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Phil. Trans. R. Soc. Lond. B 2000 **355**, 1183-1186
doi: 10.1098/rstb.2000.0663

THE ROYAL SOCIETY

doi 10.1098/rstb.2000.0663

The relationship between the position of the retinal area centralis and feeding behaviour in juvenile black bream *Acanthopagrus butcheri* (Sparidae: Teleostei)

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The topography of the neurons in the retinal ganglion cell layer of juvenile black bream *Acanthopagrus butcheri* changes during development. The region of high cell density, the area centralis (AC), relocates from a temporal (central) to a dorsal (peripheral) position within the dorso-temporal retinal quadrant. To ascertain whether the differences in the position of the AC during development are related to feeding behaviour, we monitored fishes that were given a choice of food. A range of feeding behaviour patterns was recorded in individual fishes. The smallest fishes (8–15 mm standard length (SL)) took live food from the water column. Following weaning onto pellets, fishes exhibited a preference for taking food from either the substrate or the surface (but not both). When greater than 20 mm SL, a number of individuals then divided their time between surface and substrate feeding before all fishes became exclusive benthic feeders at a stage between 50 and 80 mm SL. Three individual fishes, for which behaviour patterns were categorized, were killed and the topography of the retinal ganglion cell layer analysed. A range of positions for the AC was found with the smallest fish (12 mm SL) possessing a region of high cell density in the temporal retina. In a larger fish (70 mm SL), feeding from both the substrate and the surface, the AC was found in an intermediate dorso-temporal position. The AC of a fish (51 mm SL) preferentially taking food from the substrate was located in a dorsal position.

Keywords: fishes; development; visual axis; retinal ganglion cell

1. INTRODUCTION

The retinal ganglion cells of vertebrates exhibit regions of increased density, correlating with high photoreceptor densities and providing the retina with areas of increased resolving power (Hughes 1977). In adult teleost fishes, the position of such a region, known as the area centralis (AC), has been related to the main visual axis of feeding. For example, planktivores have a temporal AC corresponding to a region of the visual field in front of the fishes. In contrast, species that strike at prey on the substrate have an AC in the dorsal retina that provides high acuity in the visual field below the fishes (Collin & Pettigrew 1988*a*,*b*). We have recently found developmental changes in the position of the ganglion cell AC in the black bream *Acanthopagrus butcheri* (Sparidae: Teleostei) (Shand *et al.* 1999). The timing of the changes are extremely variable but, in general, the majority of juveniles between 10 and 15 mm standard length (SL), possess a region of high ganglion cell density located in temporal retina. Fishes between 15 and 80 mm SL possess an AC in either the dorso-temporal region or the dorsal retina. During relocation, the AC also moves from a central retinal position, close to the optic nerve head, to a position close to the retinal periphery. A few individuals up to at least 30 mm SL maintain a temporal AC. Fishes larger than 80 mm SL always have a dorsal AC. In this paper, we present preliminary data relating feeding behaviour to the variable position of the AC.

2. METHODS

Larval black bream were obtained from a local hatchery and initially fed on live *Artemia*. Following metamorphosis at 8–10 mm SL (*ca.* day 25 post-hatch), larvae were fed both pellets (Nippai ML[1], Fukui & Co. Ltd, 0.2–0.4 mm diameter) and *Artemia* for 20 days. Larvae greater than 15 mm SL were only fed pellets. Observations of feeding behaviour were recorded from glass aquaria, each containing four individuals, using a video camera. Fishes were monitored from metamorphosis to over six months of age (*ca.* 80 mm SL). Prior to all observations, the fishes were starved for at least 3 h and then simultaneously presented with (i) live *Artemia* that swam in the water column (until the bream were weaned at 15 mm SL), (ii) floating pellets, and (iii) soaked pellets that fell to the bottom of the tank. The percentage of pecks at food from the water column, the surface or the bottom was scored over a period of 10 min. Individual fishes for which feeding data was obtained were then killed by immersion in a lethal dose of the anaesthetic methane sulphonate salt (MS222, Sigma-Aldrich Pty, NSW, Australia). Measurements of body

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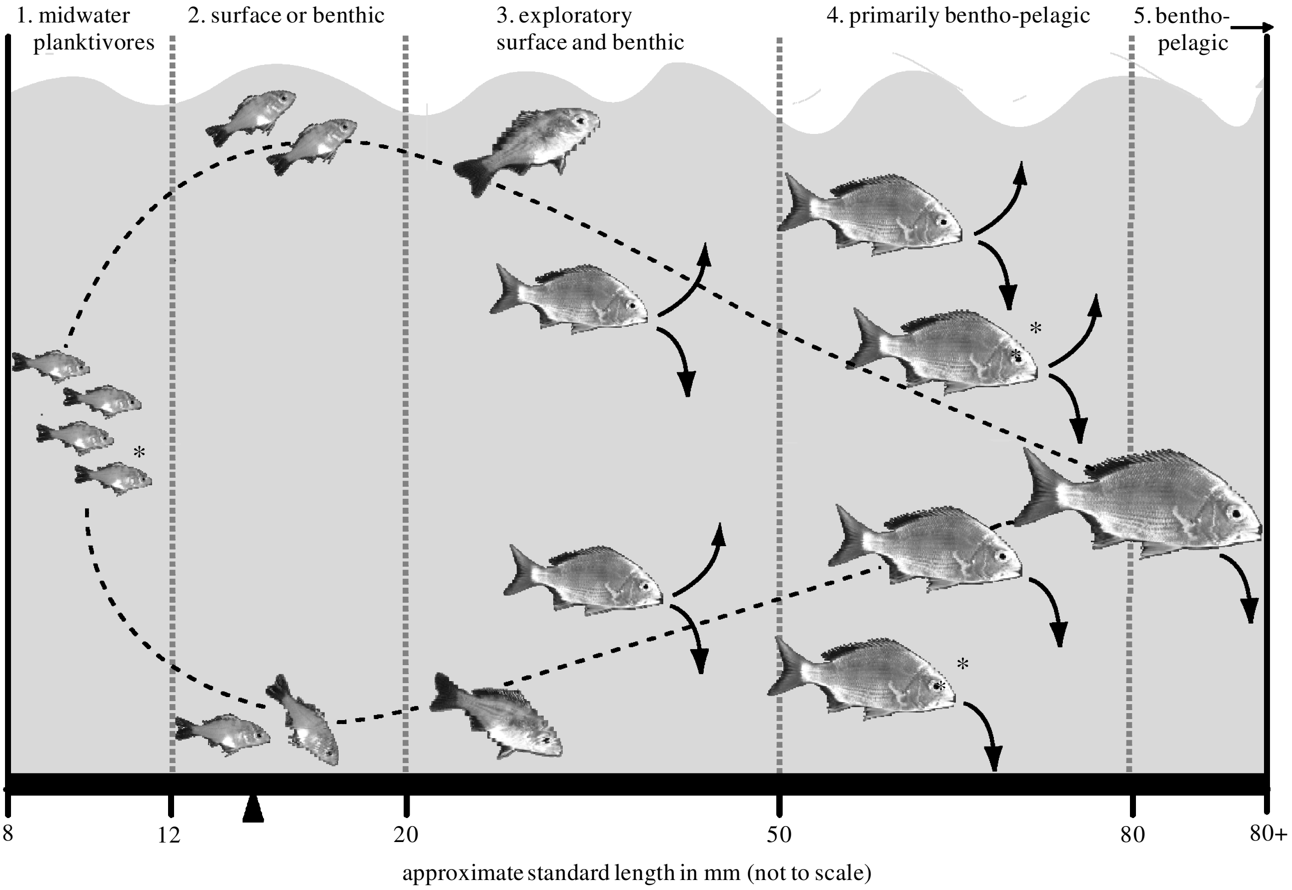

Figure 1. Schematic diagram showing the preferred feeding behaviours of aquarium-reared black bream at different stages of growth. The fishes were not fed *Artemia* after a size of 15 mm SL (arrowhead). The initial midwater planktivore phase was followed by a stage when the fishes fed either at the surface or from the substrate. After the fishes reach a size of *ca*. 20 mm SL, the majority began an exploratory stage when they fed from both the surface and the substrate (depicted by arrows), although some individuals remained as exclusive benthic feeders. During subsequent growth fishes gradually became bentho-pelagic and, after attaining a size of 80 mm SL, all adopted a position within the lower part of the water column and fed entirely from the substrate. Fishes marked with an asterisk represent individuals where their behaviour was monitored and their retinas subsequently examined (see figure 2).

length (SL) and eye and lens diameter were performed on all fishes when freshly killed. Experimental procedures were approved by the University of Western Australia Ethics Committee and followed the guidelines of the National Health and Medical Research Council of Australia. The topography of neurons in the ganglion cell layer was investigated in retinal whole mounts prepared using the methods outlined by Collin & Pettigrew (1988*a*,*b*). The orientation of the eye was recorded by a ventral cut along the falciform process in fishes of all sizes. Whole mounts were stained for Nissl substance and all neurons in the ganglion cell layer counted to provide at least a 1% count. Isodensity contour maps were constructed by hand.

3. RESULTS AND DISCUSSION

The sequence of different feeding behaviours during development was divided into five stages and represented schematically in figure 1. In general, small fishes (8–12 mm SL) fed exclusively from the water column (stage 1: midwater planktivores) before beginning to take pellets from either the substrate or the surface (stage 2: either surface or benthic). During stage 2, the smallest fishes feeding from the bottom were initially observed to 'up-end' when searching and pecking. The surface-feeding fishes then began to feed from the substrate as they grew larger (stage 3: exploratory surface and benthic). During this stage some of the black bream originally taking food only from the substrate also began to take food from the surface while others maintained the benthic feeding pattern. Larger fishes (50–80 mm SL) 'cruised' in a horizontal plane and, after sighting food, positioned themselves at an angle of 45° to peck from the substrate (stage 4: primarily bentho-pelagic). Fishes (> 80 mm SL) became bentho-pelagic (stage 5) in their feeding behaviour.

The position of the AC, together with feeding data, is shown for three individuals in figure 2. The smallest fish was a midwater planktivore, which spent the majority of its time feeding on *Artemia* in the water column prior to sacrifice, and was found to possess a region of high cell density in temporal retina (figure 2*a*). Out of the two larger fishes, one moved between the substrate and the surface to feed and had an AC in an intermediate position in dorso-temporal retina (figure 2*b*), whereas the other had been taking food from the substrate only and was found to possess a dorsal AC (figure 2*c*).

The preliminary observations reported here are to be followed by a report of more extensive behavioural analysis of a larger number of fishes (Shand *et al.* 2000*a*).

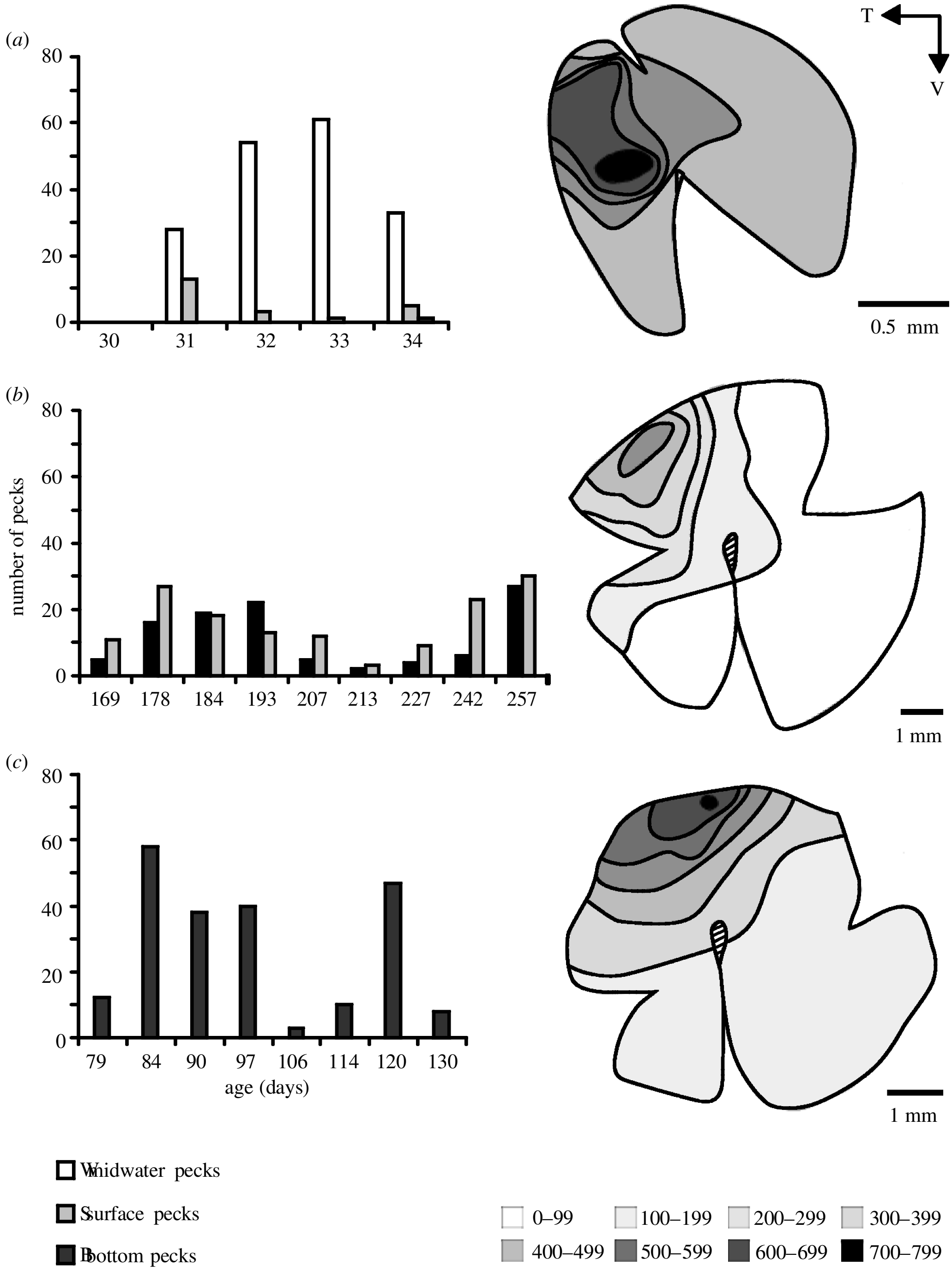

Figure 2. Records of feeding behaviour and the retinal ganglion cell layer topography for three individuals. (*a*) 12 mm SL, feeding on live food within the water column; (*b*) 70 mm SL, feeding from both the surface and the substrate; (*c*) 51 mm SL, feeding from the substrate only. Note also how the area centralis (AC) is located in a central position in small fishes with a temporal AC, but in a peripheral position in larger fishes where the AC lies in a dorsal location. T, temporal; V, ventral. Cell densities are $\times 10^2\,\mathrm{mm}^{-2}$.

However, these results show that changes in the position of the AC are related to changes in feeding behaviour during development, where fishes change their main visual axis from frontal to lower frontal as they adopt a bentho-pelagic feeding mode. We are unable to say whether the relocation of the AC is a result of exploiting a benthic food source or whether benthic feeding begins once a pre-programmed movement of the AC has taken place. It would be interesting to carry out experiments that restrict feeding from the substrate to see whether the relocation of the AC is delayed. McCormick (1999) was able to delay the morphological changes associated with metamorphosis and settlement of the coral reef fish *Acanthurus triostegus* by maintaining the pre-settlement larvae in cages in the pelagic environment. Thus, it may also be possible to delay the relocation of the AC in black bream by feeding them exclusively at the surface.

Many marine teleosts hatch as pelagic larvae and spend varying lengths of time feeding on plankton before settling to a reef or benthic mode of life (McCormick & Makey

1997). Changes in photoreceptor mosaic and visual pigment complement have also been shown to occur concomitantly with changes in behaviour, habitat and spectral light environment (for a review, see Beaudet & Hawryshyn 1999). In the case of some coral reef teleosts, changes in behaviour at settlement (or during the transition) from the oceanic pelagic environment to the coral reef habitat are abrupt, occurring over only a number of days (McCormick & Makey 1997). However, the settlement process in the black bream is more gradual and the size at which a benthic feeding mode is finally adopted, at least in aquarium-reared fishes, can vary from between 15 and 80 mm SL (i.e. over a period of six months). Black bream living in different estuaries in Western Australia are known to have different feeding strategies and growth rates, some feeding on benthic molluscs while others are omnivorous (Sarre *et al.* 2000). It is possible that variation in the timing of the formation of a dorsal AC could be a useful adaptive feature allowing black bream to exploit different food resources. Fishes with an AC located in an intermediate (dorso-temporal) location may be able to continue opportunistic foraging in the water column during the early stages of their life cycle.

The mechanisms that control the relocation and maintenance of a peripheral AC raise interesting developmental questions. Fish retinas grow by continual addition of cells at the periphery and retinal stretching (Johns 1977). Thus, the cohort of cells forming the AC must change continually. Such a situation contrasts with that observed by Easter (1992) in adult fishes, in which asymmetrical retinal growth maintains a high density of cells in temporal retina, resulting in the bending of the falciform process and the displacement of the optic nerve head towards the temporal retina. We have seen no evidence of such mechanisms in black bream during retinal growth. It is thought that differential cell addition at the retinal margins and cell death in the central retina results in the formation of a dorsal AC (Shand *et al.* 2000*b*,*c*).

We thank Greg Jenkins and Ken Frankish of the Fremantle Maritime Centre (Fremantle, Australia) for rearing and providing the black bream. Andreia Schineanu assisted with the preparation of the figures. This work was supported by a National Health and Medical Research Council (Australia) Program Grant (no. 993219).

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