

BURST-AND-COAST SWIMMING IN SCHOOLING FISH (*NOTEMIGONUS CRYSOLEUCAS*) WITH IMPLICATIONS FOR ENERGY ECONOMY

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Abstract—1. The burst-and-coast behavior and tail beat frequency were analysed to determine if an energetic saving was realized for fish when swimming in formation.

2. Individual *Notemigonus crysoleucas* were compared as they swam singly or in a school of five at 0.15 m/sec in a flow tank.

3. No significant difference was found in time intervals of bursting and coasting between leading fish in the school and solitary fish.

4. Trailing fish in the school were significantly different from the other fish with increased coast time and decreased burst time by 19%, which was calculated to provide a maximum energy saving of over 20%; however, higher tail beat frequencies of trailing fish indicate greater relative velocities compared to solitary or leading fish.

5. These results infer that energy savings through the collective use of schooling and burst-and-coast behaviors is sacrificed.

INTRODUCTION

For any organism, the effective use of energy can provide an important advantage in terms of evolutionary success as well as short term survival. Energy economy in swimming by fish has been suggested as one of a number of possible advantages to schooling (Breder, 1967, 1976; Belyayev and Zuyev, 1969; Weihs, 1973, 1975; Shaw, 1978). Swimming in polarized formations may influence the flow of water around adjacent individuals in the formation, thereby reducing drag with a concomitant decrease in the individual's energy cost of locomotion. It was hypothesized that trailing fish in a school take advantage of the flow pattern generated by leading fish for energy economy (Breder, 1965; Belyayev and Zuyev, 1969; Weihs, 1973; Abrahams and Colgan, 1985). The maximum duration of fish swimming in schools is 2–6 times longer than for single fish (Belyayev and Zuyev, 1969). Abrahams and Colgan (1985) measured the respiratory rate of fish schools and found a 13% reduction in the rate compared to the sum for individuals. Weihs (1973, 1975) proposed a hydrodynamic model that predicted a five-fold energy saving by steadily swimming in a fixed formation. Such a potential energy saving was suggested for schooling scombrids, that swim steadily in the appropriate formation (Magnuson, 1978).

In general, however, fish do not swim steadily. Many fish swim intermittently using a two-phase periodic behavior of alternating accelerations (burst phase) with glides (coast phase) (Videler and Weihs, 1982; Weihs and Webb, 1983). The burst-and-coast behavior has been shown to minimize the energy

expenditure of fish (Weihs, 1974; Videler, 1981; Videler and Weihs, 1982). Weihs (1974) estimated that an energy saving of over 50% could be attained by fish using this behavior. Energy savings are realized while coasting compared to steady swimming, because drag on an undulating fish body is greater than drag for a coasting fish (Lighthill, 1971; Webb, 1975).

The purpose of this study was to investigate the interaction of schooling and burst-and-coast swimming for possible energy economy. Examination of kinematic variables was used for comparisons of solitary and schooling fish. It was expected that trailing fish in a school would experience an energetic saving with increased coasting times and decreased tail beat frequency during the burst phase compared to other fish.

MATERIALS AND METHODS

Experimental animals

Golden shiners (*Notemigonus crysoleucas*) were obtained commercially and maintained in the laboratory in groups of at least 30 individuals. Mean fork length (\pm SE) was 7.9 ± 0.08 cm with a range from 7 to 10 cm and mean maximum width was 0.87 ± 0.01 cm. The fish were held in a 3791 aquarium with continuously filtered water and dissolved oxygen levels maintained at saturation with air stones. Water temperature was maintained between 20 and 23°C and the light cycle was 12:12 hr. Fish were fed a diet of Purina trout chow.

Flow tank

Fish were tested in a recirculating flow tank, based on a design by Vogel and LaBarbera (1978). The working section of the flow tank was constructed of 1.2 cm clear Lucite and had dimensions of 49 x 16.5 x 16 cm. The working section was bounded upstream by a grid of 4 cm long plastic straws

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(0.5 cm i.d.) that remove turbulence from the flow. The downstream end was bounded by a plastic grid (commercially termed "egg crate"). Wires attached to the downstream grid formed an electrified grid (10V DC) which was controlled with a Grass S5 Stimulator. The floor and posterior wall of the working section were marked with a grid of 2 cm squares to be used as reference points. Simultaneous lateral and dorsal views of the fish were allowed by a mirror that was positioned over the working section at a 45° angle. The dorsal view of the fish was not distorted, because no surface waves were formed due to the low test velocity.

Water speed through the working section was controlled with a variable speed electric motor (Talboys Engineering Corp. Model 101) which drove a propeller situated downstream of the working section. Water speed was determined from the time a drop of ink traversed a measured distance.

Experimental procedure

An individual fish or a group of five fish, representing a school, was obtained randomly from the holding tank and tested in the working section of the flow tank. These fish remained in the working section with no flow for a 15-min acclimation period. All fish were tested at a water speed of 0.15 m/sec and were swum continuously for no more than 15 min.

Swimming performance was recorded on video tape using a television camera (TMC-2100) equipped with a Angenieux zoom lens (1:2.8, $f = 15\text{--}150\text{ mm}$) and Panasonic video recorder (AG-6300). Filming rate was 30 frames/sec. Data were collected only for fish swimming at least 2 cm from the floor and walls of the observation section. In addition, three of the fish had to be in a configuration of two leading and one trailing before measurements were taken. Frame-by-frame analysis of video tape was used to measure position of fish in formation, coast time, burst time, and tail beat frequency. Average times were determined from five sequential burst and coast cycles.

The energy expenditure over an entire burst-and-coast swimming cycle (W_{bc}) was calculated as:

$$W_{bc} = W_b + W_c \quad (1)$$

where W_b and W_c are energies expended during burst and coast phases, respectively. Because the rate of energy expended for a body moving through water is equal to the product of drag force and velocity, equation (1) can be rewritten as:

$$W_{bc} = 1/2\rho Sa_b C_D U^3 t_b + 1/2\rho Sa_c C_D U^3 t_c \quad (2)$$

and simplified to:

$$W_{bc} = 1/2\rho SC_D U^3 (a_b t_b + a_c t_c) \quad (3)$$

where ρ is the density of water, S is wetted surface area of the fish, C_D is the coefficient of drag, U is velocity, a_b and a_c are drag augmentation factors, and t_b and t_c are times of burst and coast phases, respectively. S was estimated from the equation cited by Webb (1975) using body length (L):

$$S = 0.4L^2 \quad (4)$$

C_D was estimated from:

$$C_D = 1.33 R_L^{-0.5} \quad (5)$$

where R_L is the Reynold's Number of 1.2×10^4 calculated according to Webb (1975) and Blake (1983) and indicating laminar flow around the body. Drag augmentation factors range between 1 and 5 depending on the activity of the fish (Lighthill, 1971). When coasting, fish act like a rigid body with no increase in calculated C_D and a_c is assumed to be unity. However, drag increases in a flexing body compared to a rigid body by a factor of 3–5 (Lighthill, 1971; Webb *et al.*, 1984). To estimate the maximum effect of burst-and-coast swimming in this study, a_b was assumed to equal 5 for actively swimming fish.

RESULTS

Position of fish in school

The swimming performance of 90 fish (15 individuals; 15 schools) was examined in this study. Maximum difference in size between fish in a school was 30%, which is typical (Breder, 1976). The swimming speed of 0.15 m/sec represented a specific swimming speed of 1.9 body lengths/sec. Fish displayed no signs of fatigue over the test period.

A consistent pattern was observed between positions of leading and trailing fish in the school. Trailing fish would situate themselves downstream with an equal lateral spacing between two leading fish of 2.62 ± 0.24 cm. Trailing fish did not maintain a constant longitudinal position throughout a complete burst-and-coast cycle. From a starting position approximately 0.8 body lengths downstream of the snout of the leading fish, trailing fish were swept downstream approximately 2–6 cm by the end of the coast phase. At the beginning of the burst phase, these fish accelerated and swam upstream to the position occupied prior to coasting. Trailing fish were never observed to position themselves immediately behind another fish. Fish frequently exchanged positions with other trailing fish and with leading fish. No detectable longitudinal change in position was observed by leading fish throughout a burst-and-coast cycle. Average lateral displacements between the two leading fish was 5.23 ± 0.41 cm representing six body widths and 0.66 body lengths.

Burst-and-coast times

Mean burst-and-coast times for solitary and schooling fish are summarized in Fig. 1. Results from one-way ANOVA (Ryan *et al.*, 1976) and Tukey's test (Zar, 1984) demonstrated significant differences between solitary and schooling fish for burst ($P < 0.025$) and coast times ($P < 0.005$). No significant differences were found for burst-and-coast times between solitary and leading fish. The burst time represented approximately 70% of the total propulsive cycle for solitary and leading fish (Fig. 2), and was significantly different ($P < 0.001$) from the coast time. In addition, the burst times of solitary and trailing fish were not significantly different.

Trailing fish in a school had significantly longer coast times ($P < 0.05$) compared to solitary and

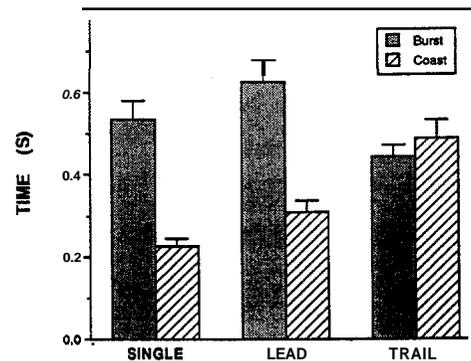


Fig. 1. Histogram of mean burst-and-coast times (\pm SE) for single fish and leading and trailing fish in a school.

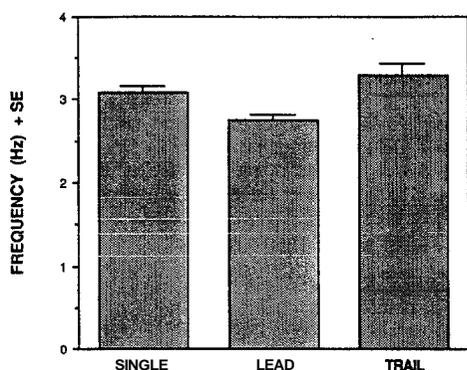


Fig. 2. Comparison of tail beat frequencies (\pm SE) during the burst phase.

leading fish (Fig. 1). Coast time for trailing fish was 58 and 115% greater than coast times for leading and solitary fish, respectively. Coast time of 0.49 ± 0.04 sec for trailing fish was nearly equal to its burst time of 0.44 ± 0.03 sec (Fig. 1). Despite longer coast times observed for trailing fish compared with other fish, no significant differences were detected for comparisons of total time of burst-and-coast cycle between fish.

Burst-and-coast swimming provides substantial energy savings to individual fish, but is particularly economical for trailing fish in a school (Table 1). Although burst-and-coast times were equal for trailing fish, the energy expended during the coast phase represented only 22% of the energy from the burst phase. In comparison to solitary fish swimming continuously and leading fish, trailing fish displayed a 29 and 21% reduction in the cost of swimming, respectively.

Tail beat frequency

Tail beat frequencies for solitary and schooling fish are summarized in Fig. 2. A significant difference ($P < 0.005$) between frequency means was found using ANOVA (Ryan *et al.*, 1976). Although no significant difference were detected from comparisons (Tukey's test) of solitary fish to schooling fish, a significant difference ($P < 0.05$) was observed between leading and trailing fish. Trailing fish were found to have a mean tail beat frequency of 3.30 ± 0.14 Hz, which was 1.2 times greater than the 2.75 ± 0.07 Hz for leading fish.

DISCUSSION

Energy savings by formation swimming is due to the undulatory movements of fish which produce thrust-type vortices shed into the wake (Weihs, 1972). This produces a vortex street composed of a series of alternating vortices periodically generated at a rate

Table 1. Comparison of the times and energy expended during burst-and-coast swimming

Behavior	Time (sec)			Energy ($\times 10^{-4}$ J)		
	Burst	Coast	Total	Burst	Coast	Total
Single (continuous)	—	—	0.76	—	—	1.92
Single (burst-coast)	0.53	0.23	0.76	1.35	0.11	1.46
Leading (burst-coast)	0.63	0.31	0.94	1.58	0.16	1.74
Trailing (burst-coast)	0.44	0.49	0.93	1.12	0.25	1.37

equal to twice the tail beat frequency and arranged as two staggered rows (Prandtl and Tietjens, 1934; Webb, 1975; Vogel, 1981; Weihs and Webb, 1983). The angular velocity in a vortex influences the relative velocity of a fish swimming in the wake (Breder, 1965; Belyayev and Zuyev, 1969; Weihs, 1973, 1975). When the trailing fish is moving in the same direction as the tangential velocity, the fish should experience a reduction of its relative velocity (Weihs, 1973; Breder, 1976). Lowered relative velocities experienced by trailing fish will decrease the drag and power output needed to maintain the swimming speed of the school.

For the thrust-type vortex trail (Weihs, 1972), a lowered relative velocity is experienced by a fish swimming diagonally behind another fish (Weihs, 1973). The optimal arrangement of the school is a diamond pattern with angles of 30° and 150° and the distance in a row is twice the width of the vortex street between adjacent fish (Weihs, 1973, 1975). This pattern is frequently observed in fish schools (van Olst and Hunter, 1970; Breder, 1976). Theoretically, trailing fish would experience a relative velocity 40–50% of the free stream velocity and a 4–6 times reduction in resistive forces (Weihs, 1975).

Our observations indicate that energy economy through the use of burst-and-coast behavior can be enhanced by swimming in formation, particularly for trailing fish. By swimming between the wakes of two leading fish, a trailing fish may experience a reduction in its relative velocity. A lowered relative velocity would allow for increased coast times and decreased burst times without a reduction of absolute Velocity. Subsequently, swimming effort is reduced for trailing fish while swimming speed is equivalent to leading fish in the school.

Energy savings proposed for golden shiners due to the interaction of burst-and-coast behavior and formation swimming, however, may be overly optimistic. For maximal savings, schooling fish with should swim continuously with antiphase tail motions (Weihs, 1973, 1975). Burst-and-coast behavior and differences expressed between leading and trailing fish would not provide the synchrony necessary for a constant and predictable vortex wake. In addition, the prolonged coast phase of trailing fish with its associated downstream displacement prevents these fish from maintaining a position for continuous energy savings.

The wake of coasting fish provides no pattern of vorticity to be exploited for energy savings by fish downstream. This is because the fish, acting as a streamlined body, has a small wake with little disturbance to the flow (Webb, 1975). Aleyev (1977) observed that a dye discharged from the gill slits of coasting fish showed no vortices in the wake. Similar results were obtained from photographs of the wake of a Zebra Danio (*Brachydanio rerio*) (McCutchen, 1977). Therefore, trailing fish in a diamond formation would experience higher relative velocities and increased energetic expense when following coasting fish.

Although a mean angle of 37.5° calculated between three shiners approached the optimum angle of 30° predicted by Weihs (1973, 1975), the trailing fish was positioned with its snout upstream of the leading fish tails. Partridge and Pitcher (1979) noted that in this

position trailing fish could not use thrust vortices produced by leading fish, because the vortices would not have sufficient time to develop before the trailing fish encountered it. Maximum energy savings were assumed when fish were downstream of leading fish at least five times the distance moved in one beat cycle (Weihs, 1975).

Higher tail beat frequency exhibited by trailing fish indicates an increase in locomotor effort compared to solitary and leading fish. This finding runs counter to the frequency arrangement hypothesized for this study and previous results (Zuyev and Belyayev, 1970). Trailing fish should show low frequencies if relative velocity is reduced due to the hydrodynamic effect of the school formation, because tail beat frequency is positively related to swimming velocity in fish (Bainbridge, 1958; Hunter and Zweifel, 1971; Webb, 1975; Stevens, 1979). Zuyev and Belyayev (1979) found that for schooling horse mackerel (*Trachurus mediterraneus ponticus*) the tail beat frequency of trailing fish was 71–85% of the frequency for leading fish. The tail beat frequency for Pacific mackerel (*Scomber japonicus*) swimming in groups was found to be lower than for solitary fish (Fields, 1990).

Differences in frequency between schools of mackerel and shiners may be due to different swimming patterns. Although mackerel periodically exhibit sharp forward bursts or glides with noticeable decelerations, swimming is uniform and position is held constant for the majority of time (Zuyev and Belyayev, 1970). High frequencies by trailing shiners results from constant use of burst-and-coast swimming. The downstream displacement caused by a prolonged coast phase requires an acceleration by the trailing fish to restore its position behind the leaders. Therefore, the trailing fish must swim at a velocity greater than the average velocity of the school incurring an increased tail beat frequency. The large accelerations during the burst will limit energy savings derived from the prolonged coast. In addition, the small size of the fish and low swimming speed examined in this study further limits energetic performance in that burst-and-coast swimming becomes more economical as Reynold's Number increases (Videler and Weihs, 1982).

The behaviors of schooling and burst-and-coast swimming offer individually the possibility of energy economy during continuous locomotion. However, simultaneous use of both behaviors restricts attainment of maximal performance by either behavior alone. The effectiveness of either strategy is compromised due to differences associated with the flow regimes for each behavior and problems of orientation and positioning within an actively swimming school. Spacing between schooling individuals is influenced by optical fixation on fellow fish (van Olst and Hunter, 1970; Breder, 1976). The leading fish is used as a reference and trailing fish more closely approach leading fish than other neighboring fish (van Olst and Hunter, 1970). The difficulty of maintaining an exact position in a school has been likened to the organization of automobiles in free-flowing traffic (Breder, 1976), where the reception of sensory stimuli and associated response times contribute to irregularities in the instantaneous structure of the

formation. Thus, energy savings due to burst-and-coast swimming by trailing fish may be incidental to maintaining position in the school.

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REFERENCES

- Abrahams M. V. and Colgan P. W. (1985) Risk of predation, hydrodynamic efficiency and their influence on school structure. *Envir. Biol. Fish.* **13**, 195–202.
- Aleyev Yu. G. (1977) *Nekton*, pp. 435. Junk, The Hague.
- Bainbridge R. (1958) The speed of swimming fish as related to size and to the frequency and the amplitude of the tail beat. *J. exp. Biol.* **35**, 109–133.
- Belyayev V. V. and Zuyev G. V. (1969) Hydrodynamic hypothesis of schooling in fishes. *J. Zool.* **9**, 578–584.
- Blake R. W. (1983) *Fish Locomotion*, pp. 208. Cambridge University Press, Cambridge.
- Breder C. M., Jr. (1965) Vortices and fish schools. *Zoologica* (N. Y.) **50**, 97–114.
- Breder C. M., Jr. (1967) On the survival value of fish schools. *Zoologica* (N. Y.) **52**, 25–40.
- Breder C. M., Jr. (1976) Fish schools as operational structures. *Fish. Bull.* **74**, 471–502.
- Fields P. A. (1990) Decreased swimming effort in groups of Pacific mackerel (*Scomber japonicus*). *Amer. Zool.* **30**, 134A.
- Hunter J. R. and Zweifel J. R. (1971) Swimming speed, tail beat frequency, tail beat amplitude and size in jack mackerel, *Trachurus symmetricus*, and other fishes. *Fish. Bull.* **69**, 253–266.
- Lighthill M. J. (1971) Large-amplitude elongated body theory of fish locomotion. *Proc. R. Soc. Ser. E* **179**, 125–138.
- Magnuson J. J. (1978) Locomotion by scombrid fishes: Hydrodynamics morphology and behavior. In *Fish Physiology: Locomotion* (Edited by Hoar W. S. and Randall D. J.), Vol. VII, pp. 239–313. Academic Press, New York.
- McCutchen C. W. (1977) Froude propulsive efficiency of a small fish, measured by wake visualization. In *Scale Effects in Animal Locomotion* (Edited by Pedley T. J.) pp. 339–363. Academic Press, London.
- Partridge B. L. and Pitcher T. J. (1979) Evidence against a hydrodynamic function for fish schools. *Nature* **279**, 418–419.
- Prandtl L. and Tietjens O. G. (1934) *Applied Hydro- and Aeromechanics*, pp. 311. Dover, New York.
- Ryan T. A., Jr, Joiner B. L. and Ryan B. F. (1976) *Minitab: Student Handbook*, PWS Publishers, Boston.
- Shaw E. (1978) Schooling fishes. *Amer. Sci.* **66**, 166175.
- Stevens E. D. (1979) The effect of temperature on tail beat frequency of fish swimming at constant velocity. *Can. J. Zool.* **57**, 1628–1635.
- van Olst J. C. and Hunter J. R. (1970) Some aspects of the organization of fish schools. *J. Fish Res. Bd. Can.* **27**, 1225–1238.
- Videler J. J. (1981) Swimming movements, body structure and propulsion in Cod (*Gadus morhua*). In *Vertebrate Locomotion* (Edited by Day M. H.), pp. 1–27. *Symp. Zool. Soc. Lond.*, no. 48, Academic Press, London.
- Videler J. J. and Weihs D. (1982) Energetic advantages of burst-and-coast swimming of fish at high speeds. *J. exp. Biol.* **97**, 169–178.
- Vogel S. (1981) *Life in Moving Fluids*, pp. 352. Willard Grant Press, Boston.
- Vogel S. and LaBarbera M. (1978) Simple flow tanks for research and teaching. *Bioscience* **28**, 638–643.
- Webb P. W. (1975) Hydrodynamics and energetics of fish propulsion. *Bull. Fish. Res. Bd. Can.* **190**, 1–159.

- Webb P. W., Kostechi P. T. and Stevens E. D. (1984) The effect of size and swimming speed on locomotor kinematics of rainbow trout. *J. exp. Biol.* **109**, 77-95.
- Weihls D. (1972) Semi-infinite vortex trails, and their relation to oscillating airfoils. *J. Fluid Mech.* **54**, 679-690.
- Weihls D. (1973) Hydromechanics of fish schooling. *Nature* **241**, 290-291.
- Weihls D. (1974) Energetic advantages of burst swimming of fish. *J. Theor. Biol.* **48**, 215-229.
- Weihls D. (1975) Some hydrodynamical aspects of fish schooling. In *Swimming and Flying in Nature* (Edited by Wu T. Y.-T., Brokaw C. J. and Brennen C.) Vol. 2, pp. 703-718. Plenum Press, New York.
- Weihls D. and Webb P. W. (1983) Optimization of locomotion. In *Fish Biomechanics* (Edited by Webb P. W. and Weihls D.) pp. 339-371. Praeger, New York.
- Zar J. H. (1984) *Biostatistical Analysis*, 2nd edn, pp. 718. Prentice-Hall, Englewood Cliffs, N.J.
- Zuyev G. V. and Belyayev V. V. (1970) An experimental study of fish in groups as exemplified by the horse mackerel (*Trachurus mediterraneus ponticus* Aleev). *J. Ichthy.* **10**, 545-549.