# Is tilting behaviour at low swimming speeds unique to negatively buoyant fish? Observations on steelhead trout, *Oncorhynchus mykiss*, and bluegill, *Lepomis macrochirus*

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When swimming at low speeds, steelhead trout and bluegill sunfish tilted the body at an angle to the mean swimming direction. Trout swam using continuous body/caudal fin undulation, with a positive (head-up) tilt angle ($\theta$, degrees) that decreased with swimming speed ($u$, cm s$^{-1}$) according to: $\theta = (164 \pm 96) . u^{(-1.14 \pm 0.41)}$ (regression coefficients; mean $\pm$ 2 S.E.). Bluegill swimming gaits were more diverse and negative (head down) tilt angles were usual. Tilt angle was $-3.0 \pm 0.9°$ in pectoral fin swimming at speeds of approximately 0.2–1.7 body length s$^{-1}$ (L s$^{-1}$; 3–24 cm s$^{-1}$), $-4.5 \pm 2.6°$ during pectoral fin plus body/caudal fin swimming at 1.2–1.7 L s$^{-1}$ (17–24 cm s$^{-1}$), and $-5.0 \pm 1.0°$ during continuous body/caudal fin swimming at 1.6 and 2.5 L s$^{-1}$ (22 and 35 cm s$^{-1}$). At higher speeds, bluegill used burst-and-coast swimming for which the tilt angle was 0.1 $\pm$ 0.6°. These observations suggest that tilting is a general phenomenon of low speed swimming at which stabilizers lose their effectiveness. Tilting is interpreted as an active compensatory mechanism associated with increased drag and concomitant increased propulsor velocities to provide better stabilizing forces. Increased drag associated with trimming also explains the well-known observation that the relationship between tail-beat frequency and swimming speed does not pass through the origin. Energy dissipated because of the drag increases at low swimming speeds is presumably smaller than that which would occur with unstable swimming.

Key words: steelhead; *Oncorhynchus mykiss*; bluegill; *Lepomis macrochirus*; stability; buoyancy.

## I. INTRODUCTION

At low swimming speeds, negatively buoyant fish ' tilt ', with the body axis subtending an angle to the axis of progression (Mackay, 1976; He & Wardle, 1986). He & Wardle (1986) showed that this behaviour increased lift generation by the pectoral fins at low swimming speeds to balance the weight of mackerel in water. Thus tilting compensates for reduced control forces that occur at low speeds (von Mises, 1945; Hoerner, 1975).

Many different species of neutrally buoyant fish appear to tilt at low swimming speeds (P. W. Webb, unpublished observation). This suggests that tilting by negatively buoyant fish may be a special case of a more general phenomenon associated with slow swimming. Therefore, I measured tilt angles of two species, both with swimbladders and typically close to neutral buoyancy, swimming at low speeds. One, steelhead trout (*Oncorhynchus mykiss* Walbaum), was chosen as representative of a less derived soft-rayed fusiform-bodied species. The second, bluegill (*Lepomis macrochirus*, Rafinesque), was chosen as a more derived species with characteristic acanthopterygian body shape and fin

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TABLE I. Lengths, mass, density of fish used in experiments. Data are means ± 2 s.e. ($n = 10$)

|  | Length (cm) | Mass (g) | Density (g cm$^{-3}$) |
|---|---|---|---|
| Steelhead trout | 12·3 ± 0·4 | 15·51 ± 2·42 | 1·0006 ± 0·0004 |
| Bluegill | 14·0 ± 0·7 | 48·85 ± 9·34 | 1·0016 ± 0·0015 |

distributions (Rosen, 1982). The objective was to determine if these fish tilted when swimming slowly and to seek insight into possible underlying principles.

## II. MATERIALS AND METHODS

Steelhead trout were obtained from a local hatchery. Bluegill were seined from local streams. Fish were held in the laboratory in 110 litre tanks at 15° C for at least 2 weeks before use. Water was replaced in the aerated holding tanks at a rate of 200% per day. Fish were fed a maintenance ration of trout chow.

Individual fish were placed in a flume (Vogel & LaBarbara, 1977), with an observation section 15 cm high, 15 cm wide and 60 cm in length. The upstream entry section was 45 cm long and contained straighteners made from 1·25 × 1·25 × 1·25 cm plastic (egg-crate) grid. The back and top were lined with Scotchlite, ruled with a grid. The front and bottom were clear plexiglass. A mirror beneath the flume allowed simultaneous observations of bottom and side views of fish swimming movements, which were recorded on video tape (framing rate, 60 Hz).

Fish were left in the flume overnight swimming at a speed of approximately 13 cm s$^{-1}$. On the following morning, flow velocity was reduced to zero, and then increased in increments of approximately 2 cm s$^{-1}$ every 5 min to a maximum speed of 4–5 body lengths s$^{-1}$ (L s$^{-1}$), the speeds at which the physostomatous trout exhaled air.

At the end of an experiment, fish were anaesthetized in the flume with 1 ppm 3-aminobenzoic acid ethyl ester (MS222). Anaesthetized fish were weighed to within $10^{-4}$ g in water of the same depth as that in the flume and then weighed in air. Fish density was calculated from weights in water and air. Total length was measured.

Video tapes were analysed field-by-field. Tilt angle was defined as the angle of the body subtended to the swimming path of the fish (He & Wardle, 1986) although the angle of the path proved essentially zero. As noted by He & Wardle (1986), tilt angle is more variable in fish with lower densities. Therefore, tilt angle was determined as the mean of measurements taken at 0·5 min intervals through every swimming period. Swimming gait was also recorded. Data were only analysed for fish swimming in the centre of the flume to minimize possible interactions with the walls (Webb, 1993a).

Data were analysed using linear regression and $t$-tests with SYSTAT (Wilkinson, 1990).

## III. RESULTS

All fish were slightly negatively buoyant (Table I), although they were very much less dense than captive mackerel (1·0377 g cm$^{-3}$; He & Wardle, 1986) and other continuously swimming negatively buoyant fish (Magnuson, 1978; He & Wardle, 1986).

At speeds <0·9 L s$^{-1}$ (11 cm s$^{-1}$), steelhead trout held station with the body tilted upwards and the pectoral fins oriented to generate negative lift as described by Arnold et al. (1991) for Atlantic salmon, Salmo salar L. At higher speeds, swimming was continuous using body/caudal fin undulation. At low swimming

speeds in particular, pectoral fins were variably flexed and extended. These movements were roughly parallel to the flow, and hence were not propulsive. Fin extensions tended to be smaller at higher speeds, as noted by others (see Videler & Wardle, 1991).

Tilt angles for swimming trout were variable, especially at lower speeds [Fig. 1(a)]. Variation was not correlated with differences in the weight of fish in water nor with pectoral fin extension. A significant ($P < 0.001$) inverse relationship was found between tilt angle ($\theta$, degrees) and swimming speed ($u$, cm s$^{-1}$) which was best described by the following equation;

$$\theta = (164 \pm 96) \, u^{(-1.14 \pm 0.41)} \tag{1}$$

where the mean $\pm$ 2 s.e. is given for regression coefficients.

Swimming behaviour of bluegill was more complex [Fig. 1(b)]. Although slightly more dense than trout, bluegill were able to hold station only to 0.2 L s$^{-1}$ (3 cm s$^{-1}$). As with trout, the body of station-holding bluegill was tilted positively at a small angle of $2.4 \pm 1.7°$ (mean $\pm$ 2 s.e.). Pectoral fins were used for swimming at speeds from approximately 0.2–1.7 L s$^{-1}$ (3–24 cm s$^{-1}$). Body/caudal fin propulsion sometimes supplemented pectoral fin swimming at speeds from approximately 1.2–1.7 L s$^{-1}$ (17–24 cm s$^{-1}$). Continuous body/caudal fin swimming occurred between 1.6 and 2.5 L s$^{-1}$ (22 and 35 cm s$^{-1}$, respectively), but burst-and-coast swimming was more common at higher speeds.

In contrast to trout, tilt angles of swimming bluegill were primarily negative (head down), and varied among gaits. Relationships between tilt angle and swimming speed within gaits were not significant (regression analysis; $P > 0.5$). Average tilt angles were $-3.0 \pm 0.9°$ during pectoral fin swimming, $-4.5 \pm 2.6°$ during swimming with the pectoral fins and body/caudal fin undulation, and $-5.0 \pm 1.0°$ during continuous body/caudal fin swimming. An exception to negative tilt angles was found during burst-and-coast swimming when angles were $0.1 \pm 0.6°$ and hence not significantly different from zero ($P > 0.1$).

## IV. DISCUSSION

Tilting behaviour was first analysed in detail for mackerel *Scomber scombrus* L. by He & Wardle (1986). They showed that tilting was a mechanism to support the excess weight of negatively buoyant fish at slow swimming speeds at which lift generated by the pectoral fins became insufficient. My observations show that tilting also occurs in neutrally buoyant fish. However, since neutrally buoyant fish have negligible weight in water, their tilting behaviour must be related to a different proximate function.

I suggest that tilting is related to stability control. All organisms are continually exposed to a variety of external destabilizing forces, as well as intrinsic variation in propulsive forces and moments. The centre of mass is typically above the centre of buoyancy, creating destabilizing rolling moments (Aleyev, 1977). Furthermore, stability problems may be large for fish which use a swimbladder to achieve neutral buoyancy. A swimbladder is well known to be unstable in depth control because its volume follows the ideal gas laws. As a result, a decrease in depth is associated with a reduction in total volume and hence an increase in density which tends to make a fish sink more and *vice versa*;
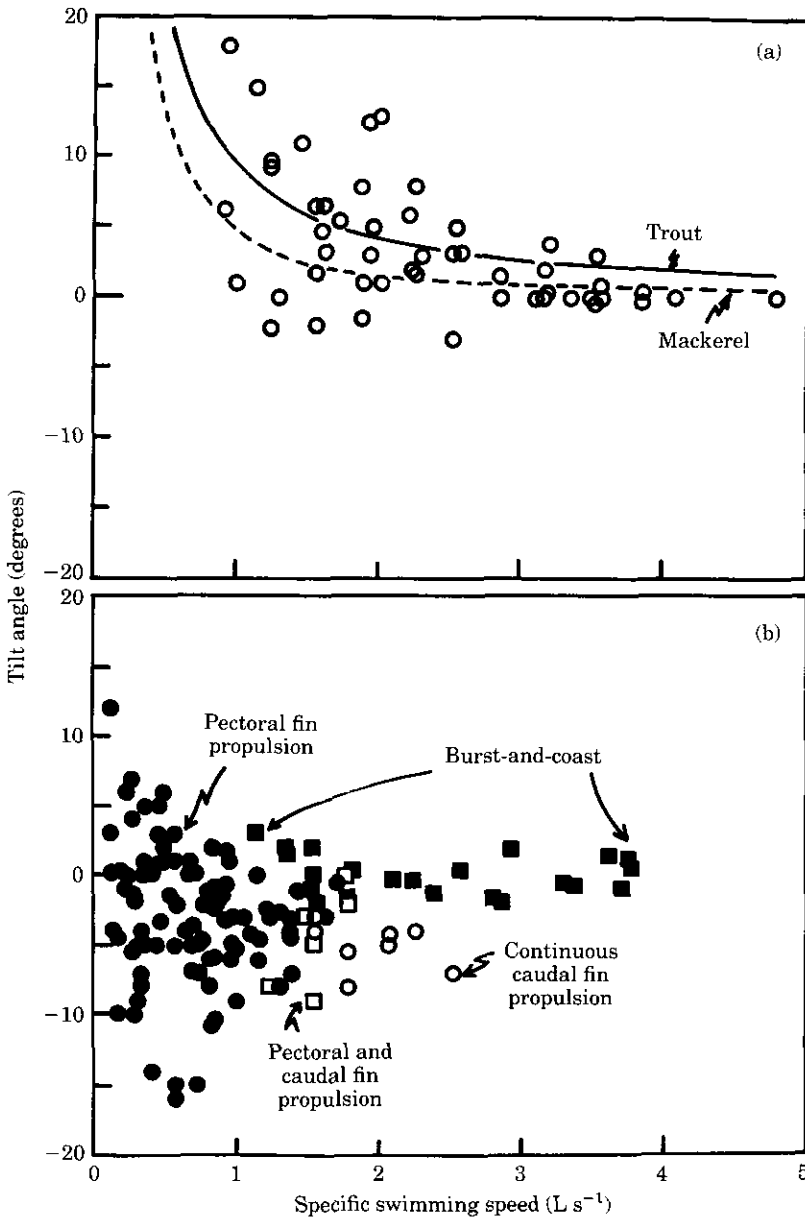
FIG. 1. The relationship between tilt angle and swimming speed for (a) steelhead trout and (b) bluegill. The solid curve for trout was fitted from equation (1). The dotted curve is for mackerel, *Scomber scombrus*; $\theta = (4 \cdot 737 \pm 3 \cdot 088) \cdot u^{(-1 \cdot 498 \pm 0 \cdot 830)}$; $r^2 = 0 \cdot 432$, $P < 0 \cdot 01$ and $\theta$ is in degrees and $u$ in L s$^{-1}$. It was determined using non-linear regression analysis of data in He & Wardle (1986). Note that linear regression using log-transformed data gives a slope with a much steeper gradient because there were fewer observations if tilting at higher speeds.

because pressure changes rapidly with depth near the water surface, fish in the productive photic zones are most likely to be unstable in hydrostatic depth regulation (Alexander, 1990). Although the swimbladder allows fish to hover and orient the body in any direction, abilities not available to negatively buoyant

fish, they must continually beat their propulsors in order to execute such behaviours.

In addition, it is well known from the design of human-engineered vehicles moving in water and air, that the effectiveness of control surfaces decreases at low speeds (von Mises, 1945; Hoerner, 1975). This is because the forces generated by control surfaces become small compared with forces, especially inertial forces, resisting the return of a vehicle to the desired orientation and/or path of motion after a perturbation. Fish face similar control problems at low swimming speeds and hence would be expected to use various mechanisms to negate falling control forces.

Fish, and human-engineered vehicles, counter destabilizing forces with trimming mechanisms. Tilting by neutrally buoyant fish may be viewed as one such mechanism, part of a behavioural repertoire for stability control at low swimming speeds. I suggest that tilting, plus the extension of passive control surfaces, increases drag. This in turn requires propulsors to beat more rapidly to provide additional thrust, and hence provide larger forces better matched to body inertia, hence facilitating stability control. Appropriate orientation of thrust is essential. This would be achieved easily by small changes in the beat plane of the paired fins, while the caudal fin and caudal peduncle contain numerous muscles to control tail shape and orientation and hence the direction of the thrust force (Thomson & Simaneck, 1977; Lauder, 1989).

It is reasonable to expect the energy costs associated with stability control are lower than those which would be incurred in the absence of control. Furthermore, it is probable that increased drag from tilting also would be smaller than that associated with unstable motions. Therefore, improved stability would be expected to lead to net energy savings. This scenario is consistent with the suggestion by Videler & Wardle (1991) that stability control is a major problem in slow swimming. I suggest a voluntary increase in drag is a general feature of this stability control, thereby requiring larger thrust forces that can be better matched to resistance that must be overcome for stability regulation. This helps explain the well known, but sometimes perplexing (Videler & Wardle, 1991) observation that the relationship between tail-beat frequency and swimming speed does not pass through the origin.

Other trimming mechanisms associated with increased beat-frequencies of propulsors are gait changes at low swimming speeds. These may or may not be used with tilting. Thus bluegills recruit paired-fin propulsors at low speeds (Alexander, 1989; Webb, 1993b), as shown in Fig. 1(a). Carp, Cyprinus carpio L., increase tail-beat frequencies at low swimming speeds by using the body/caudal fin propulsor intermittently in adopting a burst-and-coast gait (Rome et al., 1990).

Furthermore, although the proximate reasons for tilting behaviour in neutrally buoyant fish must be different from that for negatively buoyant fish, the same basic principle underlies all tilting behaviours; all are associated with reduced effectiveness of stability control surfaces at low speeds (von Mises, 1945; Hoerner, 1975). Indeed, this idea is implicit to the explanation given by He & Wardle (1986) for tilting in mackerel. They showed that tilting compensates for reduction at low swimming speed of those life forces which are essential for controlling the position of the negatively buoyant fish in the water column.

The common principle underlying tilting is reflected in behavioural similarities of neutrally and negatively buoyant fishes. For example, tilt decreases continuously with increasing swimming speed in mackerel and trout swimming with the body and caudal fin [Fig. 1(a)]. Once bluegill used body/caudal fin propulsion, tilt decreased with speed as for trout and mackerel. However, because bluegill used a wider range of body/caudal fin gaits, tilt changed discretely from $-5°$ to $0·1°$ with the change from continuous swimming to burst-and-coast body/caudal fin swimming [Fig. 1(b)].

Comparisons among species also suggest that there are two classes of *passive* and *active* trimming mechanisms used by fish for stability regulation at low swimming speeds (Weihs, 1989; Alexander, 1990). Passive mechanisms increase the area and/or the angle of attack of control surfaces. For example, negatively buoyant elasmobranchs, tuna and mackerel increase pectoral fin extension as speed decreases, and fin surface area is larger in species that routinely swim at low speeds (Magnuson, 1978; Bone & Marshall, 1982; He & Wardle, 1986). Neutrally buoyant fish also show greater fin extension at low speeds (Videler & Wardle, 1991). Tilting by negatively buoyant fish increases the angle of attack of paired fin lifting surfaces while increasing the total area generating lift by recruiting body area. Active mechanisms use propulsor motions to generate stabilizing forces, involving gait changes and tilting as discussed above.

The occurrence of a common basic principle that can explain tilting is not inconsistent with substantial variation in the role of tilting in fish with diverse life styles and living in different habitats. For example, tilt angle, which was usually negative in bluegill and positive in trout, has equal consequences for drag and propulsor activity while permitting behavioural differences. Trout and bluegill of the size used in these experiments feed on drift and zooplankton, for which positive tilt would appear advantageous. However, benthos is often an important diet component for bluegill (Osenberg *et al.*, 1992) when negative tilt would be preferable. Furthermore, visual pigments of bluegill may facilitate searching looking downwards in the water column (Lythgoe, 1979). Similarly, discrete changes in tilt associated with a wider range of gaits used by bluegill reflects a body and fin morphology of fish that typically swim slowly or intermittently in structurally complex habitats (Webb, 1983*b*). Finally, negatively buoyant mackerel (MacKay, 1976; He & Wardle, 1986) have no choice but to swim with positive tilt because of their special problem of weight support.

Species also differ in the magnitude of tilt angles which were higher and occurred over a larger range of speeds in the neutrally buoyant trout and bluegill compared with negatively buoyant mackerel (Fig. 1). Thus tilting is necessary only at speeds from $0·3$ to $0·8 \, L \, s^{-1}$ in mackerel, but occurs at swimming speeds up to $2-4 \, L \, s^{-1}$ in trout and bluegill. Differences again may relate to the magnitudes and predictability of destabilizing forces associated with differences in life style. Human-engineered marine vehicles, such as sailing vessels, use lift-producing surfaces that not only produce motive power but also stabilizing moments that are large compared with other typical destabilizing forces. This provides an overall improvement in stability (Marchaj, 1990). Negative buoyancy may provide a similar benefit in which the moments due to hydrodynamic lift from the pectoral and caudal fins is large compared with other perturbing forces. In contrast, the absence of a large reference force and instabilities

introduced by the swimbladder may present greater control problems for neutrally buoyant fish. Perhaps there are consequences for stability regulation representing costs to those adaptations for hovering and posture control that have been essential to exploiting highly productive but structured stream, reef and macrophyte habitats.

While problems of stability control are probably important reasons for tilting behaviour, additional energetic advantages might accrue to slow swimming tilted fish. A common explanation for gait changes in animal locomotion is efficient matching of muscle power to locomotor power requirements (Alexander, 1989; Webb, 1993b). Tilting may be no more than a gait variation in which drag is increased, allowing muscle to work higher on its efficiency curve, thereby achieving a net saving in total energy needs. I evaluated this possibility using swimming kinematics and performance data for steelhead trout of the same stock and of similar size to the trout used here (Webb, 1993a) but I was not able to show plausible savings.

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