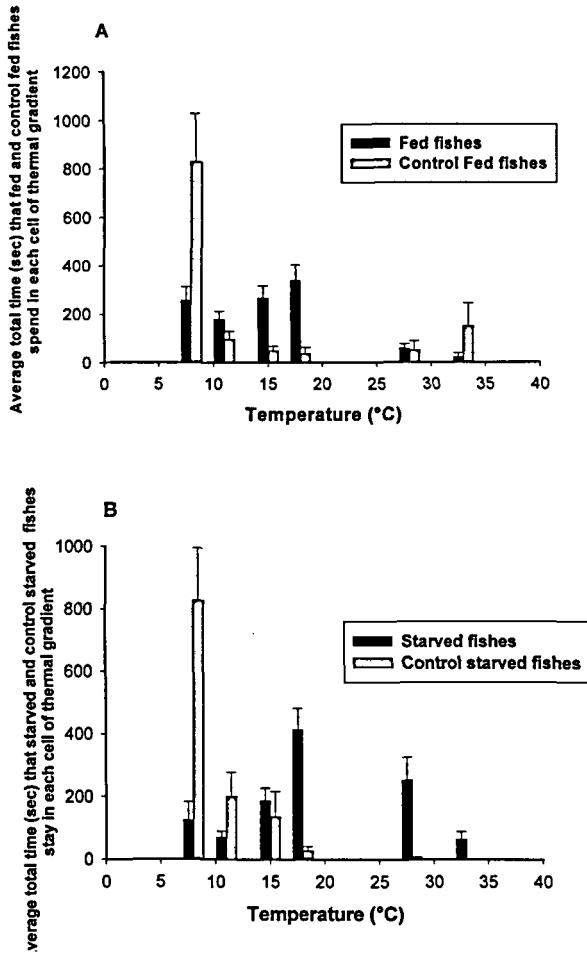
FIGURE 6   (A) Mean time that fed and control fed fishes spent in each cell of the thermal gradient. (B) Mean time that starved and control starved fishes spent in each cell of the thermal gradient. Bars indicate 1 S.E.

because of their direct dependence on ambient temperature. In fact, there is evidence that other ectotherms, such as lizards and snakes, select ambient temperature where prey detection and capture, production of young and temperatures for digestive processes are more efficient (Spotila and Standora, 1985; Tracy and Christian, 1986; Cossins and Bowler, 1987; Marken Lichtenbelt and Wesselingh, 1993; Marken Lichtenbelt, 1993;
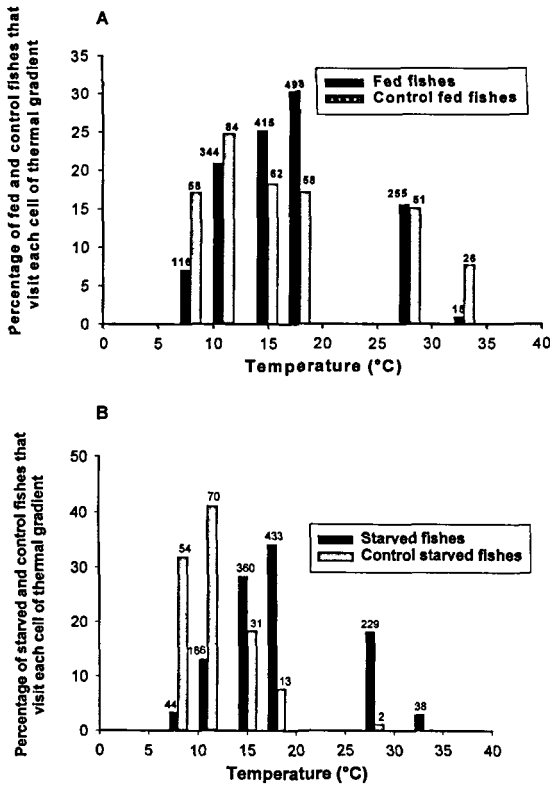
FIGURE 7  (A) Percentage of fed fishes and control fed fishes which visited each cell of the thermal gradient. (B) Percentage of starved fishes and control starved fishes which visited each cell of the thermal gradient.

Ayres and Shine, 1997). Furthermore, Dawson (1975) reported that, in an experimental thermal gradient, turtles increased their body temperatures in average of 4.5°C after feeding. Bozinovic and Rosenmann (1988) have shown under laboratory conditions that snakes increased their temperature after feeding by exposing their bodies to a radiant heat source. All these findings did not agree with our results, since fed *G. laevifrons* selected lower temperatures compared to starved fishes (Figs. 1–5). Moyle and Cech (1982) showed that some fishes may select a particular temperature in order to preserve energy or to run their metabolic enzymatic machinery more efficiently. In this context, our results are somewhat puzzling. However, the interplay between the energetics, digestion efficiency and temperature in this species within an ecological context remains to be studied.

Weiser (1991) pointed out that, because food could be temporally or spatially patchy, young fishes with high energy requirements increased their locomotor activity so as to raise the chance of finding more food. This behavior was observed in our experiments. Nevertheless, Magunson et al. (1979) and Kubb et al., (1980) indicated that fishes swimming for short periods into warm waters to forage, might be expected to feed at non-preferential temperatures if the net energy return is higher than that obtained by feeding at a preferential temperature. Our present results indicate that starved fishes swim into warmer water for longer periods than fed fishes, a behavior that would increase the chance of finding food because warmer water allows them to be more active and therefore search a greater area per unit time.

G. laevifrons is found mainly in high intertidal pools where thermal stress by high temperatures is greater than in the low intertidal zone (Metaxas and Scheibling, 1993). Our results indicate that these fishes might be found in all of the intertidal system (Figs. 1–4). In this sense, Gibson (1982) and Metaxas and Scheibling (1993) report that the distribution of fishes in intertidal systems is related to the selection of specific microhabitats and also to temperature resistance. According to Magunson et al. (1979) the temperature of an animal's habitat is one axis of its multi-dimensional niche, so this variable is used as a resource (Tracy and Christian, 1986). Further, its use could be affected by the presence of other species and interactions with other niche axis such as food. Hence, the occurrence of G. laevifrons in high intertidal pools could represent a strategy for avoiding interactions with other species (see Muñoz and Ojeda, 1997) of higher abundances in the lower intertidal zone. This behavior has also been observed in other intertidal fishes (see Nakamura, 1976).

Control fishes of both groups stayed longer at the lower cell of the system (Fig. 6A and B), and the number of total visits to each cell of control fishes was homogeneous among cells (Fig. 7A and B). This result contrasts with the behavior of fed and starved fishes, which clearly select a specific temperature, validating our experimental system.

In brief, the observed responses of G. laevifrons in the thermal gradient reveals that, because they are able to discern specific temperatures, starved fishes raise their chance of finding food by swimming in warm waters. Against our predictions, G. laevifrons seems to follow the model of behavioral thermoregulation, energy acquisition and energy use postulated by Weiser (1991), and predicted by Magunson et al. (1979) i.e. they increase their locomotor activity and forage in warm waters for short periods to increase their chance of finding food.

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