

ENTRAINMENT BY RIVER CHUB *NOCOMIS MICROPOGON* AND SMALLMOUTH BASS *MICROPTERUS DOLOMIEU* ON CYLINDERS

PAUL W. WEBB*

School of Natural Resources and Environment, University of Michigan, Ann Arbor, MI 48109-1115, USA

*e-mail: pwebb@umich.edu

Accepted 3 June; published on WWW 27 July 1998

Summary

Sympatric stream-dwelling river chub (*Nocomis micropogon*) and smallmouth bass (*Micropterus dolomieu*) were video-taped swimming in the presence of single cylinders spanning a flume. Fish were acclimated and tested at 13, 18 and 23 °C swimming in an increasing-velocity test with single vertically or horizontally oriented cylinders 6.4, 13, 19 or 25 mm in diameter. Cylinder orientation had little effect on entrainment. Both species avoided cylinders at low speeds. At intermediate speeds, some fish entrained on the cylinders, but they were displaced at higher speeds. Entrained fish made no regular swimming motions, but the median and paired fins and the body moved continuously and irregularly. The periodicity of body perturbations decreased and the amplitude

increased with current speed. These also increased with cylinder diameter, but the variability was high and differences were not significant. Chub entrained in larger numbers and for longer over a wider range of current speeds and temperatures than bass. Entrainment by chub increased with cylinder diameter up to 13–19 mm, but declined for 25 mm cylinders. Bass did not entrain on 6.4 mm and 25 mm cylinders and showed very little entrainment at 13 and 18 °C, but entrainment was similar to that of chub at 23 °C.

Key words: entrainment, swimming, river chub, *Nocomis micropogon*, smallmouth bass, *Micropterus dolomieu*.

Introduction

Structure is a major component of most fish habitats, affecting fish numbers and distributions. This is especially true in current-swept habitats where structure and current interact to create a wide variety of flow regimes (Gordon *et al.* 1994). Numerous studies have described fish taking refuge from the flow in the wake downstream of structures such as substratum waves, boulders, branches, root wads and coral heads (Breder, 1926; Cook, 1985; Fausch, 1984; Keenleyside, 1979; Gerstner, 1998; Gerstner and Webb, 1998) using visual and lateral line cues to entrain (Sutterlin and Waddy, 1975). The ability of fish to locate regions of slow flow is a bane of researchers using flumes and water tunnels and a basis for many common stream improvement practices (Ross, 1997).

In spite of the numerous field and laboratory observations of flow-refuging behavior in fishes, no experiments have been performed to determine threshold sizes and orientations for structures, with the exception of marine fish using substratum ripples (Gerstner, 1998; Gerstner and Webb, 1998). The present study examined entrainment by two stream species, river chub *Nocomis micropogon* and smallmouth bass *Micropterus dolomieu*, on cylinders. These simple structures are analogous to in-stream branches and roots commonly used as flow refuges (e.g. Probst *et al.* 1984). Observations were made using vertically and horizontally oriented cylinders from

6.4 to 25 mm in diameter, typical of branch diameters in Michigan streams. Entrainment performance was measured at three temperatures. It was expected that entrainment would increase with cylinder size, assuming that larger cylinders provide larger wakes. Temperature is a major seasonal variable in temperate streams but was expected to have little effect on entrainment. It was expected that bass would make greater use of cylinders for flow-refuging than chub, as bass are typical of the spiny-rayed fishes that are abundant in habitats characterized by complex structures (Hobson, 1974; Moyle and Cech, 1996; Sale, 1991).

Materials and methods

Fish

River chub *Nocomis micropogon* (Cope) and smallmouth bass *Micropterus dolomieu* (Lacépède) were chosen because they are sympatric representatives of soft-rayed and spiny-rayed fishes with generally similar fusiform bodies and they overlap in body length. Fish were collected using a 6 m bag seine from the same stretch of the Saline River, Michigan, USA. Bass were found in slower waters at the margin of the stream and in pools, while chub were more abundant in races.

Fish were transported to the laboratory, where they were

held in 1101 tanks for at least 2 weeks before being acclimated to test temperatures. Fish were acclimated to temperatures of 13, 18 and 23 °C at a rate of 1 °C per day, followed by at least a week at the test temperature before swimming trials began. Tanks were continuously aerated and supplied with fresh water providing 200% replacement per day. Fish quickly accepted pelleted food, which was provided to excess once per day.

Flumes

Observations were made of fish swimming in two flumes based on the design of Vogel and LaBarbera (1978). One flume had a 45 cm long upstream entry section preceding an observation section 15 cm square and 60 cm long. The observation section was delineated from the entry section by collimators constructed from 1.25 cm×1.25 cm×1.25 cm plastic grid. The second flume had a 46 cm×15 cm observation section, 85 cm in length (Fig. 1). This was preceded by a 95 cm long trapezoid entry section. The entry and observation sections were removable and could be inserted either vertically or horizontally. Baffles and collimators distributed the current uniformly over the whole cross section of the observation area and provided a rectilinear profile of microturbulent flow.

Flow was examined at a range of scales using threads, dye streams, an Ott meter and a hot-film anemometer. At a macroscopic level, dye streams and threads were used to ensure the absence of turbulence. The Ott meter and hot-film anemometer were used to measure flow profiles and hence to ensure that flow was rectilinear across the observation sections. Although large-scale turbulence was absent from the flow in

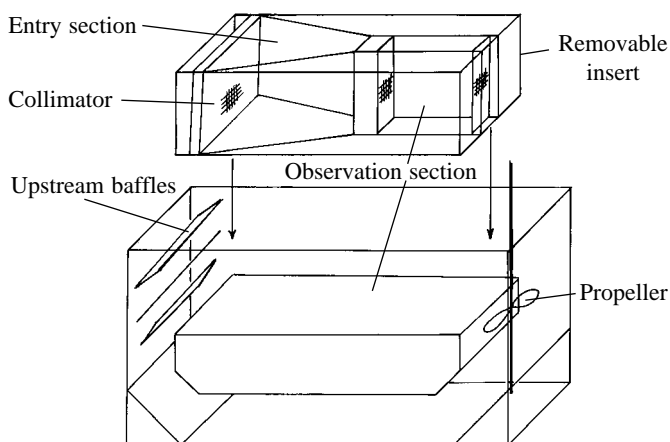


Fig. 1. Diagram of the design of a flume with a rectangular observation section. The observation section and entry section, with converging walls providing a contraction region for the flow before it enters the observation section, can be removed (upper diagram) and rotated to provide a vertical or horizontal swimming chamber for the fish. Rectilinear flow over the cross section of the observation section, especially in the vertical position, is obtained by adjusting the baffles (see lower diagram) at the corner upstream from the removable insert and by an upstream grid (collimator) 5 cm thick made of sheets of 1.25 cm×1.25 cm×1.25 cm plastic at the entry of the contraction section.

the observation sections, the hot-film anemometer showed velocity fluctuations with an intensity of turbulence of approximately 0.04, typical of microturbulent flow characteristic of flumes and water tunnels used for fish locomotion studies (Bell and Terhune, 1970; Webb, 1975).

The downstream ends of both observation sections were delimited by silver wire grids which could be electrified at 5 V d.c. to encourage fish to continue swimming. Observation sections had opaque bottoms, which were found to be essential. Without these, fish did not hold station. The observation section was illuminated with fluorescent grow-lights having a natural sunlight spectrum at an intensity of approximately 500 lx.

Fish were video-taped at 60 fields s⁻¹ from the side and from above *via* a mirror angled at 45°.

Cylinders

A single vertical or horizontal cylinder spanning the flume was placed in the center of the flume cross section, approximately one-third of the distance along the length measured from the entrance of the observation section. Cylinders were 6.4, 13, 19 and 25 mm in diameter. Fish were also observed swimming in the absence of a cylinder. All tests on the 19 and 25 mm diameter cylinders were performed in the larger flume, ensuring that all cylinders occupied much less than 10% of the cross-sectional area. Experiments on the smaller cylinders were performed in both flumes. No differences were found in the use of these small cylinders by fish in the two flumes, and the data were combined. Flow around the cylinders was examined using threads and dye streams and was found to be consistent with descriptions in the engineering literature (e.g. Hoerner, 1965; Vogel, 1994).

Procedures

A single fish was selected at random and placed in a flume with (or without) a cylinder in place and at a test temperature equal to the acclimation temperature. Cylinder diameters, cylinder orientations and water temperatures were presented in random order. Between 10 and 15 fish were tested for each combination.

Fish were left overnight in the flume swimming at a current speed of approximately 5 cm s⁻¹. On the following day, current speed was first decreased to approximately 2–3 cm s⁻¹ for 5 min. Subsequently, current speed was increased in increments, Δu , of approximately 4–5 cm s⁻¹ at 2 min intervals, Δt , until fish became entrained on the downstream screen and would not swim off. The time to exhaustion, t , following the last speed increment was recorded. The 2 min critical swimming speed, 2 min u_{crit} , was determined from: $2 \text{ min } u_{crit} = u_p + 2\Delta u/\Delta t$, where u_p is the speed preceding that at which fish were fatigued (Brett, 1964). A variety of time periods have been used between speed increments in increasing-velocity tests (Farlinger and Beamish, 1977). The short time period used here was chosen to increase the absolute speed range tested while giving time for fish to entrain. The speeds attained at fatigue in tests with a short time period, however, are likely to be limited by anaerobic capacity rather than by aerobic metabolic rate.

Video tapes were analyzed frame by frame to record the swimming behavior of fish. The use of a cylinder to avoid swimming and the percentage of time for which swimming was avoided were recorded. The body was buffeted in the wake, which was most clearly seen as rotations of the body around the nose. The amplitudes of these perturbations were measured as the angles subtended by the body axis to the flume axis. Amplitudes were calculated from the coordinates of the nose and the midpoint of the caudal peduncle in lateral and top-view video images, digitized using OPTIMAS software. The period of perturbations was calculated from the number of rotations occurring during the measured time for which fish entrained. Movements of the fins were extremely variable, but general patterns of fin motions were recorded.

At the end of an experiment, fish were weighed, and total length, body width and body depth were measured (Table 1).

Results

Swimming behavior

During acclimation to the flume, chub and bass typically swam in various parts of the flume before choosing a position where they subsequently spent most time. This position varied from upstream to downstream regions of the observation section, sometimes near the bottom, sometimes in mid-water and sometimes near the top. The location differed among individuals. Fish always swam in positions outside the wake of cylinders, when present.

Swimming gaits used in the absence of cylinders differed between river chub and smallmouth bass. At current speeds below approximately 10 cm s^{-1} , chub held position on the substratum in the parr posture (Arnold *et al.* 1991). The body was raised on the pectoral fins, which were inclined with the leading edge lower than the trailing edge. At speeds between approximately 7 and 22 cm s^{-1} , twitch-and-coast movements were occasionally seen (Webb, 1997), but at speeds from approximately 10 to 50 cm s^{-1} swimming was primarily steady using only body and caudal fin undulation. At higher speeds,

chub used burst-and-coast swimming until they became exhausted.

Smallmouth bass primarily used combinations of the pectoral, dorsal and anal fins to swim at low speeds up to approximately 20 cm s^{-1} . These were supplemented and then succeeded by body and caudal fin undulation up to a current speed of approximately 45 cm s^{-1} . As with chub, smallmouth bass used burst-and-coast swimming at higher speeds preceding exhaustion.

Swimming behavior was modified in the presence of cylinders. At low and at high speeds, fish of both species tended to swim above, below, upstream or well downstream of the cylinders, using the same gaits as in the absence of cylinders. At intermediate speeds, some fish entrained on the cylinders. Entrainment occurred within a few seconds of a speed change, suggesting that fish had fully sampled the flow regime in the flume during the acclimation period. Behavior varied among individuals. A fish might entrain at one current speed for part of the time, not entrain at another speed, and entrain for the whole period at yet another current speed.

All fish entrained in the same way, irrespective of cylinder size, temperature and current speed. The head was typically located close to, but not quite touching, the cylinder downstream from the cylinder shoulder, with the body angled into the wake (Fig. 2). For vertically oriented cylinders, fish always entrained on the upper side of the cylinder (Fig. 2B).

While entrained on cylinders, fish made no regular swimming motions. However, the blades of the dorsal, anal, caudal and paired fins were continuously in motion. Motions of both the median and paired fins of chub were primarily flexions and extensions in the plane of the fin web, roughly in the plane of the current flow. Bass also showed these movements. However, the fins of bass, especially the paired fins, often moved across the flow and fore and aft. Such motions would generate thrust. Otherwise, all fin motions were irregular, with no discernible repeating pattern, and were more pronounced in bass than in chub. Harris (1937*a,b*) also found that routine movements of the paired fins lacked discernible patterns when fish swam slowly.

Table 1. *Morphological characteristics of river chub and smallmouth bass used in experiments on the effects of single cylinders on swimming and station-holding*

Temperature (°C)	<i>N</i>	Mass (g)	Length (cm)	Depth (cm)	Width (cm)
Chub					
13	61	11.80±2.76	10.5±0.8	1.6±0.2	1.1±0.1
18	78	10.31±2.75	10.7±1.1	1.6±0.4	1.0±0.1
23	70	10.16±2.64	10.6±0.8	1.6±0.2	1.1±0.1
Smallmouth bass					
13	44	8.60±0.52	9.1±0.2	2.0±0.1	1.1±0.0
18	54	8.12±0.94	9.1±0.3	1.9±0.0	1.1±0.1
23	51	7.63±1.37	9.3±0.2	2.0±0.0	1.1±0.0

There were no significant differences in morphometrics so, for convenience, data for fish used with different-sized cylinders are combined for each test temperature.

Values are means ± 2 S.E.M.

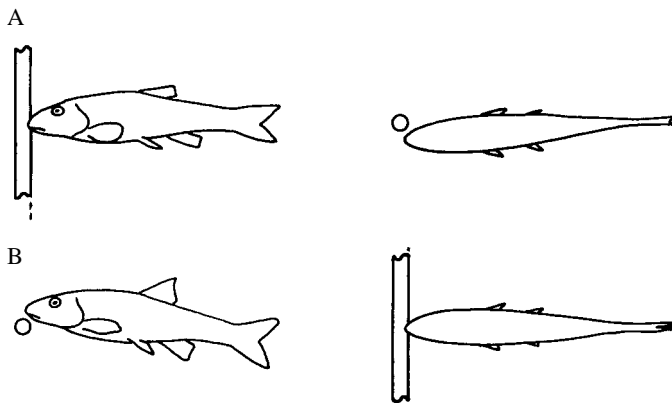


Fig. 2. Tracings from video tape of lateral and top views showing the posture of the body of a river chub when entraining at 23 °C on (A) a 13 mm diameter vertically oriented cylinder and (B) a 13 mm diameter horizontally oriented cylinder. These postures were typical of both chub and smallmouth bass entraining on cylinders of all sizes, in all temperature groups and at all speeds.

When entrained on vertically and horizontally oriented cylinders, the body moved irregularly in all planes: surge, slip and heave, and roll, yaw and pitch. Surge, slip and heave describe perturbations without rotation in the longitudinal, lateral and dorso-ventral planes of the body respectively. Roll, yaw and pitch describe rotational perturbations about the longitudinal, lateral and dorso-ventral body axes respectively. The head moved least, so that the posterior of the body and the tail tended to move relative to the head. Pitching dominated body perturbations of fish entrained on horizontally oriented cylinders, and yawing motions were most prominent with vertically oriented cylinders. The periodicity of perturbations decreased and the amplitude increased with current speed (e.g. Fig. 3). The variability in these disturbances was large, as shown by the standard errors in Fig. 3. The range and mean amplitudes of perturbations tended to be larger with larger-diameter cylinders, but, because of the large variation, these differences were not statistically significant among species entraining on cylinders of the different sizes and orientations (ANOVA, $P > 0.05$). A cylinder sheds vortices into the wake which form a Karman vortex street. The rate of vortex shedding is $f_v = u\omega/d$, where ω is the Strouhal number, taking values of approximately 0.2 at the Reynolds numbers for the cylinders, and d is the diameter of the cylinder (Vogel, 1994). For the cylinder diameters and current speeds used here, the period between vortex shedding ranged from 0.83 s for the 25 mm cylinder at a current speed of 15 cm s^{-1} to 0.04 s for a 6.4 mm cylinder at 75 cm s^{-1} . These values are very much lower than the observed periods of the perturbations of the fish body (Fig. 3A). Therefore, the buffeting of the body must be associated with other factors in addition to vortex shedding into the Karman vortex street.

At higher speeds, entraining fish were displaced from their position on a cylinder. These fish entered the current and were forced to swim. This was typically preceded by a large perturbation in which the bulk of the body shifted from the wake

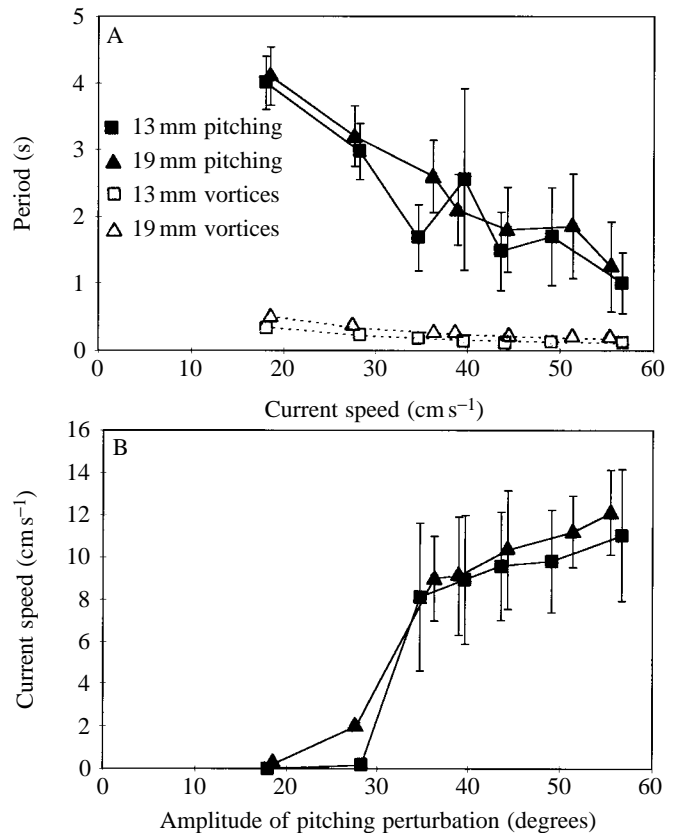


Fig. 3. The relationship between current speed and (A) the period and (B) the amplitude of perturbations for pitching movements of the body of river chub entrained on horizontally oriented cylinders at 18 °C. Values are means \pm 2 S.E.M. Sample sizes are included in Table 3. The period of the wake vortices shed by the cylinder into the Karman vortex street is also shown in A (open symbols).

into the adjacent faster flow. Displaced fish usually attempted to swim back and hold station, swimming through the wake to approach the cylinder. They were rarely successful, usually re-entraining for a few seconds at most before being displaced again.

Entrainment patterns

Proportion of fish entraining on cylinders

Differences in the proportions of chub and bass entraining on vertically and horizontally oriented cylinders were not significant (ANOVA, $P = 0.15\text{--}0.96$) for 13 mm and 19 mm diameter cylinders, but a significant effect was found (ANOVA, $P < 0.5$) for chub entraining on 6.4 mm and 25 mm cylinders (Figs 4, 5). However, in the latter situations, relatively few chub entrained compared with those entraining on intermediate-sized cylinders, differences were small and horizontally oriented cylinders were preferred in some situations (e.g. chub entraining on 6.4 mm cylinders at 18 °C), and a higher proportion of chub entrained on vertical cylinders in other situations (e.g. chub entraining on 6.4 mm cylinders at 23 °C). Overall, therefore, a convincing case for an important effect of cylinder orientation on entrainment numbers cannot be made.

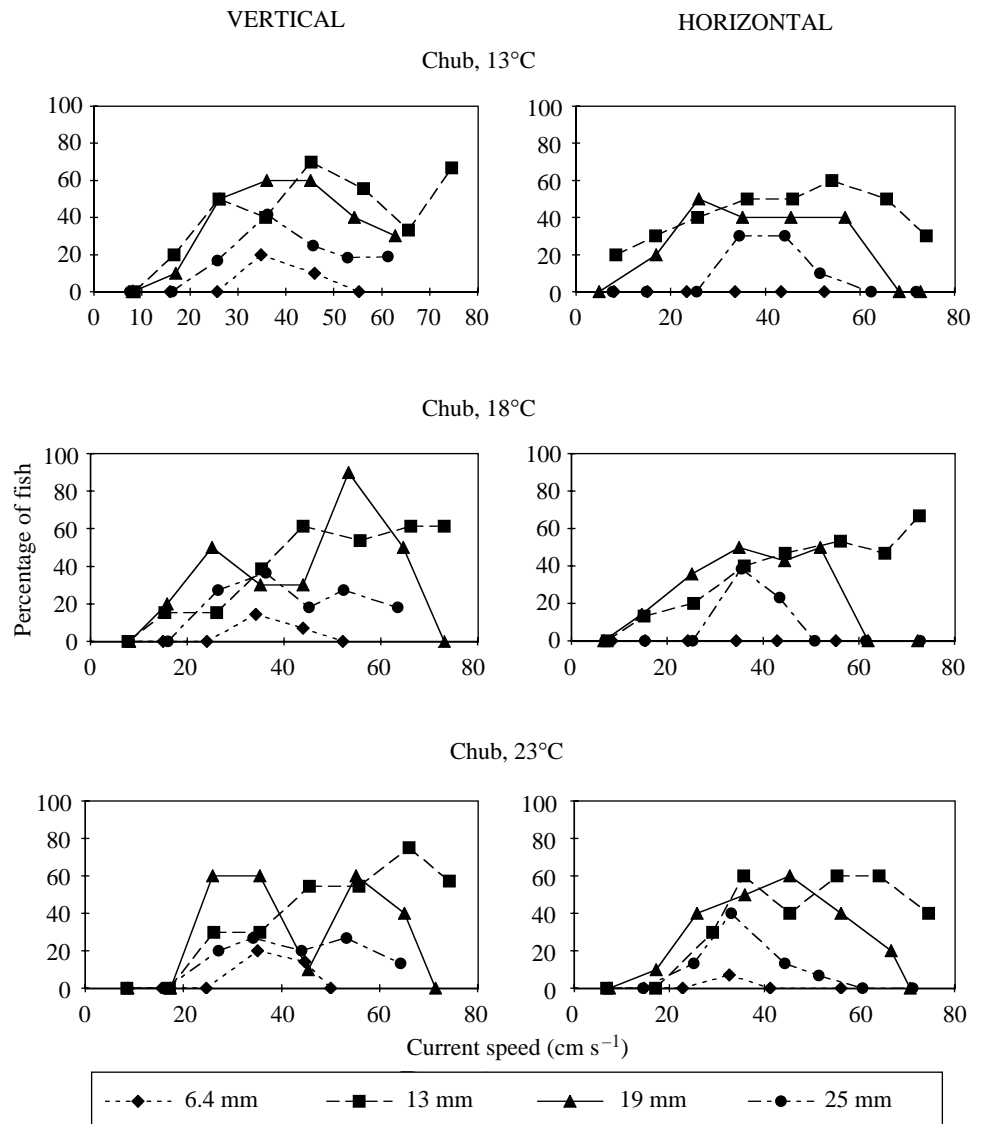


Fig. 4. The proportion of river chub entraining on vertically or horizontally oriented cylinders of various diameters and at various test temperatures with increasing current speed. Sample sizes are included in Tables 2 and 3.

Both chub and bass were most likely to entrain at intermediate current speeds. Thus, the proportion of chub entraining increased with current speed, reaching a maximum of approximately 60–80% at intermediate speeds of 25–50 cm s⁻¹; the proportion decreased at higher current speeds (Fig. 4). The highest proportions of fish entraining (up to 90% of chub) were observed with vertically and horizontally oriented cylinders of 13 mm and 19 mm diameter over all speeds investigated at all temperatures. Up to 40% of chub entrained on 6.4 mm cylinders; entrainment on these cylinders occurred over the smallest current speed range, typically 25–50 cm s⁻¹. Entrainment on 25 mm cylinders was intermediate between that for 6.4 mm and that for 13 mm and 19 mm diameter cylinders (Fig. 4).

A similar pattern was found in bass (Fig. 5), but a lower percentage of bass entrained than chub (ANOVA, $P < 0.05$). In addition, bass entrained only on the 13 and 19 mm cylinders. Bass appeared to show some preference for 19 mm cylinders at 23 °C, entraining on these larger cylinders in larger numbers at all current speeds (Fig. 5). The current speed range over

which bass entrained was generally significantly smaller than that for chub (ANOVA, $P < 0.05$), spanning speed ranges of the order of 20 cm s⁻¹, except at 23 °C when bass entrained over the same range of current speeds as chub.

Temperature had no significant effect on entrainment numbers of chub (ANOVA, $P = 0.81$). In contrast, temperature had a significant effect on entrainment by bass (ANOVA, $P < 0.001$). Fewer than 20% of the bass entrained on cylinders at 13 °C and 18 °C, but up to 70% entrained at 23 °C. The range of current speeds over which bass entrained tended to be larger at higher temperatures, ranging from approximately 25–45 cm s⁻¹ for 13 mm vertically oriented cylinders at 13 °C to 15–75 cm s⁻¹ for the same cylinder size and orientation at 23 °C.

Proportion of time fish entrained

The proportion of time that entraining fish held their positions on cylinders showed similar overall patterns to the proportion of fish entraining: fish entrained for longer at intermediate speeds and on intermediate-sized cylinders (Tables 2, 3). Chub

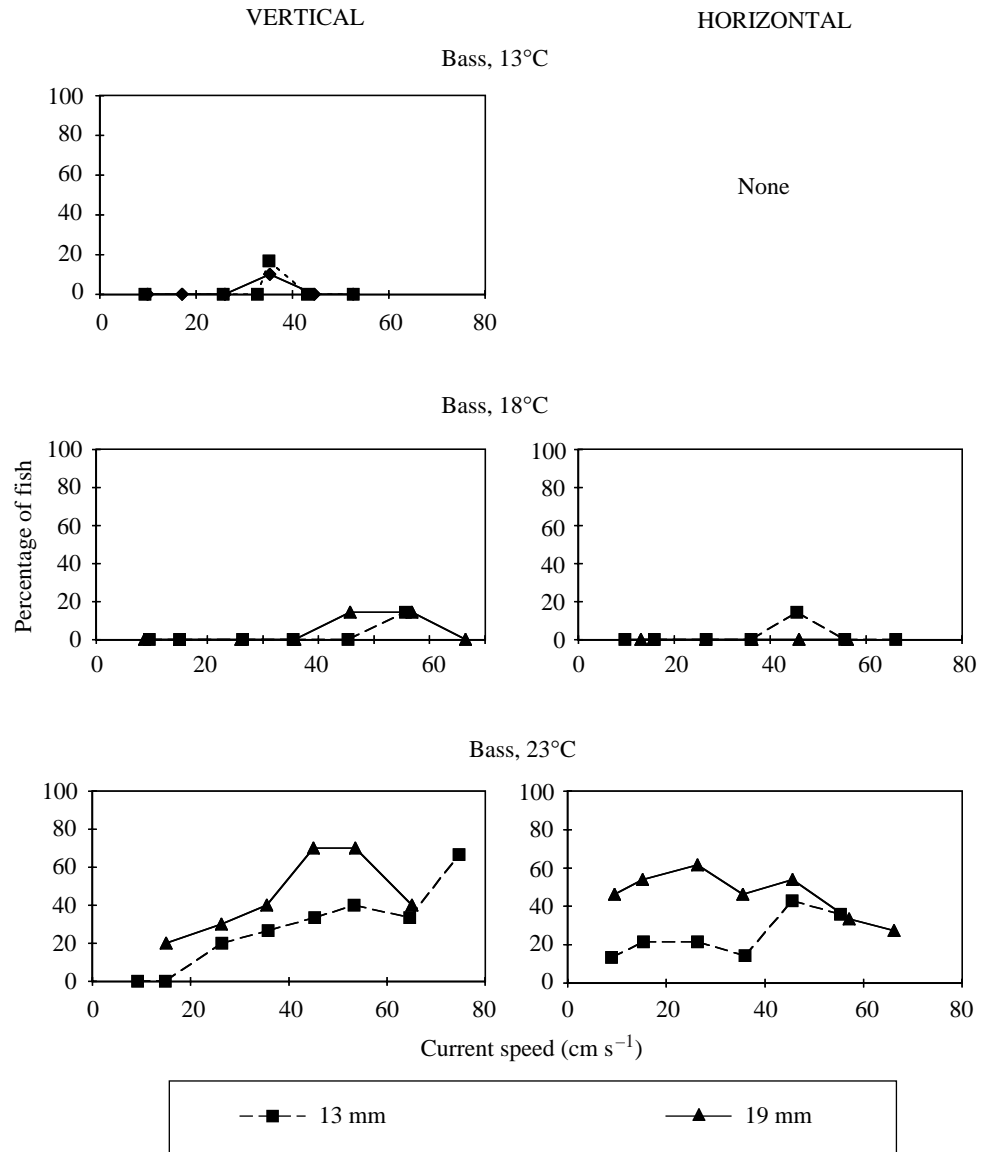


Fig. 5. The proportion of smallmouth bass entraining on vertically or horizontally oriented cylinders of various diameters and at various test temperatures with increasing current speed. Sample sizes are included in Tables 2 and 3.

entraining did so for up to 100% of the time on 13 mm vertically and horizontally oriented cylinders, for less than 60% of the time on larger cylinders and for less than approximately 20% of the time on the smallest (6.4 mm) cylinders (Table 2, 3). This suggests that chub showed some preference for 13 mm cylinders. In general, differences in entrainment times between cylinder sizes within a temperature group were significant (t -tests, $P < 0.05$), especially at current speeds above approximately 40 cm s^{-1} , but there were exceptions. For example, the 34% of time for which chub entrained on vertically oriented 13 mm cylinders at 13°C at 36 cm s^{-1} did not differ significantly from the 28% of time entraining on 19 mm cylinders of the same orientation, temperature and swimming speed. Alternatively, the 67% of time that this species spent entrained on 13 mm vertically oriented cylinders at 23°C at a current speed of 36 cm s^{-1} was significantly larger than that of 29% for 19 mm cylinders under otherwise the same test conditions. However, there was no

pattern to these exceptions, many of which were associated with small numbers of entraining fish, and the exceptions do not change the overall general conclusion that cylinder size affected entrainment time, with chub spending more time entrained on intermediate-sized cylinders at intermediate speeds.

Bass essentially entrained on cylinders only at 23°C . At this temperature and at speeds below 40 cm s^{-1} , bass showed a tendency to entrain on 13 mm cylinders for longer than on 19 mm cylinders, but the differences were not significant (t -test, $P > 0.05$). At the same temperature, bass spent significantly (t -test, $P < 0.05$) more time entrained on 19 mm cylinders than on 13 mm cylinders at higher speeds (Table 3), implying that bass had some preference for the 19 mm cylinders.

As with the proportion of fish entraining on cylinders, temperature had no significant effect on entrainment of chub (ANOVA, $P > 0.05$), whereas bass entrainment was strongly

Table 2. The percentage of time that river chub and smallmouth bass entrained on vertically oriented cylinders of four diameters and at three acclimation temperatures

River chub												Smallmouth bass																																																																																																																																																																																			
6.4 mm cylinder				13 mm cylinder				19 mm cylinder				25 mm cylinder				13 mm cylinder				19 mm cylinder																																																																																																																																																																											
<i>u</i>		Time		<i>u</i>		Time		<i>u</i>		Time		<i>u</i>		Time		<i>u</i>		Time		<i>u</i>		Time																																																																																																																																																																									
(cm s ⁻¹)	(%)	<i>N</i>	<i>N_e</i>	(cm s ⁻¹)	(%)	<i>N</i>	<i>N_e</i>	(cm s ⁻¹)	(%)	<i>N</i>	<i>N_e</i>	(cm s ⁻¹)	(%)	<i>N</i>	<i>N_e</i>	(cm s ⁻¹)	(%)	<i>N</i>	<i>N_e</i>	(cm s ⁻¹)	(%)	<i>N</i>	<i>N_e</i>																																																																																																																																																																								
13°C																																																																																																																																																																																															
8.0	0	10	0	8.4	0	10	0	8.1	0	10	0	7.5	0	12	0	9.9	0	10	0	9.4	0	12	0	15.9	0	10	0	16.7	19±16	10	2	17.0	7±0	10	1	16.2	0	12	0	17.2	0	10	0	25.7	0	12	0	25.7	0	10	0	26.1	11±7	10	5	26.2	38±8	10	5	15.7	30±22	12	2	26.0	0	10	0	32.7	0	12	0	34.8	15±7	10	2	35.8	34±13	10	4	36.1	28±7	10	6	36.1	25±9	12	5	35.3	2±0	10	2	35.2	4±0	12	2	46.0	13±0	10	1	45.3	72±10	10	7	45.2	33±9	10	6	45.6	19±13	12	3	44.6	0	10	0	43.2	0	12	0	55.3	0	10	0	56.2	68±17	9	5	54.3	40±9	10	4	52.9	9±6	11	2	52.7	0	3	0	52.7	0	2	0	65.5	100	6	2	62.8	15±0	10	3	61.3	11±10	6	2	±0	74.6	89±11	6	4																															
18°C																																																																																																																																																																																															
7.8	0	14	0	7.8	0	13	0	8.1	0	10	2	7.9	0	11	0	9.6	0	14	0	8.7	0	14	14	15.0	0	14	0	15.4	20±5	13	2	15.8	17±5	10	5	15.9	0	11	0	15.0	0	14	0	15.0	0	14	14	24.1	0	14	0	26.1	44±9	13	2	25.1	45±8	10	3	26.3	27±20	11	3	26.4	0	14	0	26.1	0	14	14	34.2	17±6	14	2	35.3	54±15	13	5	35.1	36±28	10	3	36.2	13±2	11	4	35.5	0	14	0	35.7	0	14	14	44.0	14±0	14	1	44.0	86±6	13	8	43.9	35±10	10	3	45.1	5±0	11	2	45.4	0	14	0	45.7	2±1	14	2	52.1	0	12	0	55.7	76±11	13	7	53.3	32±0	10	9	52.3	13±7	11	3	55.7	3±1	14	2	56.9	5±4	14	2	66.2	95±5	13	8	64.7	17±10	10	5	63.4	5±4	11	2	66.5	0	3	0	73.1	80±10	13	8	73.1	0	10	0																								
23°C																																																																																																																																																																																															
8.7	0	10	0	8.5	0	13	0	8.7	0	10	0	8.6	0	15	0	9.2	0	15	0	15.1	38±22	10	2	15.6	0	10	0	17.1	0	13	0	17.4	0	10	0	16.4	0	15	0	14.9	0	15	0	24.7	0	10	0	26.2	92±7	13	4	25.9	39±9	10	6	17.1	15±11	15	3	26.4	64±8	15	3	26.4	40±37	10	3	25.1	10±10	10	2	35.6	67±4	13	4	35.6	29±10	10	6	34.2	27±12	15	4	35.8	54±21	15	4	35.6	39±12	10	4	44.8	24±12	7	2	45.7	58±10	13	7	45.4	11±0	10	1	44.0	15±13	15	3	45.4	16±8	15	5	45.0	42±16	10	7	50.1	0	7	0	55.8	69±7	13	7	55.2	22±3	10	6	53.2	11±6	15	4	53.3	8±2	15	6	53.6	16±2	10	7	66.0	17±4	12	9	65.0	21±5	10	4	64.3	6±5	15	2	64.7	5±0	12	4	65.1	9±6	10	4	74.3	0	7	4	71.4	0	10	0	74.7	4±0	9	6																				

Values are means ± S.E.M.

Observations were made in an increasing-velocity test.

u is the mean current speed (cm s⁻¹), *N* is the number of fish tested and *N_e* is the number of fish that entrained on cylinders.

temperature-dependent (ANOVA, *P*<0.05). Bass spent up to approximately 70% of their time entraining on 13 mm and 19 mm cylinders at 23°C, but less than 5% of their time at 13°C and 18°C.

Two-minute critical swimming speeds

The presence of cylinders had no significant effect on the 2 min critical swimming speed of chub or bass (ANOVA, *P*>0.05). Therefore, data were combined for all treatments at each test temperature. For chub, the mean 2 min *u_{crit}* values were 59±4 cm s⁻¹ (*N*=61), 59±3 cm s⁻¹ (*N*=78) and 63±4 cm s⁻¹ (*N*=70) (means ± 2 S.E.M.) at 13, 18 and 23°C, respectively. These speeds were significant higher than those of bass of 41±6 cm s⁻¹ at 13°C (*N*=44), 53±4 cm s⁻¹ at 18°C (*N*=54) and 55±7 cm s⁻¹ at 23°C (*N*=51) (*t*-test, *P*<0.02). Temperature had no significant effect on the 2 min *u_{crit}* of chub in these experiments (ANOVA, *P*≥0.05). However, the 2 min *u_{crit}* of

bass was significantly lower at 13°C than at the two higher temperatures (*t*-test, *P*=0.03).

Discussion

Chub and bass entrained equally often on horizontally and vertically oriented cylinders but only at intermediate speeds, swimming in largely undisturbed flow at lower and higher speeds. Significant differences were found for the two species in their entrainment patterns on cylinders of various sizes at different temperatures, with chub making the most use of refuging opportunities. In general, therefore, the results differ from the predicted pattern that larger and vertically oriented cylinders would be used more commonly to avoid swimming and that bass would make greater use of the opportunities presented than chub. These experiments sought to quantify station-holding performance using simple structures and were insufficient to

Table 3. The percentage of time that river chub and smallmouth bass entrained on horizontally oriented cylinders of four diameters and at three acclimation temperatures

River chub												Smallmouth bass											
6.4 mm cylinder				13 mm cylinder				19 mm cylinder				25 mm cylinder				13 mm cylinder				19 mm cylinder			
<i>u</i>	Time	<i>N</i>	<i>N_e</i>	<i>u</i>	Time	<i>N</i>	<i>N_e</i>	<i>u</i>	Time	<i>N</i>	<i>N_e</i>	<i>u</i>	Time	<i>N</i>	<i>N_e</i>	<i>u</i>	Time	<i>N</i>	<i>N_e</i>	<i>u</i>	Time	<i>N</i>	<i>N_e</i>
(cm s ⁻¹)	(%)			(cm s ⁻¹)	(%)			(cm s ⁻¹)	(%)			(cm s ⁻¹)	(%)			(cm s ⁻¹)	(%)			(cm s ⁻¹)	(%)		
13°C																							
8.0	0	11	0	8.4	3±3	10	2	4.9	0	10	0	7.7	0	10	0								
15.1	0	11	0	16.8	5±2	10	3	16.9	10±4	10	2	14.8	0	10	0	15.7	0	11	0	16.0	0	11	0
23.4	0	11	0	25.7	14±6	10	4	25.9	16±5	10	5	25.4	0	10	0	25.5	0	11	0	25.6	0	11	0
33.6	0	11	0	36.2	37±15	10	5	35.2	33±0	10	4	34.5	24±20	10	3	35.0	0	11	0	35.4	0	11	0
43.3	0	11	0	45.8	60±18	10	5	45.4	28±11	10	4	44.1	17±14	10	3	45.0	0	11	0	44.5	0	11	0
52.5	0	11	0	54.1	65±16	10	6	56.9	4±2	10	4	51.5	2±0	10	1	53.8	0	11	0				
				65.6	69±13	10	5	68.3	0	10	0	62.4	0	10	0								
				74.0	42±36	10	3	72.8	0	10	0	71.9	0	10	0								
18°C																							
8.5	0	12	0	7.5	0	15	0	6.7	0	14	0	7.0	0	13	0	9.7	0	14	0				
15.4	0	12	0	15.2	5±4	15	2	14.6	2±1	14	2	15.2	0	13	0	15.9	0	14	0	13.1	0	12	0
24.3	0	12	0	25.5	12±9	15	3	25.2	9±8	14	5	25.3	0	13	0	26.7	0	14	0	15.6	0	12	0
34.4	0	12	0	36.1	48±12	15	6	35.0	24±9	14	7	35.4	19±11	13	5	36.0	0	14	0	26.6	0	12	0
43.0	0	12	0	44.7	57±14	15	7	44.6	36±16	14	6	43.4	26±21	13	3	45.6	4±2	14	2	36.2	0	12	0
55.2	0	12	0	56.2	50±15	15	8	52.0	29±15	14	7	50.8	0	13	0	55.5	0	14	0	46.1	0	12	0
				65.4	42±13	15	7	61.9	0	14	0	61.5	0	13	0	66.2	0	8	0	56.2	0	6	0
				72.7	37±10	6	4	72.3	0	4	0	72.8	0	3	0								
23°C																							
7.2	0	13	0	6.8	0	14	0	7.4	0	10	0	6.8	0	15	0	8.9	5±0	15	2	9.5	11±6	11	5
14.7	0	13	0	17.1	0	14	0	17.2	8±0	10	1	14.4	0	15	0	15.4	7±5	15	3	15.3	23±9	11	6
22.8	0	13	0	29.0	11±5	14	3	25.8	15±4	10	4	25.1	4±3	15	2	26.4	6±4	15	3	26.3	26±7	11	7
32.6	5±0	13	1	35.6	16±7	14	6	35.9	45±11	10	5	33.0	21±16	15	6	36.0	3±0	15	2	35.6	30±4	11	5
41.2	0	13	0	45.3	33±10	14	4	45.3	23±5	10	6	44.3	23±24	15	2	45.6	36±17	15	6	45.7	71±11	11	6
56.1	0	13	0	55.3	52±21	14	6	56.2	11±3	10	4	51.4	2±0	15	1	55.4	51±8	15	5	57.1	45±3	11	4
				64.2	44±22	14	6	66.6	3±2	10	2	60.6	0	9	0	64.2	0	13	0	66.3	1±0	11	3
				74.5	54±21	7	2	70.7	0	5	0	71.2	0	4	0	73.2	0	6	0	72.1	0	5	0

Values are means ± S.E.M.

Observations were made in an increasing-velocity test.

u is the mean current speed (cm s⁻¹), *N* is the number of fish tested and *N_e* is the number of fish that entrained on cylinders.

address the mechanisms that underlie these differences. Further studies are required to determine these mechanisms.

Cylinder orientation

Entrainment patterns of both chub and bass were similar for vertically and horizontally oriented cylinders. The maximum depth:width ratio of the fish averaged 1.5 for chub and 1.8 for bass, so that it might be expected that the vertically oriented cylinders would provide a wake better able to encompass the body. However, the fish were buffeted in the wake, so that the ability to entrain on objects such as the cylinders may depend on the performance of the fins (i.e. the control surfaces) rather than on the portion of the body immersed in the wake. The control surfaces are arranged orthogonally. The median fins were thus aligned with the cylinder and the wake of vertically oriented cylinders, while the median fins were better aligned with horizontally oriented cylinders. Therefore, the absence of an effect on cylinder orientation of entrainment may reflect

equally important contributions by these two sets of control surfaces in different planes. This could be tested by fin-amputation experiments.

Current speed

Fish behavior was irregular when entraining on cylinders. Overall, both chub and bass entrained at intermediate speeds, but not at low or high speeds. However, individuals showed variable entrainment behavior, sometimes entraining but sometimes not, with no apparent pattern. The energy cost of swimming is a significant component of the daily energy budget of fishes (Brett, 1983) and, in theory, these costs could be greatly reduced at all current speeds by fish taking refuge in the wake of a structure. Fish swam during the acclimation period such that they would have sampled the flow throughout the observation section, and a fish tended to entrain almost immediately following a speed increment. Thus, it appears that fish chose not to entrain or chose to do so for shorter periods at low current speeds. While many

fish attempted to entrain at high speeds, they were displaced quickly and chose to swim in regions of the flume where the flow was unaffected by the cylinders.

Analogous entrainment choices have been described for cod *Gadus morhua* on a rippled substratum (Gerstner, 1998). Cod used only intermediate-sized ripples with a wavelength of approximately twice the length of the body to obtain refuge from the current at intermediate speeds, avoiding shorter and longer ripples at low and high speeds.

The basis for variation among individual fishes and entrainment at intermediate speeds only is not known. Variation among individuals in swimming behavior is well known and is especially well described for delta smelt *Hypomesus transpacificus* (Swanson *et al.* 1998). Mechanical factors may also be important. Perhaps the need for continuous regulation of stability in the wakes of small cylinders results in a fatigue–recovery cycle for the control system.

Other energetic factors might explain the choice to begin entraining at an intermediate speed. Stability and mechanically similar maneuvers are associated with high energy costs which increase at low speeds (Blake, 1979; Videler, 1993; He and Wardle, 1986; Webb, 1991, 1993, 1997; Boisclair and Tang, 1993; Krohn and Boisclair, 1994). In contrast, translocation costs increase with speed (Beamish, 1978; Videler, 1993). Perhaps fish try to entrain when stability costs, which decline as speed increases, become smaller than translocation costs, which increase with speed.

The upper limit to the speeds at which fish entrain apparently occurs when postural control is overwhelmed by increasingly large perturbations at high current speeds.

Critical swimming speeds determine upper limits of performance. The 2 min u_{crit} would be expected to increase with cylinder diameter, which would provide an increasingly large refuge for the body. However, in practice, fish did not entrain at higher current speeds. Therefore, 2 min u_{crit} was unaffected by the presence of the cylinders in these experiments.

Cylinder diameter

Similarly, fish were expected to entrain in larger percentages and for longer as cylinder diameter increased. Chub did entrain in larger percentages (Fig. 4) and for longer (Tables 2, 3) as cylinder diameter increased from 6.4 to 13 mm, but entrainment was similar for 19 mm cylinders and tended to decrease for 25 mm cylinders. Bass did not entrain on 6.4 mm or 25 mm cylinders, but entrained in approximately similar numbers (Fig. 5) and for similar proportions of time (Tables 2, 3) on 13 mm and 19 mm cylinders. The cylinder diameters on which fish entrained were of the same order as body depth and width. Experiments using fishes with a wider range of body cross-sectional dimensions could determine whether there is a relationship between body depth and width and the diameter of structures on which fish entrain.

The small number of fish entraining on 25 mm cylinders and the short entrainment periods were unexpected. However, low-frequency body perturbations such as those illustrated in Fig. 3 tended to be larger with larger cylinders. Thus, fish were

probably displaced more easily from large cylinders in the same way that larger-amplitude disturbances appear to displace them from cylinders at higher speeds.

Low entrainment on 25 mm diameter cylinders does not mean that cylinders larger than this will be avoided. Woody debris with very much larger diameters is well known to be used by stream fish as a flow refuge (Ross, 1997). Large-diameter objects provide extensive regions of low-speed flow which can fully encompass the fish. Similarly, branched structures provide a larger region of retarded flow compared with that of the components individually (von Mises, 1945; Hoerner, 1965). Therefore, as cylinder diameter increases above 25 mm, it is likely that a size is reached at which fish again entrain: fish may also be able to entrain on more complex structures of smaller average diameter.

Temperature effects and differences in stability strategies

Entrainment by chub on cylinders of a given size was independent of temperature. In contrast, bass essentially entrained only at 23 °C (Fig. 5). One possible explanation for this unexpected result might be that different muscle systems are involved in the two species, perhaps with chub making greater use of glycolytic muscle and bass relying more on temperature-dependent slow oxidative muscle. Alternatively, different stabilizing strategies may be involved: chub appeared to use self-correcting dynamic control (von Mises, 1945; Hoerner, 1965, 1975), in which a perturbation increases the angle of attack on the fins such that the resulting increased lift force counteracts the displacement (Weihs, 1989, 1993). The flexion and extension of the median and paired fins in the plane of the fin web would vary the magnitude of lift forces tuning the control system. In contrast, bass tended to move their fins normal to the fin-web plane, so the fins must have actively generated thrust. The median fins of bass were similarly employed, although to a lesser extent. While thrust forces are dynamic in origin, I define such thrust-based stability regulation as powered control.

Powered control requires accurate phasing of correction forces with perturbations, without which a correction may amplify a displacement (induced error). The response times involved in sensing, analyzing and reacting to a perturbation typically decrease with temperature, even for thermally acclimated fish such as those used in these experiments. As a result, the probability of induced error with powered control systems is likely to decrease as temperature increases. This would result in temperature-dependent entrainment as observed for bass. In contrast, the self-correction feature of dynamic control will be less dependent on temperature and would result in entrainment patterns consistent with those observed for chub. Furthermore, dynamic control would be expected to correct the larger-magnitude vorticity more effectively in the wake of large-diameter cylinders and the higher-frequency vorticity expected with small-diameter cylinders (Vogel, 1994). Therefore, the hypothesis that bass rely more on powered control than do chub can explain the observed differences in entrainment patterns between the two species at various temperatures and cylinder diameters.

This hypothesis is also consistent with the general life-styles and habitat preferences of soft-rayed and spiny-rayed fishes. Dynamic control would be expected to favor persistence in the high-current and more turbulent habitats in which soft-rayed fish are typically dominant members of the community (Moyle and Cech, 1996). Powered control probably provides for accurate body-positioning. Combined with suction feeding, power-based stability and maneuvering provides a very effective system for cropping a food resource of small items in the productive lentic surface waters (Lauder, 1983; O'Brien *et al.* 1986) in which spiny-rayed fish are prevalent.

This research was supported by the National Science Foundation, grant numbers IBN 9017817 and DCB-9017817. I also thank two anonymous referees for their valuable suggestions.

References

- ARNOLD, G. P., WEBB, P. W. AND HOLFORD, B. H. (1991). The role of the pectoral fins in station-holding of Atlantic salmon (*Salmo salar* L.). *J. exp. Biol.* **156**, 625–629.
- BEAMISH, F. W. H. (1978). Swimming capacity. In *Fish Physiology*, vol. 7, *Locomotion* (ed. W. S. Hoar and D. J. Randall), pp. 101–187. New York: Academic Press.
- BELL, W. H. AND TERHUNE, L. D. B. (1970). Water tunnel design for fisheries research. *Fish. Res. Bd Can. Tech. Rep.* **195**, 1–69.
- BLAKE, R. W. (1979). The energetics of hovering in the mandarin fish (*Synchropus picturatus*). *J. exp. Biol.* **82**, 25–33.
- BOISCLAIR, D. AND TANG, M. (1993). Empirical analysis of the swimming pattern on the net energetic cost of swimming in fishes. *J. Fish Biol.* **42**, 169–183.
- BREder, C. M. (1926). The locomotion of fishes. *Zoologica* **4**, 159–297.
- BRETT, J. R. (1964). The respiratory metabolism and swimming performance of young sockeye salmon. *J. Fish. Res. Bd Can.* **21**, 1183–1226.
- BRETT, J. R. (1983). Life energetics of sockeye salmon. In *Behavioral Energetics: The Cost of Survival in Vertebrates* (ed. N. P. Aspey and S. I. Lustock), pp. 29–63. Columbus, OH: Ohio State University Press.
- COOK, P. H. (1985). The behaviour of plaice (*Pleuronectes platessa* L.) in relation to bottom currents and sediment type. PhD thesis, University of East Anglia, Norwich, UK.
- FARLINGER, S. AND BEAMISH, F. W. H. (1977). Effects of time and velocity increments in the critical swimming speeds of largemouth bass (*Micropterus salmoides*). *Trans. Am. Fish. Soc.* **106**, 436–439.
- FAUSCH, K. D. (1984). Profitable stream positions for salmonids: relating specific growth rate to net energy gain. *Can. J. Zool.* **62**, 441–451.
- GERSTNER, C. L. (1998). Use of substratum ripples for flow refuging by Atlantic cod, *Gadus morhua*. *Env. Biol. Fish.* **55**, 455–460.
- GERSTNER, C. L. AND WEBB, P. W. (1998). The station-holding performance of plaice, *Pleuronectes platessa*, on artificial substratum ripples. *Can. J. Zool.* **76**, 260–268.
- GORDON, N. D., MCMAHON, T. A. AND FINLAYSON, B. L. (1994). *Stream Hydrology*. New York: John Wiley & Sons.
- HARRIS, J. E. (1937a). The mechanical significance of the position and movements of the paired fins in the Teleostei. *Papers Tortugas Lab. Carnegie Inst.* **31**, 173–189.
- HARRIS, J. E. (1937b). The role of fin movements in the equilibrium of fish. *A. Rep. Tortugas Lab., Carnegie Inst.* **1936–37**, 91–93.
- HE, P. AND WARDLE, C. S. (1986). Tilting behavior of the Atlantic mackerel, *Scomber scombrus*, at low swimming speeds. *J. Fish Biol.* **29** (Suppl. A), 223–232.
- HOBSON, E. S. (1974). Feeding relationships of teleostean fishes on coral reefs in Kona, Hawaii. *Fishery Bull. Fish. Wildl. Serv. U.S.* **72**, 915–1031.
- HOERNER, S. F. (1965). *Fluid-dynamic Drag*. Brick Town, NJ: Hoerner Fluid Dynamics.
- HOERNER, S. F. (1975). *Fluid-dynamic Lift*. Brick Town, NJ: Hoerner Fluid Dynamics.
- KEENLEYSIDE, M. H. A. (1979). *Diversity and Adaptation in Fish Behaviour*. Berlin: Springer-Verlag.
- KROHN, M. M. AND BOISCLAIR, D. (1994). Use of a stereo-video system to estimate the energy expenditure of free-swimming fish. *Can. J. Fish. aquat. Sci.* **51**, 1119–1127.
- LAUDER, G. V. (1983). Food capture. In *Fish Biomechanics* (ed. P. W. Webb and D. Weihs), pp. 280–311. New York: Praeger Scientific.
- MOYLE, P. B. AND CECH, J. J. (1996). *Fishes: an Introduction to Ichthyology*. Upper Saddle River, NJ: Prentice-Hall.
- O'BRIEN, W. J., EVANS, B. I. AND HOWICK, G. L. (1986). A new view of the predation cycle of a planktivorous fish, white crappie (*Pomoxis annularis*). *Can. J. Fish. aquat. Sci.* **43**, 1894–1899.
- PROBST, W. E., RABENI, C. F., COVINGTON, W. G. AND MARTENEY, R. E. (1984). Resource use by stream-dwelling rock bass and smallmouth bass. *Trans. Am. Fish. Soc.* **113**, 283–294.
- ROSS, M. R. (1997). *Fisheries Conservation and Management*. London: Prentice-Hall.
- SALE, P. F. (1991). *The Ecology of Fishes on Coral Reefs*. San Diego, CA: Academic Press.
- SUTTERLIN, A. M. AND WADDY, S. (1975). Possible role of the posterior lateral line in obstacle entrainment by brook trout (*Salvelinus fontinalis*). *J. Fish. Res. Bd Can.* **32**, 2441–2446.
- SWANSON, C., YOUNG, P. S. AND CECH, J. J. (1998). Swimming performance of delta smelt: maximum performance and behavioral and kinematic limitations on swimming at submaximal velocities. *J. exp. Biol.* **201**, 333–345.
- VIDELER, J. J. (1993). *Fish Swimming*. New York: Chapman & Hall.
- VOGEL, S. (1994). *Life in Moving Fluids*. Princeton, NJ: Princeton University Press.
- VOGEL, S. AND LABARBERA, M. (1978). Simple flow tanks for research and teaching. *BioScience* **26**, 638–643.
- VON MISES, R. (1945). *Theory of Flight*. New York: Dover.
- WEBB, P. W. (1975). Hydrodynamics and energetics of fish propulsion. *Bull. Fish. Res. Bd Can.* **190**, 1–159.
- WEBB, P. W. (1991). Composition and mechanics of routine swimming of rainbow trout, *Oncorhynchus mykiss*. *Can. J. Fish. aquat. Sci.* **48**, 583–590.
- WEBB, P. W. (1993). Is tilting at low swimming speeds unique to negatively buoyant fish? Observations on steelhead trout, *Oncorhynchus mykiss* and bluegill, *Lepomis macrochirus*. *J. Fish Biol.* **43**, 687–694.
- WEBB, P. W. (1997). Swimming. In *The Physiology of Fishes*, second edition (ed. D. D. Evans), pp. 3–24. Marine Science Series, Boca Raton, FL: CRC Press.
- WEIHS, D. (1989). Design features and mechanics of axial locomotion in fish. *Am. Zool.* **29**, 151–160.
- WEIHS, D. (1993). Stability of aquatic animal locomotion. *Contemp. Math.* **141**, 443–461.