

substrates that are colonized by fungi that produce mycotoxins such as the trichothecenes. Over the 1-h period that metabolism was monitored, *C. hemipterus* detoxified MAS at a rate that was 8–10 times (on a per mg protein basis) that of caterpillars that may also encounter the trichothecenes, but are not adapted to feeding on material containing them. The increased rates of MAS metabolism by *C. hemipterus* relative to *S. frugiperda* and *H. zea* may contribute to the lower toxicity of trichothecenes to *C. hemipterus*. This information, which represents the first study of trichothecene metabolism by insects, indicates that insects are capable of adapting to a range of naturally occurring toxins which also includes mycotoxins through enzymatic detoxification.

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4 The mention of firm names or trade products does not imply that they are endorsed or recommended by the U.S. Department of Agriculture over other firms or similar products not mentioned.

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## Limitations on visual food-location in the planktivorous antarctic fish *Pagothenia borchgrevinki*

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**Summary.** The visual threshold for food-location in the antarctic fish *Pagothenia borchgrevinki*, is compared with light conditions and food availability under the ice. Even under the most favourable conditions for vision, *P. borchgrevinki* is operating close to its visual threshold and must often depend on non-visual mechanisms of prey detection.

**Key words.** Antarctic fish; vision; lateral line; prey detection.

The area immediately beneath the annual sea-ice of polar regions has been termed the cryopelagic habitat<sup>2</sup>. In McMurdo Sound, Antarctica, *P. borchgrevinki* is the only common species of fish occupying this zone. During the austral spring these fish feed on macrozooplankton located in the water column<sup>3</sup>. Observations of fish striking lures indicate that feeding can be visually mediated. However, it has also been shown that the mechanosensory lateral line system of these fish is well suited to the

detection of planktonic prey<sup>4,5</sup>. This system may be particularly important not only during winter, but also in summer when snow and ice cover, and phytoplankton and algal blooms, reduce ambient light levels.

What is the lowest light level at which these fish are still able to locate food visually? To answer this question fish were taken from beneath the sea-ice in McMurdo Sound, Antarctica (water temperature  $-1.9^{\circ}\text{C}$ ) and kept in aquaria under controlled lighting conditions. For elec-

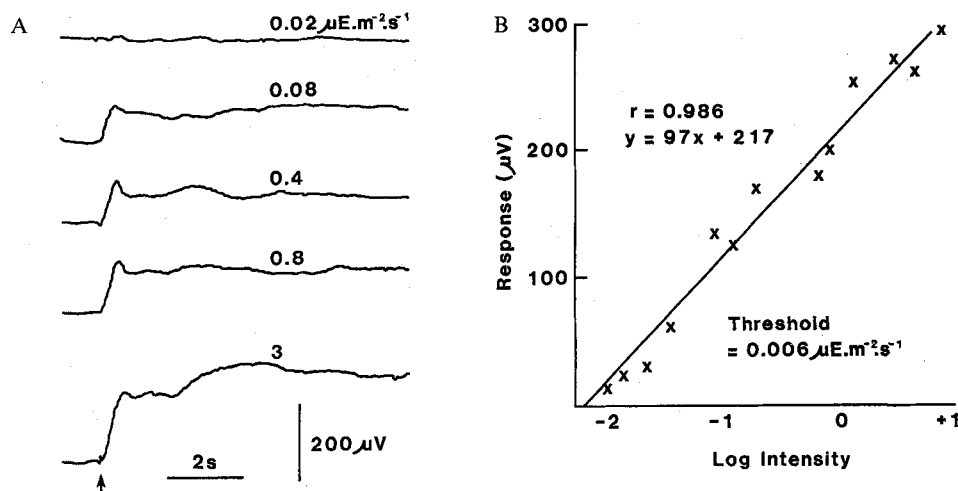


Figure 1. A Sequence of ERG traces (DC – 100 Hz) showing the effects of increasing stimulus intensity. A small spike-like negative 'A' potential is visible on some traces, followed by a clear 'B' wave and slower 'C' wave.

B The measured height of the 'B' wave is plotted against the log of the stimulus intensity, and threshold obtained by extrapolation of the regression line to the 'O' response level.

troretinogram (ERG) experiments, the brain was destroyed by pithing, and the fish laid on its side in an aquarium with the gills irrigated continuously with  $-1.0^{\circ}\text{C}$  to  $-1.5^{\circ}\text{C}$  seawater. A chlorided silver wire was inserted into the eye to record the electrical response of the retina to 200-ms flashes of white light. All preparatory procedures were conducted under dim red light. The ERG response consisted of a small initial negative potential ('A' wave), a clear positive peak ('B' wave) and a long slow 'C' wave (fig. 1). Responses were measured as the height of the 'B' wave, and showed a very good linear relationship when plotted against the log of the stimulus intensity (fig. 1). Electoretinogram thresholds were thus obtained by extrapolation of the regression line to the 'O' response level. For light-adapted fish the mean ERG threshold was  $0.01 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$  ( $\pm 0.001$  SE,  $N = 7$ ), and for dark-adapted fish  $0.0014 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$  ( $\pm 0.0004$  SE,  $N = 7$ ). Histological examination of the retinæ of light and dark adapted fish showed that dark-adaptation resulted in retraction of retinal screening pigment from the outer segment of the rods.

To obtain a behavioural threshold for visual feeding, a group of fish were captured on barbless hooks and placed in a large aquarium. For each behavioural trial, the experimental area was darkened, and a recently killed euphausiid shrimp, suspended on a piece of cotton was placed in the aquarium. The fish were observed on an infrared video system, and light intensity increased stepwise until a clear orientation or strike response was recorded. The lowest light level at which a positive response was recorded was  $0.005 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ . In 13 trials at light intensities less than this, no positive response was recorded, and in trials at higher light intensities 10 out of 14 responses were positive. It is argued here that photopic vision is probably required for prey detection and that the behavioural threshold, which is at the bottom end of the range of the light-adapted ERG

thresholds, best represents the lower boundary of light intensities at which visual food-location is possible.

In order to compare visual thresholds with environmental light levels, vertical profiles of downwelling light were obtained at the fishing site. Snow and ice cover dramatically reduce light intensity as has been previously report-

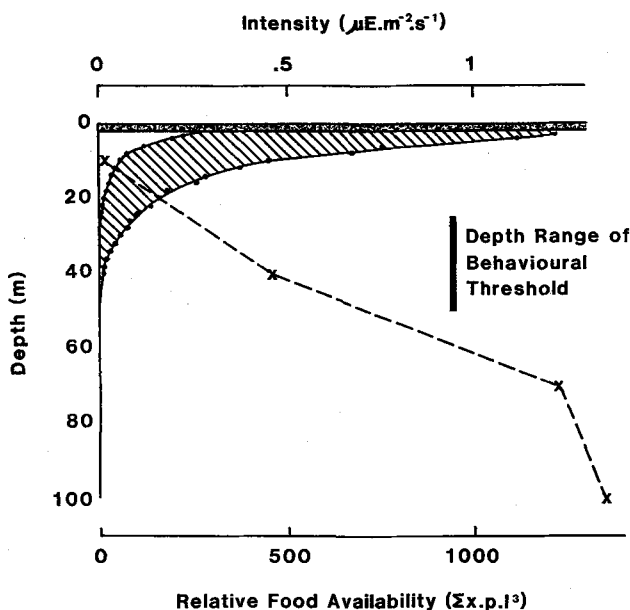


Figure 2. Depth profiles of light intensity and food availability. The shaded layer at the water surface represents the ice cover. Two examples of the relationship between depth and light intensity (upper axis) are plotted on the figure, and the area between them cross-hatched. The lowest light values were obtained by doing a light profile at night when the sun angle was low. The highest light values were found during the middle part of the day. The depth range of light values corresponding to the behavioural threshold for feeding is illustrated on the right of the figure. Also shown is the vertical profile of food availability. The numerical value for food availability at each depth was obtained by summing over prey plankton species, their density ( $x$ ) times their proportional representation in the diet of *P. borchgrevinki* ( $p$ ) times the cube of the length of an average specimen ( $l^3$ ).

ed<sup>5</sup>. Below the ice, light intensity decreases exponentially (fig. 2). Under the best conditions for light penetration (daytime, clear water in early spring) the threshold intensity for visual feeding is reached at about 50 m. With lower sun angles (23.00 h) these light levels are reached at about 25 m (fig. 2). Also indicated in figure 2 is a relative index of food availability. This was obtained by determining the densities of prey plankton at different levels in the water column, and then weighting their density by a measure of their respective importance in the diet of *P. borchgrevinki*. No diurnal movement of these plankton species was observed in these studies. The surprising result is that food availability shows a marked reduction in the upper levels of the water column. This pattern of distribution is unlikely to be caused by hydrological processes, since the smaller non-prey plankton species were uniformly distributed over this depth range. Fish densities, and food intake rates are too low to account for the reduction in terms of removal by fish predation<sup>7</sup>, leaving the most likely explanation as a behavioural response on the part of the plankton. Species subject to fish predation avoid the upper part of the water column where the fish are able to see.

The limitations to visual feeding are thus determined by the animals' own capabilities, environmental light condi-

tions, and the distribution of its prey. It is concluded that, even during the most favourable conditions for visual food-location, *P. borchgrevinki* must be operating close to its visual threshold. In these circumstances non-visual sensory systems such as the lateral line may well be of assistance. When conditions for visual feeding deteriorate due to lower ambient light levels (increased snow and ice cover, sub-ice algal blooms, phytoplankton blooms, low sun angle, and winter darkness) it is to be expected that reliance on non-visual systems will be increased.

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## Testing hypothesized causes of within-island geographic variation in the colour of lizards

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**Summary.** Within the island of Tenerife the lizard *Gallotia galloti* shows geographic variation in a range of features, most notably the colour pattern of breeding males. Numerous (7) specific causal hypotheses, both phylogenetic and ecogenetic, are proposed or plausible for this geographic variation and these are simultaneously tested against the observed multivariate pattern. The hypotheses based on the divergence in allopatry (e.g. the secondary contact of populations from the precursor islands of Anaga and Teno and the separation of high- and low-altitude populations by encircling cloud) are rejected. The hypothesis that the pattern is caused by topographically determined climatic differences within the island is not rejected. The climate may influence the balance between selection for signalling colouration for sexual/territorial purposes and natural selection for crypsis.

**Key words.** Geographic variation; natural selection; sexual selection; multivariate analysis; crypsis.

The study of geographic variation within individual islands has practical advantages. Since the number of species tends to be low the abundance of individuals per species tends to be high; this is an advantage when obtaining samples for quantitative work. Moreover, environmental conditions and character states can change over very short distances with consequent logistic advantages.

On the island of Tenerife (Canaries) the lizard *Gallotia galloti* is very abundant and shows spatial heterogeneity (microgeographic variation) in a range of features<sup>1-3</sup>, the most obvious of which is the colour pattern of sexually mature males<sup>4</sup>. Whilst the colour pattern and behaviour of juveniles and females is cryptic to avoid predation from mainly aerial predators, e.g. *Falco tinnunculus*, breeding males adopt prominent positions and are