Interrelation of Feeding Behavior and Accommodative Lens Movements in Some Species of North American Freshwater Fishes

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Accommodation, in response to atropine and pilocarpine, was measured retinoscopically and photographically in seven species of freshwater fishes. These species accommodate in varying magnitudes and directions by means of lenticular movements. The common white sucker (Catostomus commersoni) and the goldfish (Carassius auratus) accommodate mainly in the lateral direction (5-10 diopters), whereas the common bluegill (Lepomis macrochirus), northern rock bass (Ambloplites rupestris), and yellow perch (Perca flavescens), exhibit a larger accommodative ability which occurs primarily along the rostral-caudal axis (up to 40 diopters in the yellow perch). The rainbow trout (Salmo gairdneri) accommodates equally along the lateral and rostral-caudal axes. No accommodative response occurs in the northern black bullhead (Ictalurus melas). Reference to the diets and feeding habits of the above species suggests that the magnitude and principal direction of accommodation is a response to the visual demands of a particular life history.


In the first major study of accommodation in fishes, Beer (1894) concluded that they were myopic and that during accommodation the lens moved toward the retina via contraction of the retractor lentis muscle. Studies by Verrier (1927, 1928, 1934, and 1947), Rochon-Duvigneaud and Verrier (1927), Bourguignon and Verrier (1930), and Baron and Verrier (1951) suggested that the retractor lentis is not contractile, that fish are hyperopic, and that they accommodate by increasing the axial length of the eye. More recent work (Tamura 1957; Kimura and Tamura 1966; Meyer and Schwassmann 1970) agree with the accommodative mechanism proposed by Beer and indicate that the primary axis of accommodative lens movements is rostral-caudal. Pumphrey (1961) has suggested that accommodative lens movements occur principally along the rostral-caudal axis in order to maintain a constant lens-to-retina distance for different directions of regard. Baylor (1967) reported accommodative changes toward hyperopia which

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were associated with aggressive displays induced by fright.

The accommodative changes observed in the studies mentioned above were, for the most part, induced by electrical stimulation of the retractor lentis muscle or by the use of pharmacological agents. Little attention has been directed at the neural control of accommodation in fishes. However, evidence is available (Meader 1936a, 1936b, Nicol 1952) implicating the parasympathetic nervous system. The first portion of the present study was designed to test the validity and reliability of using parasympathomimetics and parasympatholytics to stimulate and relax the accommodative system of living fishes by demonstrating a repeatable gradient of accommodative response to treatment dose level. The second portion of the study was designed to determine the magnitude and axis of accommodative lens movements in several species of North American freshwater fishes of differing visual requirements.

**Materials and Methods**

In drug-dosage experiments the following procedure was employed. Three goldfish were injected intraperitoneally, at minimum intervals of 3 days, with varying levels of atropine sulphate or pilocarpine hydrochloride. The refractive error was measured retinoscopically before and after treatment, the difference being the magnitude of the induced accommodative change.

Measurements were made in a lateral direction of regard only. No effort was made to control ocular movement. However, measurements were made only when the pupil plane of the test eye appeared to be perpendicular (as indicated by maximum iridial reflection) to the axis of retinoscopic observation; i.e. perpendicular to the side of the test aquarium. Both eyes were tested to determine the bilaterality of the accommodative response. In several instances, heart rate was recorded using external electrodes (Hester 1968) to provide some indication of parasympathetic activity at the extreme dose levels.

In the second portion of the study the accommodative response was measured along various directions of regard. A test aquarium specifically constructed to permit retinoscopic observation along various axes was employed (Fig. 1). Curare was administered to prevent ocular movement.

The accommodative response found retinoscopically was verified by photography. This method consisted of measuring the lens movements photographically, calculating the refractive power of the lens from its photographic dimensions, and then determining the change in refractive error due to the movement in question.

In many fishes the pupil is elongated at the rostral margin; the lens therefore does not extend to the rostral margin of the pupil. Walls (1967) referred to this as the "aphakic space" and considered it a means of enlarging the binocular field of vision. In those species with an aphakic space, one assumes that the major accommodative effort would occur along the rostral-caudal axis. This possibility was strengthened by preliminary results for the goldfish accommodative response. These data suggested that the goldfish, which does not have an aphakic space, accommodates primarily along the lateral axis.

The following fishes were studied: northern black bullhead, Ictalurus melas melas; goldfish, Carassius auratus; coast rainbow trout, Salmo gairdneri irideus; common bluegill, Lepomis macrochirus macrochirus; northern rock bass, Ambloplites rupestris rupestris; and yellow perch, Perca flavescens. In the bullhead, sucker, and goldfish, the pupil is round or almost round. In the rainbow trout, bluegill, rock bass, and yellow perch the rostral pupil elongates increasingly in the order mentioned.

Aqueous solutions of atropine sulphate and pilocarpine hydrochloride (respective inhibitor and excitor of the parasympathetic nervous system) were administered intraperitoneally. Dosage was a function of subject size, species, and desired magnitude of accommodative effort. Atropine sulphate concentrations varied from 2 to 20

![Fig. 1. Test aquarium with fish in place indicating the directions and facets through which retinoscopic measurements were made.](image-url)
Fig. 3. Dorsal view of the left eye of a yellow perch under the influence of atropine (a) and pilocarpine (b). The diameter of the dark bar alongside the cornea is 1.0 mm. Rostrum is to the right.

Sivak — J. Fish. Res. Board
TABLE 1. Refractive errors (with pilocarpine/with atropine) indicating accommodative lens movements in seven North American species of freshwater fishes. Abbreviations for the axis of lens movement are as follows: R = rostral, D-R = dorsal-rostral, V-R = ventral-rostral, L = lateral, D = dorsal, V = ventral, D-C = dorsal-caudal, V-C = ventral-caudal, C = caudal. All values are raised to the nearest $10^6$ diopter. Unless indicated as (-) all values indicate hyperopia.

<table>
<thead>
<tr>
<th>Species</th>
<th>R</th>
<th>D-R</th>
<th>V-R</th>
<th>L</th>
<th>D</th>
<th>V</th>
<th>D-C</th>
<th>V-C</th>
<th>C</th>
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<tr>
<td>northern black bullhead</td>
<td>4.5/4.5</td>
<td>4.5</td>
<td>12.7/12.5</td>
<td>7.0</td>
<td>7.0/7.0</td>
<td>7.0/7.0</td>
<td>7.0/7.0</td>
<td>7.0/7.0</td>
<td>7.0/7.0</td>
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<td>6.0/6.0</td>
<td>9.0/9.0</td>
<td>9.0/9.0</td>
<td>8.0/8.0</td>
<td>8.0/8.0</td>
<td>8.0/8.0</td>
<td>8.0/8.0</td>
<td>8.0/8.0</td>
</tr>
<tr>
<td>avg</td>
<td>5.8/5.8</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>5.5/5.5</td>
</tr>
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<td>common white sucker</td>
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<td>-16/16.0</td>
<td>8.5/4.3</td>
<td>6.0/4.0</td>
<td>-9.0/-12.0</td>
<td>-0.5/-1.5</td>
<td>0.0/-0.5</td>
<td>1.5/-1.5</td>
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<tr>
<td>sucker</td>
<td>10.5/9.5</td>
<td>11.5/9.0</td>
<td>6.0/5.0</td>
<td>16.0/11.0</td>
<td>11.0/10.5</td>
<td>12.0/10.0</td>
<td>11.0/9.5</td>
<td>8.0/6.0</td>
<td>10.0/8.5</td>
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<tr>
<td>avg</td>
<td>6.7/5.5</td>
<td>5.4/4.1</td>
<td>-7.3/-7.7</td>
<td>11.8/7.2</td>
<td>7.7/6.5</td>
<td>-4.3/-3.3</td>
<td>4.3/3.7</td>
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<td>4.4/2.8</td>
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<td>-7.5/-7.5</td>
<td>4.0/-5.0</td>
<td>-3.0/-6.0</td>
<td>-4.0/-7.0</td>
<td>-1.0/-0.8</td>
<td>-0.5/-0.1</td>
<td>0.0/-0.3</td>
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<tr>
<td>avg</td>
<td>2.3/0.9</td>
<td>2.2/0.8</td>
<td>1.2/0.5</td>
<td>11.4/0.4</td>
<td>5.1/2.3</td>
<td>4.0/1.7</td>
<td>7.5/7.8</td>
<td>4.9/1.0</td>
<td>7.1/9.1</td>
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<td>rainbow trout</td>
<td>11.0/7.0</td>
<td>7.0/5.0</td>
<td>4.5/5.0</td>
<td>15.0/7.0</td>
<td>8.0/10.0</td>
<td>8.0/7.0</td>
<td>4.8/6.5</td>
<td>6.0/7.5</td>
<td>4.5/11.0</td>
</tr>
<tr>
<td>avg</td>
<td>6.5/0.5</td>
<td>4.8/3.0</td>
<td>1.8/-1.0</td>
<td>11.0/5.0</td>
<td>7.0/-8.5</td>
<td>5.5/4.5</td>
<td>4.5/6.5</td>
<td>4.8/7.0</td>
<td>5.0/9.5</td>
</tr>
<tr>
<td>avg</td>
<td>6.8/3.5</td>
<td>4.0/-1.0</td>
<td>4.0/-1.5</td>
<td>12.0/5.0</td>
<td>7.7/-7.5</td>
<td>6.5/5.2</td>
<td>3.8/5.8</td>
<td>4.9/7.0</td>
<td>4.2/9.3</td>
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<td>common bluegill</td>
<td>9.0/-17.0</td>
<td>1.5/-18.0</td>
<td>3.0/-16.0</td>
<td>13.0/6.5</td>
<td>9.0/8.0</td>
<td>3.0/6.0</td>
<td>-5.0/-16.0</td>
<td>-2.5/-15.5</td>
<td>0.0/-20.0</td>
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<tr>
<td>avg</td>
<td>9.0/-12.2</td>
<td>3.3/-16.3</td>
<td>3.7/-16.3</td>
<td>12.5/3.3</td>
<td>5.7/4.2</td>
<td>2.7/3.7</td>
<td>-5.0/-11.3</td>
<td>-3.8/-12.8</td>
<td>-4.3/16.0</td>
</tr>
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<td>northern rock bass</td>
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<td>4.5/-11.3</td>
<td>3.0/-10.3</td>
<td>11.0/1.5</td>
<td>5.0/0.5</td>
<td>3.0/3.5</td>
<td>1.0/5.0</td>
<td>1.0/7.0</td>
<td>0.0/4.0</td>
</tr>
<tr>
<td>avg</td>
<td>6.3/-15.0</td>
<td>4.5/-15.3</td>
<td>0.3/-16.0</td>
<td>11.0/-0.5</td>
<td>6.0/-1.0</td>
<td>3.0/0.0</td>
<td>1.0/-8.5</td>
<td>0.5/0.9</td>
<td>2.0/10.0</td>
</tr>
<tr>
<td>avg</td>
<td>8.5/-20.0</td>
<td>4.5/-18.0</td>
<td>-4.5/-18.0</td>
<td>12.0/-1.0</td>
<td>8.0/-4.0</td>
<td>-1.5/-4.0</td>
<td>0.5/7.5</td>
<td>-6.5/9.5</td>
<td>0.5/14.0</td>
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<td>yellow perch</td>
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<td>9.0/-6.0</td>
<td>7.0/-27.0</td>
<td>15.0/-1.0</td>
<td>11.0/4.0</td>
<td>1.0/-24.0</td>
<td>-1.0/-6.5</td>
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<td>0.5/-10.0</td>
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<tr>
<td>avg</td>
<td>9.0/-20.0</td>
<td>6.0/-17.0</td>
<td>4.0/-22.0</td>
<td>15.0/-2.5</td>
<td>9.5/4.0</td>
<td>0.5/-39.5</td>
<td>0.0/-13.5</td>
<td>-3.5/-7.5</td>
<td>-0.8/-14.0</td>
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<tr>
<td>avg</td>
<td>8.2/-25.3</td>
<td>6.3/-11.0</td>
<td>4.5/-37.0</td>
<td>13.3/-1.8</td>
<td>9.2/3.7</td>
<td>-2.2/-34.2</td>
<td>0.8/10.2</td>
<td>-2.7/4.3</td>
<td>1.2/11.7</td>
</tr>
</tbody>
</table>
The refractive index of the lens is 1.654 (Matthiesson 1880).

The lens radius was calculated from measures of chord.

Indices of the aqueous and vitreous humors may be assumed (Walis 1967) to be 1.33 while the effective eye was relatively simple since the lens is the only refractive axis.

It was possible to compare the magnitude of movement along the rostral-caudal axis with that along the lateral axis.

A short focal lens and a micrometer controlled movable image screen; a flat glass plate was mounted in front; a range of refractive errors was measured retinoscopically in air and in water (through the aquarium wall). No significant difference was recorded.

Because the lens of most fishes protrudes beyond the pupil plane and is therefore easily visible, it is possible to independently verify the accommodative response as measured retinoscopically by an alternate method (Kimura and Tamura 1966). The following procedure was employed: The eye was photographed from above with a camera mounted on dissecting microscope, with the subject submerged to minimize excessive respiratory movements. Illumination was provided by way of a dissecting microscope light mounted beneath the aquarium. With the fish properly positioned the angles formed by the points joining the center of each facet to the fish's body was parallel to the horizontal axis of the aquarium. With the fish properly positioned the angles formed by the points joining the center of each facet to the center of the pupil were as follows: rostral and caudal = 15°; dorsal and ventral = 22°; lateral = 90°; dorsal-rostal, ventral-rostal, dorsal-caudal and ventral-caudal = 18°. With the above test aquarium it was possible to measure directional accommodative responses for the left eye only. To determine the dose-response of accommodation to atropine sulphate and pilocarpine hydrochloride, measurements were made along the lateral axis only. The test aquarium in this case was similar in size to the one described above but lacked the domed extension. In this situation, observations of both eyes were made by simply turning the aquarium 180°.

**Results**

**Accommodative Response to Variable Doses of Atropine and Pilocarpine**

The accommodative response of a goldfish (as determined from the change in refractive error along the lateral axis) is presented as an example of the three fish studied in this manner (Fig. 2). Injection of pilocarpine results in a shift in refractive error in the direction of hyperopia while atropine results in a shift toward myopia. Both functions are curvilinear. Once accommodation leveled off, a further increase in dosage was fatal unless countered with an injection of the antagonistic drug. The difference in maximum accommodative changes induced with the above drugs indicated an accommodative range of 12 diopters (ranges of 9 and 13 diopters were measured for the other two goldfish.) The response is bilateral.

Recording of heart rate at maximum dose levels resulted in consistently higher heart rates following injections with atropine than following injection...
with pilocarpine. In one example the average heart rate, based on an average of three separate experiments, was 99/min with atropine and 60/min with pilocarpine as opposed to a rate of 72/min with no drugs.

**Discussion**

These results agree with the type of accommodative mechanism first proposed by Beer (1894). The changes in heart rate induced with atropine and pilocarpine agree with those changes implicating the parasympathetic nervous system, as shown by Randall (1966). This supports the anatomical findings which suggest that the retractor lentis muscle is innervated by the parasympathetic nervous system. Furthermore, by controlling dosage it is possible to regulate the magnitude of the accommodative response or determine the maximum magnitude of accommodation.

Several of the teleost species studied possess an accommodative ability of considerable magnitude. Except for the northern black bullhead and the common white sucker the accommodative ranges of the species studied exceed or equal that of most terrestrial vertebrates, and that of the yellow perch is exceeded only by certain birds and lizards (Walls 1967).

A problem with this interpretation is whether the large drug-induced accommodative changes in the pupil plane also occur under natural circumstances. This question is important in view of the finding that large rostral movements of the lens occurred only following fairly extensive injection with atropine sulphate. The response to pilocarpine hydrochloride and to moderate levels of atropine sulphate occurred primarily along the lateral axis. This question was examined in a separate study of northern rock bass accommodation under natural conditions (J. G. Sivak and H. C. Howland un-
published data). It was found (by using a television monitoring system) that large rostral lens movements (e.g. equivalent to 20 diopters) do occur in response to a feeding stimulus.

The measurement of an accommodative response in the goldfish disagrees with the findings of Kimura and Tamura (1966) who reported no accommodative ability for this species. This difference may be due to the variation in eye development among different strains of goldfish or perhaps to the difference in experimental methods.

In attempting to understand the significance of the accommodation differences in the species studied, two observations must be emphasized. First, extreme accommodative ranges (>20 diopters) occur only along the pupil plane (rostral-caudal) and not along the lateral axis. Second, a considerable accommodative range in the pupil plane is associated with an elongation of the rostral margin of the pupil. These observations suggest that large accommodative efforts in the pupil plane (more specifically, movement of the lens toward the rostrum) are responses made necessary by the need for good visual acuity close to and in front of the snout. Tamura (1957) concluded that accommodative differences in fishes is related to feeding behavior.

Bullheads are inhabitants of muddy waters and are exclusively nocturnal feeders (Keast and Welsh 1968; Adams and Hankinson 1928). The relatively small eye and the profusion of barbels around the mouth suggest that this is not a “visual” animal. Suckers are described by Marshall (1966) as scavengers “that feed on detritus, particles of broken-down organic matter that fall to the bottom.” They “grub along the bottom drawing in the deposits and contained organisms through their highly protrusable jaws, which bear thick, fleshy lips.” Goldfish feeding habits and diet are difficult to categorize since they rarely appear in the wild. However, by analogy with their close relatives the carp they may be described as omnivorous in diet and not predacious (Kuhne 1939; Webster 1941).

Although the above groups of fish are not, in general, sight feeders, the other species studied are. The diets of rainbow trout, common bluegill, northern rock bass, and yellow perch consist mainly of small crustaceans, molluscs, aquatic insects, and aquatic insect larvae (Kuhne 1939; Emig 1966; and Webster 1941). However, the rainbow trout is somewhat piscivorous as well, (McAfee 1966) and, therefore, may not be as dependent on “good” near visual acuity in front of the rostrum.

The three latter species are diurnal (Keast and Welsh 1968) sight feeders (Kuhne 1939; Snow et al. 1960; and Webster 1941). Common bluegill feeding behavior is described by Snow et al. (1960) as follows: “With hatches of insects, bluegills will keep a wary eye on the surface, edge up to the insect and suck him with a resounding smack of his mouth.” Webster (1941) describes yellow perch as “crusing slowly over weed beds, picking up organisms living on the vegetation.” From the above descriptions it is apparent that the differences in axis and magnitude of accommodation is determined by the visual needs imposed by the feeding habits and particular diet of each species investigated.

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MATTHESSEN, L. 1880. Untersuchungen über dem Aplanatismus und die Periscopie der Kristallinen


