Does food quality influence thermoregulatory behavior in the intertidal fish *Girella laevifrons*?

José M. Pulgar*, Marcela Aldana, Francisco Bozinovic, F. Patricio Ojeda

Center for Advanced Studies in Ecology and Biodiversity, Departamento de Ecología, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Santiago 6513677, Chile

Abstract

Algal and invertebrate species are less abundant towards higher zones of the intertidal, where the greatest variations in physical environmental conditions occur. Mobile predators such as fishes that inhabit high intertidal rockpools are thus exposed to wide variations in physical conditions and to a low abundance and quality of food. We used an aquarium with a temperature gradient in the laboratory to assesed whether dietary quality differences modify temperature preferences of *Girella laevifrons*, one of the most abundant transitory fishes inhabiting rocky shores along the coast of Chile. Our results indicate that food quality clearly modifies temperature preferences in this species. Animals fed on high quality bivalves selected intermediate temperatures (16–18°C) while those fed on lower quality algae selected lower temperatures (10–12°C). Control fish not subjected to the temperature gradient did not select portions of the aquarium differentially. The thermal selectivity of *G. laevifrons* in relation to the optimization of digestive processes and mechanisms of energy conservation are discussed.
© 2003 Elsevier Ltd. All rights reserved.

1. Introduction

Both biotic and abiotic environmental conditions are known to be heterogeneous. Among abiotic factors, temperature has been documented as one of the most important factors determining distributional patterns of ectotherms, particularly among marine organisms (Norris, 1963; Spicer and Gaston, 1999; Somero, 2002; see Tomanek and Helmuth, 2002 and related papers in the symposium), as it affects biological processes such as food assimilation and growth rates (Pulgar et al., 1999; Morgan and Metcalfe, 2001), together with life history strategies (Tracy and Christian, 1986; Cossins and Bowler, 1987; Wieser, 1991; Lenski and Bennett, 1993; Parsons, 1993; Stephen and Porter, 1993). In the context of energetics, heat and food energy budgets interact through their effects on body temperature and metabolism (Porter and Gates, 1969; Dent and Lutterschmidt, 2003).

Heat exchange sets the body temperature but is modified by thermoregulatory behavior. Metabolism is temperature dependent but also tends to raise body temperature and may alter behavior (Spotila and Standora, 1985). In essence, an overall framework that combines both heat and food energy budgets could help us understand the roles of heat exchange and resource allocation in the life histories of animals. More specifically, ambient temperature, together with body size, and the quality of food have are the three principal factors determining rates of assimilation (Kooijman, 2000).

In the intertidal system, rockpools represent a particular environment characterized by their discrete

*Corresponding author. Tel.: +56-2686797; fax: +56-26862621.

E-mail address: jpulgar@genes.bio.puc.cl (J.M. Pulgar).

nature in time and space, as well as by their daily and seasonal variability in temperature, oxygen concentration and salinity (Newell, 1970; Stephenson and Stephenson, 1972; Truchot and Duhamel-Jouve, 1980; Metaxas and Scheibling, 1993; Horn et al., 1999). These variations, especially in temperature, depend on a pool's localization along the intertidal vertical gradient, which determines the length of time that a pool remains isolated from the subtidal system (Gibson, 1982; Horn et al., 1999). On the other hand, the abundance and quality of food available for mobile predators such as fishes also varies along a vertical gradient in the intertidal zone (Raffaelli and Hawkins, 1986; Metaxas and Scheibling, 1993). Green algae (e.g., *Ulva* sp. and *Enteromorpha* sp.) usually dominate the mid to high sectors of intertidal habitats, while brown algae and corallines are dominant on the lower sectors of the intertidal zone (Metaxas and Scheibling, 1993). Further, species richness and abundance of invertebrates decreases towards the higher sectors of rocky intertidal areas (Raffaelli and Hawkins, 1986).

Assemblages of intertidal fishes are composed of resident and transitory species, which possess highly contrasting life histories (Horn and Gibson, 1999). Resident species inhabit the intertidal zone along their entire post-plancktonic lives (e.g. Blenniidae), while transient species (e.g. Kyphosidae) do so only during juvenile or early developmental stages; later completing their life cycles in shallow subtidal habitats (Horn and Gibson, 1988). In contrast to resident species, transitory species have been reported to occupy those rockpools most distant from the subtidal zone, remaining isolated from it for a number of tidal cycles (Thompson and Lehner, 1976). Consequently, these species would be exposed to highly variable physical habitat conditions as well as that of the abundance and quality of food available.

We assess if food quality modifies the thermal preferences of juvenile individuals of the fish species *Girella laevifrons* (Kyphosidae), which is the most abundant transitory fish species inhabiting high intertidal rockpools along the coast of Chile (Pulgar et al., 1999). This species lives in tidepools for a period of ca. 2 years, and then migrates to shallow subtidal areas, where it completes its life cycle (Stepien, 1990; Varas and Ojeda, 1990). *G. laevifrons* fed on algae and small invertebrates, but macroalgae is the preferred dietary item, being a 56% of total food items while bivalves represent a 12% of total food items Muñoz and Ojeda, 1997). Because ectotherms require an external heat source for digestion and nutrient processing (Cossins and Bowler, 1987), we hypothesized that an interaction between dietary quality and ambient temperature modifies the thermal preferences of the intertidal fish *G. laevifrons*.

2. Materials and methods

2.1. Sampling and acclimation

Fish were collected from eight tide pools at the locality of Isla Negra in central Chile (33°26′S, 71°41′W). Seawater temperature of each pool was recorded on the surface, bottom, and under boulders. Depth of tidepools ranged from 20 to 90 cm. All these measurements were taken during low tide at ca. mid-day. Eighty juvenile *G. laevifrons* (4–6 cm Lt) specimens were captured with hand nets after the application of the anaesthetic MS-222 to the tidepools. All sampled fish were immediately deposited in a 20 l cooler containing fresh seawater, and transported to the laboratory. Fish were later separated into two groups of 30 individuals each, and maintained for 40 days at 14°C and under the same conditions, of constant aeration, water recycling, and a 12:12 h photoperiod. The two groups were fed different foods. The first group received a diet of green algae consisting of *Enteromorpha* sp. and *Ulva* sp., while the second was fed fresh bivalves *Perumitylus* sp.

3. Dietary energy content

The energetic content of each of the two diets was determined using a computerized Parr 1261 bomb calorimeter. Two replicates were determined to be ash free and were considered reliable when the difference between two measurements was less than 1%. Analysis of energetic content indicated that fresh bivalves contained 21.9 kJ/g and green algae contained 11.7 kJ/g.

4. Experimental thermal gradient

Temperature selectivity (T_s) experiments were conducted in a vertical aquarium ($30 \times 30 \times 60 \, cm^3$) containing a thermal gradient. The depth of the aquarium tank used was within the depth range of the intertidal pools from where fish were collected. This aquarium was split into six 10 cm cells, separated by a perforated acrylic sheet, which contained four $7 \, cm^2$ holes each, allowing fish free passage among the different cells of the aquarium. The bottom of the aquarium was immersed into a thermoregulated bath with a temperature of nearly 10°C. A heater set to 31°C was positioned on the superior portion of the aquarium. This way, after 2 h, an experimental system with a well-established water temperature (T_w) gradient was obtained, which ranged between 10°C on the bottom and 30°C on the top (Table 1). Prior to the commencement of the T_s experiments, T_w of each of the cells along the thermal gradient was monitored through a digital thermometer connected to Cu-constantan thermocouples. The

Table 1
Average temperature (°C) ± 1 SD, registered at each cell in the thermal gradient

Cell	Average temperature (°C)
6	30.9 ± 1.22 (top)
5	25.3 ± 1.11
4	18.6 ± 2.56
3	16.4 ± 1.76
2	12.9 ± 1.30
1	10.3 ± 0.3 (bottom)

Cells are shown from upper-most cell (cell 6) to lower-most (cell 1) with 22 replicates (11 *G. laevifrons* of each experimental group.

stability of the experimental system was tested by registering T_w of each cell immediately before depositing a fish specimen and immediately after registering the amount of time that the specimen stayed within each cell.

5. Thermal selectivity experiments

Eleven *G. laevifrons* individuals of each group were placed, one per trial, on the upper side of the thermal gradient (Table 1). Each fish specimen was maintained within the experimental system for a total period of 40 min. Previous experience indicated that *G. laevifrons* takes only 20 min to explore and recognize the complete thermal gradient (Pulgar et al., 1999). During the following 20 min the total amount of time that each fish stayed within each cell of the thermal gradient was registered using a stop-watch. After each trial, water was renewed and aerated for 20 min. Finally, control trials were conducted with the aquarium at a constant T_w of 15°C and using five individuals (one per run) that had been maintained under each quality diet. Dissolved oxygen concentration was measured in each cell using a CHEMests colorimetric kit K-7510, and ranged from 7 mgO$_2$/l in cell 6 to 8 mgO$_2$/l in cell 1.

6. Data analyses

In order to simplify the statistical analysis for an assessment of fish T_s as a function of diet, thermal cells were grouped into high, intermediate, and low temperature cells. This way, the time spent by fish in the two high temperature cells (cells 5–6), two intermediate temperature cells (cells 3–4), and two low temperature cells (cells 1–2) were summed. Thus, we obtained (1) the type of diet with two levels, algae and bivalves, (2) water gradient temperature with three levels, high, medium, and low, and (3) the presence or absence of the thermal gradient, with two levels.

Thermal selectivity of each of the two groups fed on different quality diets was tested via one-way repeated measurements ANOVA (Siegel and Castellan, 1988) applied on the time spent by the fish at each thermal sector of the aquarium (low, medium, and high temperature sectors). This analysis allow us to determine selectivity within each experimental group. Then, differences in the amount of time spent at each temperature were tested via a three-way repeated measures ANOVA, with two dietary levels (algae and bivalves), temperature gradient with two levels (absence and presence), and water temperature with three levels (low, medium, and high). This analysis allow us to test for differences among experimental groups. Finally, we used a repeated measurement test because fish were continuously recorded during 20 min and consequently they visited different areas in the experimental set-up. Thus, we recorded the same individual through time.

7. Results

Mean T_w of tidepools varied from 18.5°C (± 0.6 SD) under boulders to 20.5°C (± 0.6 SD) on the bottom, and 22.0°C (± 0.3 SD) on the surface. Water temperature within each cell of the experimental thermal gradient is shown in Table 1. Temperature ranged between 11°C and 28°C.

The analysis of the amount of time that individuals spent at high, intermediate, and low temperature cells indicated that specimens fed on fresh bivalves spent a significantly greater amount of time in intermediate temperature cells (16–19°C) than at high and low temperatures (Anova $F_{(2,20)} = 14.57$, $P < 0.001$, a posteriori Scheffe test $P < 0.05$, Fig. 1). On the other hand, fish fed on algae spent a significantly greater amount of time in low temperature cells (10–13°C) than at intermediate and high T_w's (Anova $F_{(2,20)} = 38.6$, $P < 0.001$, a posteriori Scheffe test, $P < 0.05$, Fig. 1). This way, fish fed on bivalves showed a clear preference for intermediate temperatures while those fed on algae selected cells with the lowest water temperatures (Fig. 1). In contrast, neither fish fed on bivalves nor those fed on algae showed preferences for any of the different sectors of the aquarium in control trials. (Fish fed on bivalves: Anova $F_{(2,8)} = 0.26$, $P < 0.77$. Fish fed on algae: Anova $F_{(2,8)} = 3.1$, $P < 0.09$, Fig. 2). Fish subjected to the experimental thermal gradient showed clear preferences for different sectors of the experiment gradient (Fig. 1) while control fish (not subjected to the thermal gradient) did not show significant preferences for any of the sectors within the aquarium (Anova $F_{(2,56)} = 11.32$; $P < 0.0001$, Figs. 1 and 2, Table 2).
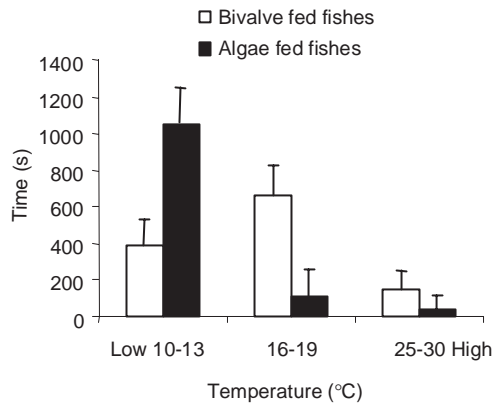
Fig. 1. Mean amount of time (s) ± 1 SE that fishes fed on algae (black barr) and on fresh bivalves (white barr) stayed at low, intermediate, and high temperature cells of the thermal gradient. Total duration of each trial (fish) was 60 min, and 11 replicates were conducted per experimental group.
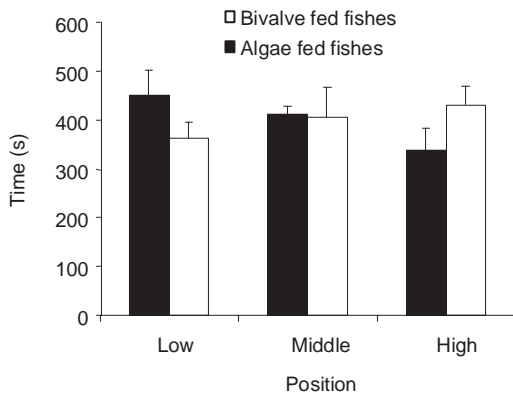

Fig. 2. Mean amount of time (s) ± 1 SE that fishes fed on algae (black barr) and on fresh bivalves (white barr) stayed within the various cells of the aquarium during control trials (no thermal gradient). Total duration of each trial (fish) was 60 min, and 11 replicates were conducted per experimental group.

8. Discussion

The main three factors that determine feeding ates are body size, food availability and temperature (Kooijman, 2000). Optimality theory assumes that the overall fitness of an animal increases as a function of net rate of energy intake, having been utilized to understand how individuals select particular environmental conditions as a function of the flexibility of their physiological responses and the environmental variability (Krebs and Davis, 1978; Dent and Lutterschmidt, 2003). This approach has been used to propose unified energy budget models combining heat and food energy budgets through their effects on body temperature and metabolism (Spotila and Standora, 1985). Environmental temperature has been shown to have direct effects on the digestive processes and energetic costs of ectotherms (Cossins and Bowler, 1987). Numerous studies have demonstrated that lizards, snakes, and turtles select environmental temperatures where the detection and capture of prey, reproduction, and digestive processes are most efficient (Dawson, 1975; Spotila and Standora, 1985; Tracy and Christian, 1986; Marken Lichtenbelt and Wesselingh, 1993; Marken Lichtenbelt, 1993; Ayres and Shine, 1997; Bozinovic and Rosenmann, 1988).

In this study, we evaluated the effect of diet quality on T_s of the intertidal fish G. laevifrons. Our results indicate that food quality (algae vs. bivalves) modifies thermal preferences of this species, as fish fed on algae selected low temperatures (10–13°C), while those fed on bivalves preferred more intermediate temperatures (16–19°C) (Fig. 1). Even though acclimation and photoperiod can modify the preferred temperature in fishes (Kelsch and Neill, 1990; Bridges, 1993), variations in the temperature selectivity observed among treatments are related to differences in food quality because all specimens used in this study were maintained under the same experimental conditions (14°C and photoperiod (12:12) for 40 days).

The performance and fitness of ectotherms are profoundly affected by body temperature (Huey and Kingsolver, 1993). This way, energy conservation among ectotherms can be achieved via behavioral

Table 2
Results of a three-way analysis of variance on time spent by fishes fed on two diets in each cell of thermal gradient

Factor	Df factor	CM factor	Df error	F	P
Diet	1	417	28	0.43	0.52
Gradient/control	1	435	28	0.47	0.51
Temperature	2	159 617	56	29.9	0.00001
Diet*gradient/control	1	430	28	0.44	0.51
Diet*temperature	2	459 092	56	16.9	0.00001
Gradient/control*temperature	2	477 049	56	9.38	0.0003
Diet*gradient/control*temperature	2	575 152	56	11.31	0.0001

Diet = algae, invertebrates; gradient/control = presence or absence of the thermal gradient; Temperature = low, medium, high.

mechanisms that result in a reduction in body temperature (Sibly and Calow, 1986; Cossins and Bowler, 1987; Sogard and Olla, 1996). Fry sockeye salmon *Oncorhynchus nerka* save considerable energy by daily vertical migration; feeding at the surface at dawn and dusk and digesting food and processing chemical energy at lower temperatures in deep water during the day (Brett et al., 1983). On the northern coasts of California, survival and growth of juvenile coho salmon *O. kisutch* under natural conditions, where food is limiting, may be possible only in a narrower range of temperatures than can be tolerated under artificial conditions (Hartwell et al., 2001). Streams with high temperatures may not be adequate as rearing habitats for coho salmon in the absence of extremely high food availability, which might mitigate elevated metabolic rates of fish in these habitats (Welsh et al., 2001). Our results indicate that fish subjected to a low quality diet (algae), selected the lowest temperatures of the experimental system (10–13°C), suggesting that an energy conservation strategy was being adopted by these fishes. On the other hand, animals fed on a high quality diet (bivalves), selected intermediate temperatures of the thermal gradient (16–19°C), a response that suggests that these fish were selecting conditions that could bring about an optimization of their digestive processes, and an increase in their energetic returns (Fig. 1).

Temperature has been shown to play a very important role in determining both vertical distribution and survival of intertidal fishes (Bridges, 1993); in fact, variations in the abundance of intertidal fishes have been indicated to be mainly associated with changes in water temperature and the search of specific microhabitats (Horn and Gibson, 1988; Bridges, 1993; Metaxas and Scheibling, 1993). A bioenergetic model developed by Crowder and Magnuson (1983) evaluates fish foraging behavior in a heterogeneous temperature environment. The model suggests that fish areas of foraging depends on the interaction between the presence of food and the temperature of the habitat. This way, fish would optimize the use of habitat resources by making choices among the various spatial components according to the food–temperature conditions in which they find themselves. In this sense Dent and Lutterschmidt (2003) demonstrated the diversity of physiological responses in two fish species, *Lepomis macrocirrhus y L. megalotis*, to different physical and food conditions of the colonized environment. In our study, fish selected temperatures differentially (Fig. 1). An intertidal fish species such as *G. laevifrons* that is exposed to an environment that is heterogeneous in terms of temperature conditions, as are intertidal rockpools (Truchot and Duhamel-Jouve, 1980; Metaxas and Scheibling, 1993) and variable in food quality and availability, as observed along the intertidal gradient (Raffaelli and Hawkins, 1986), would be expected to be spatially segregated within the intertidal zone. Hernández et al. (2002) indicated that the largest-sized specimens of *Graus nigra* (Kyphosidae) reached their metabolic maximum response at lower temperatures compared to small fishes. In the intertidal zone, the largest-sized individuals of *G. nigra* primarily occupy tidepools located in the lower sectors (habitats with the greatest richness and abundance of prey and that is least variable in terms of thermal conditions). In summary, the thermoregulatory behavior of *G. laevifrons* depends on the interaction between environmental temperature and the quality of food available, an interaction that should be taken into account when evaluating fish distributional patterns as a function of environmental temperature.

Acknowledgements

References

Ayres, D.Y., Shine, R., 1997. Thermal influences on foraging ability: body size, posture and cooling rate of an ambush predator, the python *Morelia spilota*. Funct. Ecol. 11, 342–347.

Brett, J.T., Shelbourn, J.E., Shoop, C.T., 1983. Growth rate and body composition of fingerling sockeye salmon, *Oncorhynchus nerka*, in relation to temperature and ration size. J. Fish. Res. Board Can. 26, 2363–2393.

Bozinovic, F., Rosenmann, M., 1988. Energetics and food requirements of the female snake *Phillodryas chamissons* during the breeding season. Oecologia 75, 282–284.

Bridges, C.R., 1993. Ecophysiology of intertidal fish. In: Ranking, J.C., Jensen, F.B. (Eds.), Fish Ecophysiology. Chapman & Hall, London, pp. 375–400.

Cossins, A.R., Bowler, K., 1987. Temperature Biology of Animals. Chapman & Hall, University Press, Cambridge, USA, 390pp.

Crowder, L.B., Magnuson, J.J., 1983. Cost–benefit analysis of temperature and food resource use: a synthesis with examples from the fishes. In: Aspey, W.P., Lustick, S.I. (Eds.), Behavioral Energetics, the Cost of Survival in Vertebrates. Ohio State University Press, Columbus, pp. 189–221.

Dawson, W.R., 1975. On the Physiological Significance of the Preferred Body Temperature of Reptiles. In: D.M. Gates and R.B. (Eds.), On the Physiological Significance of the Preferred Body Temperature of Reptiles.

Dent, L., Lutterschmidt, W.L., 2003. Comparative thermal physiology of two sympatric sinfishes (Centrarchidae: Perciformes) with a discussion of microhabitat utilization. J. Thermal Biol. 28, 67–74.

Gibson, R.N., 1982. Recent studies on the biology of intertidal fishes. Oceanogr. Mar. Biol. Ann. Rev. 20, 263–414.

Hartwell Jr., H.W., Hodg son, G.R., Harvey, B.C., 2001. Distribution of juvenile Coho Salmon in relation to water temperature and tributaries of the Mattole River, California. N. Am. J. Fish. Manag. 21, 464–470.

Hernández, C.E., Neill, P.E., Pulgar, J.M., Ojeda, F.P., Bozinovic, F., 2002. Water temperature fluctuations and territoriality in the intertidal zone: two possible explanations for the elevation distribution body size in Graus nigra. J. Fish Biol. 61, 472–488.

Horn, M.H., Gibson, R.N., 1988. Intertidal fishes. Scient. Am. 258, 54–60.

Horn, M.H., Martin, K.L., Chotkowski, M.A., 1999. Intertidal Fishes. In: Horn, M., Martin, K., Chotkowski, M. (Eds.), Life in Two Worlds. Academic Press, San Diego, CA, USA, 399pp.

Huey, R.B., Kingsolver, J.G., 1993. Evolution of resistance to high temperature in ectotherms. Am. Nat. 142, S21–S46.

Kelsh, S.W., Neill, W.H., 1990. Temperature preferences versus acclimation in fishes: selection for changing metabolic optima. Trans. Am. Fish. Soc. 119, 601–610.

Kooijman, S.A.L.M., 2000. Dynamic Energy and Mass Budget in Biological Systems. Cambridge University Press, Cambridge.

Krebs, J.R., Davis, N.B., 1978. Behavioral Ecology and Evolutionary Approach. Sinahuer Associates, Inc, Sunderland, MA.

Lenski, R.E., Bennett, A.F., 1993. Evolutionary responses of Escherichia coli to thermal stress. Am. Nat. 142, S47–S64.

Marken Lichtenbelt, W.D., 1993. Optimal foraging of a herbivorous lizard, the green iguana in a seasonal environment. Oecologia 95, 246–256.

Marken Lichtenbelt, W.D., Wesselingh, R.A., 1993. Energy budget in free-living green iguanas in a seasonal environment. Ecology 74, 1157–1172.

Metaxas, A., Scheibling, R.E., 1993. Community structure and organization of tidepools. Mar. Ecol. Prog. Ser. 98, 187–198.

Morgan, I.J., Metcalfe, N.B., 2001. The influence of energetic requirements on the preferred temperature of overwintering juvenile Atlantic salmon (Salmo salar). Can. J. Fich. Aquat. Sci. 58, 762–768.

Muñoz, A.A., Ojeda, F.P., 1997. Feeding guild structure of a rocky intertidal fish assemblage in central Chile. Environ. Biol. Fish. 49, 471–479.

Newell, R.C., 1970. Biology of Intertidal Animals. Mrine Ecological Survey Ltd., UK.

Norris, K.S., 1963. The functions of temperature in the ecology of the percoid fish Girella nigrans (Aires). Ecol. Monogr. 33, 23–62.

Parsons, P.A., 1993. The importance and consequences of stress in living and fossil populations: from life-history variation to evolutionary change. Am. Nat. 142, S6–S20.

Porter, W.P., Gates, D.M., 1969. Thermodynamic equilibria of animals with environment. Ecol. Monogr. 39, 245–270.

Pulgar, J., Bozinovic, F., Ojeda, F.P., 1999. Behavioral thermoregulation in the intertidal fish Girella laevifrons (Kyphosidae): the effect of starvation. Mar. Fresh. Behav. Physiol. 32, 27–38.

Raffaelli, D., Hawkins, S., 1986. Intertidal Ecology. Chapman & Hall, London, UK, 356pp.

Sibly, R.M., Calow, P., 1986. Physiological Ecology of Animals: An Evolutionary Approach. Blackwell Scientific Publications, Oxford, 179pp.

Siegel, S., Castellan, N.J., 1988. Nonparametric Statistics for the Behavioral Sciences. McGraw Hill, New York, 399pp.

Sogard, S.M., Olla, B.L., 1996. Food deprivation affects vertical distribution and activity of a marine fish in a thermal gradient: potential energy-conserving mechanism. Mar. Ecol. Progr. Ser. 133, 43–55.

Somero, G.N., 2002. Thermal physiology and vertical zonation of intertidal animals: optima, limits and costs of living. Integ. Comp. Biol. 42, 780–789.

Spicer, J.I., Gaston, K.J., 1999. Physiological Diversity and its Ecological Implications. Blackwell Scientific Publications, Oxford, 256pp.

Spotila, R.J., Standora, E.A., 1985. Energy budgets of ectothermic vertebrates. Am. Zool. 25, 973–986.

Stephenson, T.A., Stephenson, A., 1972. Life Between Tidemarks on Rocky Shore. W.H. Freeman & Co., San Francisco, 425pp.

Stephen, C.A., Porter, W.P., 1993. Temperature, activity, and lizard life histories. Am. Nat. 42, 273–293.

Stepien, C.A., 1990. Population structure, diets and biogeographic relationship of a rocky intertidal fish assemblage in central Chile. High levels of herbivory in a temperate system. Bull. Mar. Sci. 47, 598–612.

Thompson, D.A., Lehner, C.E., 1976. Resilience and rocky intertidal fish community in a physically unstable environment. J. Exp. Mar. Biol. Ecol. 22, 1–29.

Tomanek, L., Helmuth, B., 2002. Physiological ecology of rocky intertidal organisms: a synergy of concepts. Integ. Comp. Biol. 42, 771–775.

Tracy, C.R., Christian, K.A., 1986. Ecological relations among space, time, and thermal niche axes. Ecology 67, 609–615.

Truchot, J.P., Duhamel-Jouve, A., 1980. Oxigen and carbon dioxide in the marine intertidal environment: diurnal & tide changes in rockpools. Respir. Physiol. 39, 241–254.

Varas, E., Ojeda, F.P., 1990. Intertidal fish assemblage of the central Chilean coast: diversity, abundance and trophic patterns. Rev. Biol. Mar. (Valparaiso) 25, 59–70.

Welsh Jr., H.H., Hodgson, G.R., Harvey, B., 2001. Distribution of juvenile Ciho Salmon in relation to water temperatures in tributaries of the Mattole River, California. N. Am. J. Fish. Manag. 21, 464–470.

Wieser, W., 1991. Limitation of energy acquisition and energy use in small poikilotherms: evolutionary implications. Funct. Ecol. 5, 234–240.