

## VISUAL FUNCTION IN FOUR ANTARCTIC NOTOTHENIID FISHES

BY N. W. PANKHURST<sup>1</sup> AND J. C. MONTGOMERY<sup>2</sup>

<sup>1</sup>Leigh Marine Laboratory and <sup>2</sup>Department of Zoology, University of Auckland, Private Bag, Auckland, New Zealand

Accepted 14 November 1988

### Summary

Visual function was investigated in the antarctic fish *Pagothenia borchgrevinki* (Boulenger), *Trematomus bernacchii* Boulenger, *T. centronotus* Regan and *T. hansonii* Boulenger. All *Trematomus* species have large anterior aphakic spaces (indicating a forward feeding vector), whereas *Pagothenia* does not. *Pagothenia* and *T. hansonii*, which both feed in the water column, lack the corneal iridescence displayed by *T. bernacchii* and *T. centronotus*. This is thought to relate to the importance of downwelling light for image formation in *Pagothenia* and *T. hansonii*. Absolute sensitivity thresholds to white and monochromatic light were measured using electroretinogram (ERG) responses in light- and dark-adapted *Pagothenia* and dark-adapted *Trematomus* species. Dark-adapted fish (retinal screening pigment withdrawn from rod outer segments) had thresholds of  $1\text{--}3 \times 10^{-3} \mu\text{E m}^{-2} \text{s}^{-1}$  to a 200 ms pulse of white light, whereas that of light-adapted *Pagothenia* (rod outer segments covered by the retinal screening pigment) was  $1.9 \times 10^{-2} \mu\text{E m}^{-2} \text{s}^{-1}$ . We suggest that the thresholds approximate threshold stimuli for rods and cones, respectively. Measurement of thresholds of light-adapted *Pagothenia* made using a behavioural measure (feeding responses) gave a threshold of  $5 \times 10^{-3} \mu\text{E m}^{-2} \text{s}^{-1}$ . Limits for photopic and scotopic vision are predicted to be reached at depths of 20–40 and 30–60 m, respectively, under snow and ice conditions typically encountered at this time of year. ERG-determined spectral sensitivity curves peaked around 500 nm in all four species and matched the spectral irradiance under the ice. Shifts to longer wavelengths in spectral irradiance caused by sub-ice phytoplankton growth may degrade visual ability. Flicker fusion frequencies (FFFs) reached a maximum value of 15 Hz in *Pagothenia* at the maximum stimulus intensity used, but at environmentally realistic light intensities they were less than 8 Hz. FFFs were lower in all *Trematomus* species than in *Pagothenia*.

### Introduction

The teleost fauna of McMurdo Sound, Antarctica, is dominated by members of the family Nototheniidae, which has undergone extensive species radiation (MacDonald *et al.* 1987). The photic environment encountered by the fish is of low

Key words: fish vision, antarctic fish, *Pagothenia*, *Trematomus*, Nototheniidae.

intensity, even at maximum levels of illumination during summer (Littlepage, 1965; Sullivan *et al.* 1983), yet casual observation of at least one species (the planktivorous *Pagothenia*) suggests that under adequate photic conditions feeding is visually mediated (Foster *et al.* 1987). It might, then, be expected that nototheniid fishes would display visual modifications similar to those of species from other low-light environments (e.g. deep sea), where fish commonly have increased retinal sensitivity (Pankhurst, 1987). However, structural examination of nototheniid retinæ suggests that there has been no specific adaptation, at least among shallower species, for vision in low light (Meyer-Rochow & Klyne, 1982; Eastman, 1988). Eastman (1988) has suggested that there may be sufficient light penetration during summer to permit ocular function in morphologically unspecialized eyes.

Here we investigate some functional correlates of previously reported retinal structure in three benthic (*T. bernacchii*, *T. centronotus* and *T. hansonii*) and a cryopelagic (*Pagothenia borchgrevinkii*) nototheniid fish. Visual function was assessed in relation to habitat, feeding mode and ambient light levels, by recording electroretinograms (ERGs) to establish thresholds to white and monochromatic light, and flicker fusion frequencies.

Earlier workers have used ERGs to investigate visual function in fish (reviewed by Ali & Muntz, 1975). More recently, the technique has fallen into disfavour among visual physiologists because it is not precise enough to allow assignment of electrical changes to the activity of particular cell types. However, ERGs are relatively simple to record and are considered to be useful for comparative investigations of vision in relation to retinal morphology or environmental conditions (Ali & Muntz, 1975). Visually mediated feeding behaviour was used as an additional assessment of photopic visual threshold in *Pagothenia*.

### Materials and methods

Fish were captured from McMurdo Sound, Antarctica, during October and November 1987, by fishing with baited hooks or small metal lures through holes drilled in the sea ice. *Trematomus* species were captured by fishing on the bottom at 20–30 m, whereas *Pagothenia* were captured from just under the sea ice over 200 m of water. At capture, fish were placed in plastic aquaria in a mobile laboratory (ice-hole marine lab, IHML) stationed over the fishing hole. Sea water at ambient temperature ( $-1.86^{\circ}\text{C}$ ) was circulated through the holding aquaria using a submersible pump placed in the ice hole. Fish were either maintained for up to several days until the experiment, or killed immediately for morphometric studies. Fish were killed by spinal transection, and total length was measured. Eyes were then excised from selected fish chosen to cover a full size range, pierced laterally to allow penetration of fixative, and fixed for 24 h in Bouin's fixative, before storage in 70% ethanol. Fixed material was dehydrated in an ethanol series, embedded in paraffin, and median transverse sections ( $7\ \mu\text{m}$ ) were stained with haematoxylin and eosin.

*Electroretinograms*

Electroretinograms (ERGs) were recorded from pithed fish that were partially submerged lateral surface upwards in a flow-through chamber. Water flow was maintained over the gills *via* a tube placed in the mouth and connected to an overhead reservoir. Reservoir temperature was  $-1.86^{\circ}\text{C}$ , whereas the temperature in the chamber rose slowly over the course of an ERG run (30–60 min) to  $0-1.5^{\circ}\text{C}$  owing to the higher air temperature of IHML. A chlorided silver wire was inserted through a small hole in the cornea and the amplified and filtered (d.c., 100 Hz) ERGs were recorded on FM tape for later analysis. Single flash stimuli (duration 200 ms) were delivered using a fibre-optic light guide placed normally to the eye at a distance of 1 cm from the corneal surface, and connected in series to a filter box, camera shutter and Schott KL 1500 halogen light source (colour temperature 3000 K). Stimulus duration was controlled using the camera shutter, and stimulus intensity by insertion of neutral density filters (Kodak Wratten no. 96, density = 1.0) in the filter box. Monochromatic single flash stimuli were produced using Kodak Wratten band pass filters. Filter numbers, band widths (greater than 10% peak transmittance) and peak transmittance were measured with an HP8452 diode array spectrophotometer, and were as follows. Filter 70,  $>662$  nm, peak 700 nm; filter 72B, 588–634 nm, peak 604 nm; filter 73, 558–598 nm, peak 570 nm; filter 74, 510–562 nm, peak 528 nm; filter 75, 462–518 nm, peak 482 nm; filter 50, 430–474 nm, peak 450 nm. Stimulus intensity was measured at the corneal surface using a LiCor LI-185A quantum meter with an LI-190S quantum sensor and, for monochromatic stimuli, intensities were corrected for the spectral response of the meter (Lambda Instruments Co. data). Because the neutral density filters used have lower transmittance below 500 nm than at the other wavelengths used, intensities obtained using combinations of Wratten band pass and neutral density filters were measured directly to the detection limits of the sensor ( $0.002 \mu\text{E m}^{-2} \text{s}^{-1}$ ), rather than extrapolated from the nominal values of the neutral density filters. Stimulus intensities below the detection limit of the sensor (for 528 and 482 nm only) were extrapolated from nominal filter values, after correction for the differential absorbance of the neutral density filters. Multiple flash stimuli were produced by introducing a mechanical strobe wheel into the light path between the light source and the camera shutter.

All fish were tested using a standard protocol. Sensitivity thresholds to white and monochromatic light were established by recording ERG responses to increasing light intensity. The ERG response was standardized as the height of the b wave, and plotted against the logarithm of light intensity (I). The response showed strong linearity, and thresholds were determined by calculating zero intercepts from linear regression of  $\log I$  on response. Curves with a correlation coefficient of less than 0.9 were discarded from the analysis. Flicker fusion frequencies (FFFs) were determined by exposing fish to stimulus trains of frequency 1, 2.5, 5, 7.5, 10, 12.5 and 15 Hz (stimulus duration of 12, 10.6, 9.5, 8.4, 7.6 and 7.0 ms, respectively). Fish used for ERG recording were either light- or dark-adapted before experiment. Light adaptation was achieved by maintaining

fish in ambient IHML light ( $0.2\text{--}0.6 \mu\text{E m}^{-2}\text{s}^{-1}$ ) for 2 h or more. Dark-adapted fish were kept in complete darkness for 2–4 h and briefly exposed (up to 5 min) to an orange photographic safelight (peak transmittance 600 nm) of intensity  $0.15 \mu\text{E m}^{-2}\text{s}^{-1}$ , for electrode placement. Experiments were conducted in the dark. The effects of light- and dark-adaptation were examined in *Pagothenia* in sectioned retinae from fish that had either been transferred from IHML ambient light to complete darkness for 1, 2 or 4 h, or transferred from complete darkness (12 h) to IHML ambient light for 0.5, 1, 2 or 5 h. In addition, retinae were removed from selected fish of all species at the end of ERG runs and processed for histology. Retinal sections were examined for shifts in the position of retinal screening pigment and cone ellipsoids.

#### *Behavioural thresholds*

Light intensity thresholds of intact light-adapted *Pagothenia* were assessed using a behavioural technique. Twelve fish were captured on barbless hooks and transferred with minimal handling to an opaque white plastic tank (dimensions 600 mm × 900 mm × 500 mm deep) filled to a depth of 180 mm. Approximately half the water surface was covered with a floating polystyrene sheet to provide overhead cover. Fish were allowed to settle for 24 h before experiment. A silicone diode video camera attached to a recorder and monitor was positioned over the exposed portion of the water surface, and the tank illuminated obliquely with an infrared light source. Behavioural responses to food items were then recorded over a range of stimulus intensities ( $<0.002\text{--}0.4 \mu\text{E m}^{-2}\text{s}^{-1}$ ). Initial experiments were conducted using foil lures suspended on a fine thread; however, consistent orientation or strike responses were only obtained when the visual stimulus was combined with an olfactory stimulus (minced fish odour). Subsequent trials were therefore conducted with dead euphausiids (*Euphausia crystallorophias*) 10–26 mm long attached to a fine thread. For each trial, the hut was darkened and a euphausiid introduced into the tank, suspended from a thread. Bait position and fish response were viewed on the video monitor. Light intensity was increased in steps until an orientation (confirmed turn or point towards the bait), approach or strike was recorded. In practice, turns or approaches were nearly always followed by a strike. The bait was then replaced, the tank returned to full darkness and the trial repeated. Eleven trials were conducted at approximately 30 min intervals over a 6 h period. Fish fed enthusiastically on minced fish at the beginning and end of the experiment, indicating that nil responses were not due to satiation.

#### *Ambient sub-ice light profiles*

Ambient light intensities under the sea ice were measured using an LI-192SA underwater quantum sensor attached to the LiCor meter. Light profiles were measured at IHML (depth 200 m, discontinuous snow cover) at 15.00 and 23.00 h, at a sampling hole near McMurdo Base (depth 20 m, continuous snow cover) at 16.00 h, and through a natural crack in the sea ice near the Erebus Ice Tongue,

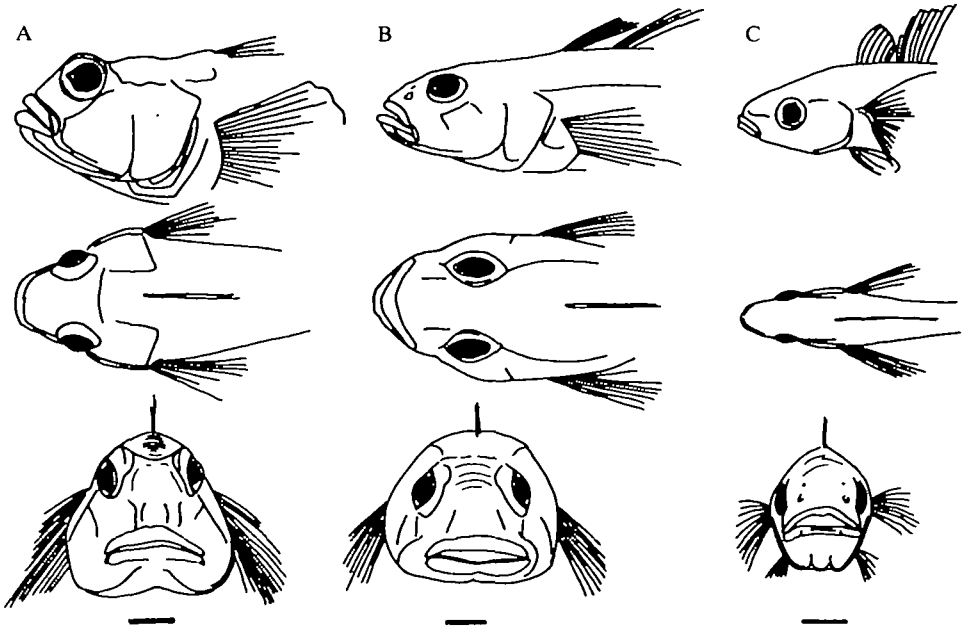


Fig. 1. Lateral, dorsal and frontal profiles of (A) *Trematomus centronotus*, (B) *T. hansonii*, (C) *Pagothenia borchgrevinkii*, drawn from photographs. Scale bars, 2 cm.

McMurdo Sound (depth >40 m, continuous snow cover) at 17.00 h, during the second week of November. Ice thickness was 2–4 m at all sites.

#### Statistics

Spectral sensitivity values of light- and dark-adapted *Pagothenia* were compared using two-way analysis of variance (ANOVA) and SNK tests on arc-sin transformed data. Exponential curves were fitted to intensity–depth profiles of underwater light using the ‘Grapher’ program package.

### Results

#### Visual morphology

Features of the external eye morphology of the four species examined are shown in Fig. 1. *T. bernacchii* and *T. centronotus* have similar ocular morphology, with laterally directed eyes situated high on the head, a large anterior aphakic space and obvious corneal iridescence. In *T. hansonii* the eyes occupy a dorsolateral position with the visual axis directed obliquely upwards. An anterior aphakic space is present, but there is no obvious corneal iridescence. *Pagothenia* has centrally located, laterally oriented eyes with only small aphakic spaces and, as in *T. hansonii*, no corneal iridescence. Examination of the retinal structure of the species confirmed the reports of earlier workers (Meyer-Rochow & Klyne, 1982; Eastman, 1988).

Table 1. *Threshold intensities ( $\mu\text{E m}^{-2} \text{s}^{-1} \times 10^{-3}$ ) for initiation of ERGs by a 200 ms flash of white light*

Species	Fish length (range) (mm)	Threshold intensity	
		Light-adapted	Dark-adapted
<i>Pagothenia borchgrevinki</i>	123–245	19.3 ± 11.5 (N = 7)	1.4 ± 0.4 (N = 8)
<i>Trematomus bernacchii</i>	168–233	–	3.0 ± 0.6 (N = 4)
<i>T. centronotus</i>	171–259	–	1.0 ± 0.3 (N = 3)
<i>T. hansonii</i>	176–218	–	1.0 ± 0.1 (N = 3)

Threshold intensities were obtained from ERG–response curves (details in text).  
Values are means ± s.e.

Retinal sections from light-adapted fish had retinal screening pigment that was fully extended over the rod outer segments. Sections from sequentially sampled dark-adapting *Pagothenia* showed fully extended pigment after 1 h in the dark, half sclerad retraction after 2 h in the dark, and full retraction after 4 h. Dark-adapted *Pagothenia* (12 h) showed a small vitread extension of the screening pigment after 30 min in the light, and full vitread pigment extension after 1 h in the light. No displacement of cone ellipsoids was detected. Retinae of fish sampled after ERG recording showed pigment retraction and extension following dark- and light-adaptation, respectively.

#### *Electoretinograms*

ERG traces showed classic a, b and c waves at high stimulus intensities, but merged to a single peak at near-threshold intensities. Stimulus–response curves were strongly linear, although in some cases responses saturated at the highest stimulus intensities. Plateau regions were edited from the curves before regression analysis. Average thresholds to single flashes of white light were  $1\text{--}3 \times 10^{-3} \mu\text{E m}^{-2} \text{s}^{-1}$  for dark-adapted fish, whereas the threshold of light-adapted *Pagothenia* was an order of magnitude higher (Table 1). There was no apparent relationship between fish size and light threshold in any of the species.

As with thresholds to white light, monochromatic light thresholds were lower in dark- than in light-adapted fish (Table 2). The relationship between sensitivity (the reciprocal of threshold) and stimulus wavelength is shown for *Pagothenia* in Fig. 2. Spectral sensitivity curves for *Trematomus* species were very similar (data not shown). Maximum sensitivity occurred at 482 nm, with a rapid fall-off in sensitivity at longer and shorter wavelengths. There was no difference between the spectral sensitivities of *Pagothenia* in the light- or dark-adapted states.

Changes in flicker fusion frequencies (FFFs) with stimulus intensity are shown for *Pagothenia* in Fig. 3. At stimulus intensities of  $1 \mu\text{E m}^{-2} \text{s}^{-1}$  or above, curves were similar for both light- and dark-adapted fish. Below  $1 \mu\text{E m}^{-2} \text{s}^{-1}$ , FFFs of light-adapted fish fell away quickly whereas those of dark-adapted fish declined steadily with decreasing stimulus intensity. Responses were beginning to saturate

Table 2. Threshold intensities ( $\mu\text{E m}^{-2} \text{s}^{-1} \times 10^{-3}$ ) for initiation of ERGs by a 200 ms flash of monochromatic light

Wavelength (nm)	<i>Pagothenia borchgrevinki</i>		<i>Trematomus bernacchii</i> (N = 3)	<i>T. centronotus</i> (N = 3)	<i>T. hansonii</i> (N = 2)
	Light (N = 6)	Dark (N = 8)			
700	>80	>80	>80	>80	80, 80
604	60 ± 10	33 ± 9	51 ± 15	25 ± 11	55, 14
570	37 ± 12	19 ± 7	16 ± 2	11 ± 5	18, 3
528	7 ± 3	1.5 ± 0.7	5 ± 2	0.9 ± 0.4	1.0, 1.4
482	4.5 ± 1.9	1.0 ± 0.5	1.4 ± 0.9	0.3 ± 0.07	0.3, 0.6
450	14 ± 8	5 ± 1.5	6 ± 3	0.8 ± 0.3	1.0, 0.7

Threshold intensities were obtained from ERG-response curves (details in text).

Values are means ± s.e., except for *T. hansonii* where both values are given.

All *Trematomus* measurements are from dark-adapted fish.

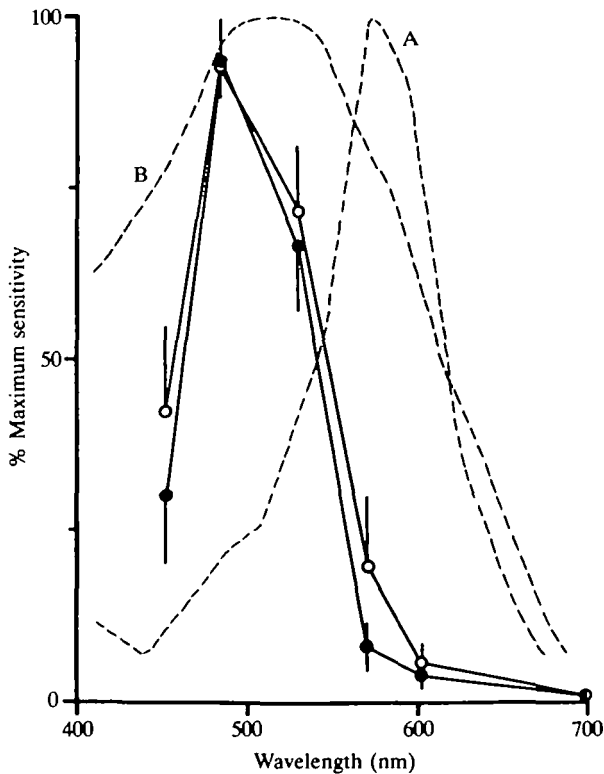


Fig. 2. Relationship between spectral sensitivity ( $1/\text{threshold}$ ,  $\mu\text{E m}^{-2} \text{s}^{-1}$ ) and stimulus wavelength in light- (open circles,  $N = 6$ ) and dark-adapted (closed circles,  $N = 8$ ) *Pagothenia* (mean ± s.e.). Downwelling spectral irradiances as a percentage of maximum with (A) and without (B) sub-ice microbial flora are shown as dashed lines (data from Sullivan *et al.* 1983).

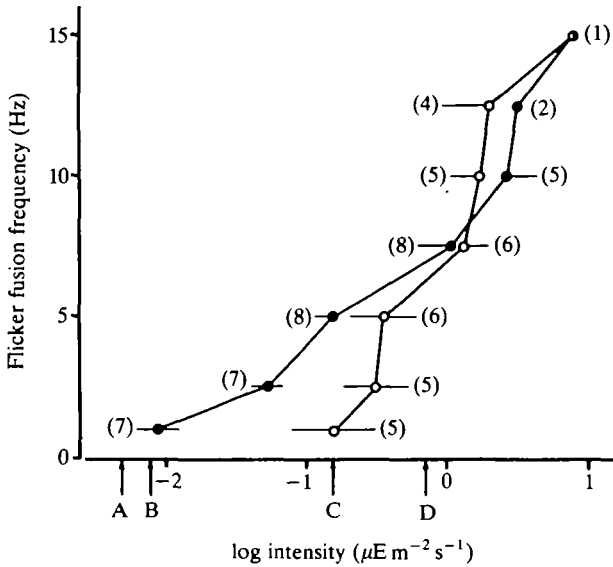


Fig. 3. Change in mean flicker fusion frequency  $\pm$  s.e., with stimulus intensity for light- (open circles) and dark-adapted (closed circles) *Pagothenia*. Number of measurements is given in parentheses. Markers on the intensity scale show photopic behavioural threshold (A), and downwelling intensities (IHML 15.00 h) at 40 (B), 20 (C) and 5 m (D).

at the highest stimulus intensity available. Threshold intensities at 1 Hz flicker were all higher than thresholds for 200 ms pulses, with ranges of  $0.3\text{--}2.0 \times 10^{-2}$  ( $N = 8$ ),  $1.2\text{--}7.6 \times 10^{-2}$  ( $N = 4$ ),  $1.2\text{--}41.0 \times 10^{-2}$  ( $N = 3$ ) and  $3.0\text{--}79.0 \times 10^{-2}$   $\mu\text{E m}^{-2} \text{s}^{-1}$  ( $N = 3$ ) for *Pagothenia*, *T. bernacchii*, *T. centronotus* and *T. hansonii*, respectively. At the maximum stimulus intensity used ( $7.4 \mu\text{E m}^{-2} \text{s}^{-1}$ ) FFFs were 12.5–15.0, 7.5–10.0, 5.0–10.0 and 5.0 Hz for the four species, respectively. At stimulus intensities near the maximum ambient light level recorded ( $0.5 \mu\text{E m}^{-2} \text{s}^{-1}$ ), FFFs were 5.0–10.0, 2.5–5.0, 1.0–5.0 and 2.5 Hz for the four species, respectively, and approaching or below threshold for 1 Hz flicker at intensities near the ambient levels recorded at 20 m.

#### Behavioural thresholds

Light intensity thresholds for feeding behaviour in *Pagothenia* are shown in Table 3. At the lowest intensity ( $<0.002 \mu\text{E m}^{-2} \text{s}^{-1}$ ), there were no responses to euphausiid baits. At low intensities ( $0.002\text{--}0.01 \mu\text{E m}^{-2} \text{s}^{-1}$ ) fish showed positive responses in about half the trials, whereas at higher intensities most trials resulted in feeding responses. The lowest intensity at which a response was recorded was  $0.005 \mu\text{E m}^{-2} \text{s}^{-1}$ ; below this value, fish in all 13 trials showed no response, whereas above this value there were feeding responses in 10/14 trials. Accordingly, the behaviourally determined threshold for feeding is thought to lie at about  $0.005 \mu\text{E m}^{-2} \text{s}^{-1}$ .



Table 3. *Threshold intensities for feeding behaviour in Pagothenia borchgrevinki presented with dead euphausiids*

Number of trials	Light intensity ( $\mu\text{E m}^{-2} \text{s}^{-1} \times 10^{-3}$ )			
	2	2-10	10-50	>50
No response	11	5	1	1
Response	0	3	3	4
Total	11	8	4	5

Response = orientation or strike (details in text).

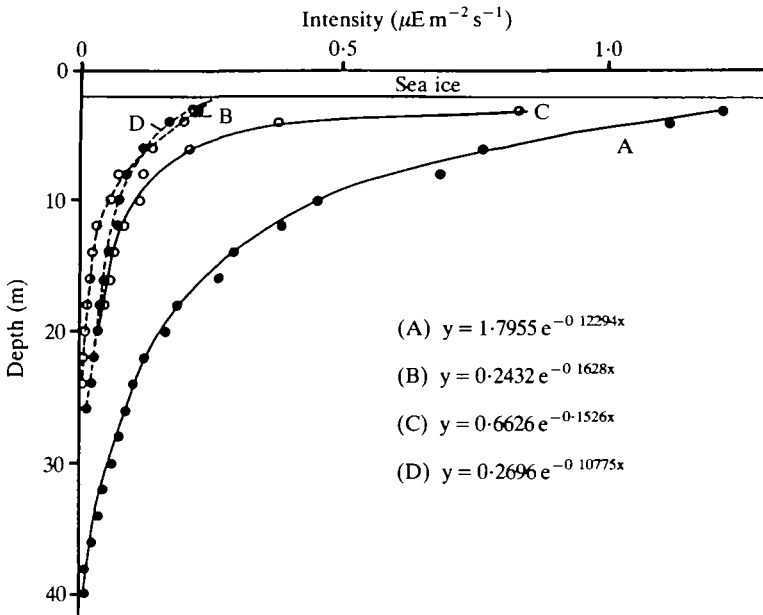


Fig. 4. Depth-intensity profiles of downwelling light measured at (A) IMHL 15.00 h, (B) IHML 23.00 h, (C) McMurdo fish-hut 16.00 h and (D) Erebus ice-crack 17.00 h.

*Ambient sub-ice light profiles*

Highest light intensities were recorded at IHML at 15.00 h, with measurable light penetration ( $0.002 \mu\text{E m}^{-2} \text{s}^{-1}$ ) to 40 m (Fig. 4). At 23.00 h, light levels immediately under the ice were a log unit lower, and measurable light was attenuated at 24 m. Profiles similar to IHML values at 23.00 h were found at the McMurdo and Erebus ice-crack sites during the day, where the snow cover was more complete. Laterally incident light fell to immeasurable levels at one-third to half the depth for downwelling light.

### Discussion

Eye position in the four fish appears to be primarily related to feeding vectors. The two benthic species that utilize benthic prey (*T. bernacchii* and *T. centro-notus*) have laterally directed vision, as does the cryopelagic *Pagothenia*. *T. hansonii* is also benthic but appears to feed mainly from the water column overhead (B. A. Foster & J. C. Montgomery, unpublished data), and has eyes that are dorsolateral rather than lateral. Aphakic spaces are present in all the species, but are most prominent in the three species of *Trematomus*. Aphakic spaces are thought to allow accommodation of the lens along a visual axis (Sivak, 1973) and/or to increase peripheral vision (Munk & Frederiksen, 1974). In either case, the direction of the aphakic space indicates the direction of greatest visual interest (Lythgoe, 1979). The large anterior aphakic space in *Trematomus* indicates that there is a forward feeding vector, whereas for the planktivorous *Pagothenia* the area of visual interest may extend over a wider arc.

Neither of the species that feed from the water column (*Pagothenia* and *T. hansonii*) has obvious corneal iridescence. Iridescent corneas, most common among benthic and demersal species, are thought to screen out bright downwelling light that would otherwise mask less bright laterally incident light from the region of maximum visual interest (Lythgoe, 1979). The absence of iridescence in the water-column feeders suggests that downwelling light is of some interest, and this may be related to the detection of pelagic prey as silhouettes. In contrast, the benthic feeding *Trematomus* species rely more on laterally incident light and may need to screen out some of the downwelling light. Downwelling light was four times brighter than laterally incident light on the bottom at the sample site in this study.

Rod numbers are low in all four species (Meyer-Rochow & Klyne, 1982; Eastman, 1988; this study) compared with other shallow marine teleosts (27/30 species from shallow New Zealand waters have higher rod densities), outer segment lengths are similar to or shorter than those of shallow New Zealand species, and convergence ratios (rods: bipolars) are lower than those of 26/30 New Zealand species (N. W. Pankhurst, unpublished data). This is in agreement with the contention of Eastman (1988) that antarctic nototheniids do not show specific retinal adaptations to enhance sensitivity.

ERG thresholds to white light occurred at light intensities as low as  $4 \times 10^{-4} \mu\text{E m}^{-2} \text{s}^{-1}$  in dark-adapted fish but were 1–2 orders of magnitude higher in light-adapted *Pagothenia*. Although it is possible that cone activity contributes to the b wave of the ERG even at low stimulus intensities, the downward shift in threshold of dark-adapted *Pagothenia* indicates that a new population of photoreceptors (i.e. rods) has been recruited by the process of dark-adaptation. Histological examination of retinæ showed that the retinal screening pigment was retracted from the outer segments only in the dark-adapted fish. It is therefore reasonable to assume that ERG thresholds in the light- and dark-adapted states approximate the absolute thresholds for cone- and rod-mediated vision, respectively.

Downward extrapolation of ambient light profiles (Fig. 4) suggests that the average depth limits for visual function under the variety of snow and ice conditions encountered lie in the range of 30–60 m and 20–40 m for scotopic and photopic vision, respectively. With the exception of silhouettes, most visual information is derived from light reflected from surfaces of visual interest rather than downwelling light itself (Dartnall, 1975), so the depth limits for laterally oriented vision may be considerably shallower than the values measured in this study. Although *Pagothenia* is thought to occur mainly in the cryopelagic zone, the depth ranges of *T. bernacchii*, *T. centronotus* and *T. hansonii* are reported to extend down to 550, 200 and 550 m, respectively, in McMurdo Sound (Eastman & DeVries, 1982). This suggests that even during summer *Trematomus* species are dependent on nonvisual systems over a substantial part of their distribution range.

Minimum ERG thresholds of the nototheniids in this study fall at the lower end of the range determined for a variety of dark-adapted shallow marine species (approximately  $6 \times 10^{-4}$  to  $3 \times 10^{-1} \mu\text{E m}^{-2} \text{s}^{-1}$ ) by Kobayashi (1962) using similar methods. As in the present study, light adaptation resulted in an increase in the ERG threshold. More recent work by Glass *et al.* (1986) has suggested that behavioural measures of absolute sensitivity give much lower estimates of visual thresholds. The Atlantic mackerel *Scomber scombrus* has a threshold for schooling behaviour (which is thought to be visually mediated) of  $1 \times 10^{-7} \mu\text{E m}^{-2} \text{s}^{-1}$ . Although it is possible that ERG techniques underestimate intensity thresholds, it is to be expected that *Scomber* thresholds should be lower than those of nototheniids. The rod density in the retina of *Scomber* is two orders of magnitude higher than that of the species examined here (Meyer-Rochow & Klyne, 1982; N. W. Pankhurst & J. C. Montgomery, unpublished data). Clearly there is some need to confirm ERG scotopic thresholds using a behavioural measure, but a suitable response criterion has not yet been found.

Behaviourally determined thresholds for feeding in light-adapted *Pagothenia* ( $0.005 \mu\text{E m}^{-2} \text{s}^{-1}$ ) are consistent with minimum ERG thresholds ( $0.006 \mu\text{E m}^{-2} \text{s}^{-1}$ ) and are thought to represent the minimum light level for recruitment of cones. Cone-mediated feeding behaviour by *Pagothenia* in early summer is probably limited to the upper 40 m of the water column. At deeper levels, fish would have to detect larger prey as contrast changes *via* rods and use nonvisual senses. The proposed photopic threshold for *Pagothenia* is higher than the value of about  $1 \times 10^{-4} \mu\text{E m}^{-2} \text{s}^{-1}$  determined for *Gadus morhua* by Anthony (1981) using a cardiac conditioning technique, but within the range for enhanced (visually mediated) predatory activity in *Abramis brama* ( $9 \times 10^{-5}$  to  $2.4 \times 10^{-2} \mu\text{E m}^{-2} \text{s}^{-1}$ , Townsend & Risebrow, 1982).

Temporal resolving power reached maximum values of 15 Hz in *Pagothenia* at maximum stimulus intensity, but at light levels equivalent to the highest intensity recorded under the ice, FFF averaged 7.5 Hz. FFF fell quickly to 1 Hz at intensities well above the average threshold of light-adapted *Pagothenia* to a 200 ms pulse. This suggests that the ability to fix moving images on the retina degrades rapidly with depth, and at the limits of photopic function only slow moving or stationary

prey could be detected. Dark-adapted *Pagothenia* showed similar FFFs to light-adapted fish at high intensities, but FFFs fell more slowly with decreasing intensity than in light-adapted fish. This supports the contention that a different class of photoreceptors is active in dark-adapted fish at low light intensities. Maximum FFF was lower in *Trematomus* species (5–10 Hz) than in *Pagothenia*, which may be related to vision in the generally lower light levels of the benthic habitat. The lowest FFF values were found in *T. hansonii* which has the highest rod density of the four species examined. Low temporal acuity may be the price of enhanced contrast discrimination in this species.

The observation that absolute thresholds to 1 Hz flicker (12 ms pulse) were higher than thresholds determined for single 200 ms pulses indicates that, at or near threshold, stimulus duration exerts an effect on the value of absolute threshold. An effect of this type might explain the apparent disparity between ERG and behaviourally determined thresholds (Glass *et al.* 1986). Behavioural criteria will generate lower thresholds if the visual stimulus on which they are based is persistent relative to the stimuli presented during ERG studies.

FFF values for a number of shallow temperate marine species at light intensities near the maximum value used in this study (about  $9.5 \mu\text{E m}^{-2} \text{s}^{-1}$ ) recorded at 10–20°C are surprisingly close to values for *Pagothenia* (e.g. *Halichoeres* 13 Hz, *Sillago* 22 Hz, *Lagocephalus* 20 Hz, *Fugu* 16 Hz, *Chysophrys* 18 Hz; Kobayashi, 1962). FFF values of fish have been shown to be very temperature-sensitive (reviewed by Ali, 1975), which suggests that *Pagothenia* shows considerable temperature compensation in terms of temporal resolving power. This is consistent with other studies showing that antarctic fish display neural cold adaptation (MacDonald *et al.* 1987). The lower FFF maxima recorded from *Trematomus* species may indicate less temperature compensation than in *Pagothenia*. However, in view of the similarities of the visual systems of *Pagothenia* and *Trematomus* species, it seems more likely that the lower temporal resolving power in *Trematomus* is related to vision at generally lower light levels.

Spectral sensitivity measurements indicate that overall retinal sensitivity peaks around 500 nm. This presumably reflects the absorptive maximum of rod pigment or pigments in the dark-adapted state and, as there was no shift in spectral sensitivity with light adaptation in *Pagothenia*, possibly that of the dominant cone pigments as well. Retinal spectral sensitivity is blue-shifted relative to the spectral response of the quantum meter used to record light levels in the present study (response at 500 nm = 76% of peak response at 660 nm). As a result, absolute sensitivities to white light may have been underestimated to a small degree, and the rate at which visually relevant light is attenuated with depth will have been overestimated. The nature of the light meter used does not allow us to establish the level of error that this might introduce; however, the similarity between thresholds to white and monochromatic light suggests that the error is not large.

Downwelling spectral irradiance under hard ice with a minimal platelet layer peaks at 490–550 nm (Sullivan *et al.* 1983) but shows a marked red shift with the development of the sub-ice microbial community later in the summer. Nototheniid

visual function under these conditions is likely to be considerably impaired. The shift in spectral irradiance with phytoplankton growth may also be associated with decreasing water clarity and increased light attenuation (El-Sayed *et al.* 1983). A combination of shift in spectral irradiance, increasing light scatter and decreasing light intensity as a result of summer phytoplankton growth may make vision during the later part of the summer as intractable a problem as during the period of winter darkness.

In summary, the retinae of the nototheniids examined in this study do not show structural specialization for vision in light of low intensity. Behavioural and ERG experiments indicate that visual function will be minimal below about 60 m under sea ice, and that visually mediated feeding will be restricted to relatively large slow-moving prey. Spectral sensitivity would appear to be appropriate for the ambient spectral irradiance for only part of the antarctic summer. Visual function does not appear to have been modified as a response to the specific demands of the antarctic environment. Fish probably use vision preferentially to feed under optimal photic conditions, but it seems clear that for much of the year nonvisual sensory systems of the type described by Montgomery & MacDonald (1987) for *Pagothenia* would dominate. The successful radiation of the Nototheniidae appears to have been mainly the result of their ability to cope with very low temperature (MacDonald *et al.* 1987) and, in the absence of major competition from other fish groups, sensory systems may only have to be adequate rather than optimized for specific features of the environment.

Thanks are extended to Heiko Weix and John Cargill for technical assistance, and to Georgina Andersen for the preparation of histological material. This study was funded by the University Grants Council of New Zealand, and logistic support was provided by the Antarctic Division of the Department of Scientific and Industrial Research.

### References

- ALI, M. (1975). Temperature and vision. *Rev. can. Biol.* **34**, 131–186.
- ALI, M. & MUNTZ, W. R. A. (1975). Electroretinography as a tool for studying fish vision. In *Vision in Fishes* (ed. M. A. Ali), pp. 159–167. New York: Plenum Press.
- ANTHONY, P. D. (1981). Visual contrast thresholds in the cod *Gadus morhua* L. *J. Fish Biol.* **19**, 87–104.
- DARTNALL, H. J. A. (1975). Assessing the fitness of visual pigments for their photic environment. In *Vision in Fishes* (ed. M. A. Ali), pp. 543–563. New York: Plenum Press.
- EASTMAN, J. T. (1988). Ocular morphology in Antarctic Notothenioid fishes. *J. Morph.* **196**, 283–306.
- EASTMAN, J. T. & DEVRIES, A. L. (1982). Buoyancy studies of notothenioid fishes in McMurdo Sound, Antarctica. *Copeia* **1982**, 385–393.
- EL-SAYED, S. Z., BIGGS, D. C. & HOLM-HANSEN, O. (1983). Phytoplankton standing crop, primary productivity and near surface nitrogenous nutrient fields in the Ross Sea, Antarctica. *Deep Sea Research* **30**, 871–886.
- FOSTER, B. A., CARGILL, J. M. & MONTGOMERY, J. C. (1987). Planktivory in *Pagothenia borchgrevinki* (Pisces: Nototheniidae) in McMurdo Sound, Antarctica. *Polar Biol.* **8**, 49–54.
- GLASS, C. W., WARDLE, C. S. & MOJSIEWICZ, W. R. (1986). A light intensity threshold for schooling in the Atlantic mackerel *Scomber scombrus*. *J. Fish Biol.* **29**, 71–81.

- KOBAYASHI, H. (1962). A comparative study of electroretinogram in fish, with special reference to ecological aspects. *J. Shimonoseki Coll. Fish.* **11**, 407–538.
- LITTLEPAGE, J. L. (1965). Oceanographic investigations in McMurdo Sound Antarctica. *Biol. Antarct. Seas* **2** (Antarctic Res. Ser. 5), 1–37.
- LYTHGOE, J. N. (1979). *The Ecology of Vision*. Oxford: Clarendon Press. 244pp.
- MACDONALD, J. A., MONTGOMERY, J. C. & WELLS, R. M. G. (1987). Comparative physiology of Antarctic fishes. *Adv. Mar. Biol.* **24**, 321–388.
- MEYER-ROCHOW, V. B. & KLYNE, M. A. (1982). Retinal organisation of the eyes of three nototheniid fishes from the Ross Sea (Antarctica). *Gegenbaurs morph. Jahrb. Leipzig* **128**, 762–777.
- MONTGOMERY, J. C. & MACDONALD, J. A. (1987). Sensory tuning of lateral line receptors in Antarctic fish to the movements of planktonic prey. *Science* **235**, 195–196.
- MUNK, O. & FREDERIKSEN, R. D. (1974). On the function of aphakic apertures in teleosts. *Vidensk. Meddel. fra Dansk Naturhist. For.* **137**, 65–94.
- PANKHURST, N. W. (1987). Intra- and interspecific changes in retinal morphology among mesopelagic and demersal teleosts from the slope waters of New Zealand. *Env. Biol. Fish.* **19**, 269–280.
- SIVAK, J. G. (1973). Interrelation of feeding behaviour and accommodative lens movement in some species of North American freshwater species. *J. Fish. Res. Bd Can.* **30**, 1141–1146.
- SULLIVAN, C. W., PALMISANO, A. C., KOTTMEIER, S., MCGRATH GROSSI, S., MOE, R. & TAYLOR, G. T. (1983). The influence of light on development and growth of sea-ice microbial communities in McMurdo Sound. *Antarct. J. U.S.* **18**, 177–179.
- TOWNSEND, C. R. & RISEBROW, A. J. (1982). The influence of light level on the functional response of a zooplanktivorous fish. *Oecologica* **53**, 293–295.