COVER ILLUSTRATION

From the top down

Body symmetry in animals came very early as shown by the metazoan imprints from the Ediacaran period (600–543 million years ago). Even now, symmetry represents a sign of fitness.

Why, then, did the approximately 500 species of flatfish of the order *Pleuronectiformes* discard such a predominant characteristic primarily with the eye and orbit?

Flatfish, as represented by the sand dab, *Citharychthys*, on the cover, hatch from eggs as bilaterally symmetrical, transparent fry that live near the ocean surface more or less as plankton and have the same fusiform body shape as most other fish. In these animals, transparency, except for the pigment in the eye, is a camouflage technique and is common to many piscine species. High in the water column these young flatfish feed on smaller planktonic creatures until metamorphosis. Their metamorphosis is vastly different from other species of fish because they become flattened and compressed and simultaneously move to deeper water to become bottom dwelling. That alone would not be so unusual, but along with the bodily compression, one eye, with corresponding bony changes, migrates to the opposite side of the body to join the other eye as seen in the sand dab on the cover. The now asymmetric fish settle to ocean floor lying on their blind side. This surprising transformation illustrates the plasticity of evolutionary development to satisfy a specialised niche. In their adult form, some species of these odd fish will have both eyes exclusively on the left side, some on the right side, and some species may have predominantly, but not exclusively, one side or the other.

This odd transformation of 90 degrees requires body modifications that leave only one anal and dorsal fin, assorted gastrointestinal tract modifications, a pale benthic or floor-facing side, and bony changes to accommodate the migrated eye. Once the transformation is complete, both eyes will have migrated (at least to some degree) and only the eye that will have changed sides will have a complete bony orbit. When compared to other fish, the extraocular muscles of an adult flatfish have a similar neuronal input and

Winter flounder.

compensatory eye movements, and the eyes have the same spatial orientation as each other as before metamorphosis, although some changes in extraocular muscle sizes occur. Surprisingly, there is little change in the semicircular canals and otoliths of the vestibular system. This means that metamorphosis must also include substantial changes to the neural pathways in order to maintain a normal vestibulo-ocular reflex. Symmetry around the visual axes, and visual fields is maintained. It is almost as if the eyes retained their position and the body of the fish rotated beneath them (Graf W, *et al*, *J Neurophysiol* 1985;54:887). To satisfy that extreme makeover, the brain rearranges itself in response, suggesting that it is visual symmetry that is ultimately important.

More surprising changes can be seen during this transition. The fry, high in the water column, have only one class of photoreceptors—single cones in a hexagonal pattern. The opsin contained in those photoreceptors has a peak sensitivity at approximately 520 nm in the winter flounder (fig). That would be in the “green” range, but with no other visual pigment, these young fish live their lives in a monochromatic world. Not surprisingly, this fits well with the animal’s ecology as its environment is full of light with little need for rods. Cone distribution resembles the adults of many other fish (*BJO* cover, October 2004) with a concentration of these cells in the temporal aspect to permit visualisation and discrimination of prey directly in front of it (Evans IE, Fernald RD, *Vis Neurosci* 1993;10:1055).

Metamorphosis, driven by thyroid hormone, brings ecological change, and the retina must accommodate that as

well. In a dramatic transformation of the retina reminiscent of the dramatic changes seen in the frog visual system (*BJO* cover, November 2004), flatfish develop rods and three different varieties of cones. The retinal mosaic changes from a regularly spaced hexagonal pattern to a square one consisting of four double cones surrounding a central single cone. The visual pigments are restricted to a specific variety of cone. For example, all single cones have opsins that are short wavelength at approximately 461 nm—or “blue,” and all double cones have two opsins, one in each of the two cones—529 or “green” and 547 or “red.” Note that even the opsin from the pre-metamorphic retina changed too. The dorsal retina develops a higher concentration of cones (as opposed to a temporal concentration in the pre-metamorphic fish) and a higher concentration of photoreceptors overall, compared to the ventral retina.

What is the ecological purpose of this change and why abandon symmetry? The benthic (bottom dwelling) character and omnivorous, opportunistic nature of the adult means that it stays flat on the bottom or even nestled under the mud with only its eyes showing, allowing it to burst into the water column to capture unwitting prey often near the bottom. Predation comes from above, and in the lower light levels of the ocean floor (even if it is only 40–50 metres) rods would be required to see forms and movement in lower light levels. Additionally, in bright light, these fish can change colour, at least to some extent, and will do so to match their background. Cones with visual pigments sufficient to permit colour vision are required to interpret the colour of the surround.

From the top down this is indeed an interesting transformation, although we still do not understand how a single variety of opsin in the pre-metamorphic fish develops into four different opsins in the adult, nor do we fully understand the purpose and transformation of the photoreceptors into double cones.

I R Schwab

University of California Davis, 4860 Y Street,
Suite 2400, Sacramento, CA 95817, USA;
irschwab@ucdavis.edu

Photograph by James Brandt.