

## KINEMATICS OF PECTORAL FIN PROPULSION IN *CYMATOGASTER AGGREGATA*

By P. W. WEBB\*

*Fisheries Research Board of Canada,  
Pacific Biological Station, Nanaimo, B.C.*

(Received 8 May 1973)

### INTRODUCTION

Studies of fish locomotion have concentrated on body and caudal fin swimming modes. This applies equally to all facets of locomotion (e.g. see Bone, 1966; Gray, 1968; Lighthill, 1969; Webb, 1971 *a, b*, 1973; Brett & Glass, 1973). In contrast, little work has been done on other swimming modes. Breder (1926) has classified various non-body swimming modes, and some of these have been further qualitatively discussed (Harris, 1937, 1953; Breder & Edgerton, 1942; Lissman, 1961). Brett & Sutherland (1965) noted that *Lepomis gibbosus* shifted from pectoral fin propulsion to caudal fin propulsion when swimming speed increased above approximately 12 cm/sec (1 L/sec).

However, no quantitative studies relating kinematic parameters, metabolic costs, etc. with performance have been made on these non-body/caudal fin modes. Therefore, this paper attempts to evaluate the kinematics for one such mode, pectoral fin propulsion of *Cymatogaster aggregata*, and to examine interactions between various kinematic parameters in relation to swimming speed.

### MATERIALS AND METHODS

#### *Fish*

Fifteen shiner seaperch (*Cymatogaster aggregata*) were caught in Departure Bay, Vancouver Island, B.C., using a baited hook and line. Fish were immediately transferred to 197 l holding tanks, described by Alderdice, Brett & Sutherland (1971). Temperature was initially held at  $12.0 \pm 0.2$  °C, the temperature of the local water from which fish were caught. Fish were held for 6 weeks prior to testing. During the first 4 weeks the temperature was slowly raised to  $15.0 \pm 0.2$  °C, the test temperature, and subsequently maintained at this level. The acclimation temperature approximated to the local sea-water temperature of the fishes natural habitat in late summer when the experiments were performed.

At all times the holding tanks were flushed with sea water at 150 l/h. Dissolved oxygen levels were maintained close to 100% air saturation by means of air stones.

It was found that fish were easily excited and tended to try and jump out of holding tanks unless cover was provided. Cover with a strong vertical green pattern (submerged bottles) was found to be most effective. Water was continuously recirculated in the

\* Present Address: School of Natural Resources, The University of Michigan, Ann Arbor, Michigan 48104, U.S.A.

tanks, the mean velocity outside the cover area being 20 cm/sec, to facilitate self-cleaning.

Fish were fed to excess twice a day on Abernathy pellets. Fish readily accepted this artificial food. Fish were starved for 48 h prior to testing.

### *Experimental procedure*

Nine healthy, intact fish were selected for testing. Single fish were transferred to the fish-chamber of a water-tunnel respirometer (Brett, 1964). Following recovery, the water velocity was set at 10 cm/sec. Fish swam regularly in the current, and training was rarely necessary. The downstream electrified grid was not required for training.

The following day (never less than 16 h after placing the fish in the chamber) the pectoral-fin movements were recorded during the course of a standard increasing-velocity performance test (Brett, 1964). Swimming speed was increased in 7.5 cm/sec. increments every 45 min, until the fish was exhausted. The critical swimming speed (45 min.  $U_{crit}$ ) was calculated in the usual way (Brett, 1964; Webb, 1971*a, b*, 1973). To ensure that fish were exercised to exhaustion, the downstream electrified grid was intermittently used if fish drifted too far downstream. Fish only drifted downstream prior to exhaustion. The grid was therefore rarely used, and no electrolysis products accumulated.

Pectoral fin and body movements were recorded in vertical and horizontal planes using cine-film at 54 f.p.s. as described by Webb (1973). Visual observations were also made of fish swimming in the holding tanks at very low speeds and at zero speeds.

Water was continuously flushed through the respirometer, with the exception that water flow was temporarily interrupted in order to measure oxygen consumption at each swimming speed. These data will be reported elsewhere (P. W. Webb, in preparation). At no time was the dissolved oxygen level permitted to fall below 90% air saturation.

At the end of an experiment fish were weighed to the nearest 0.01 g, and total length was measured to the nearest 1 mm. Weight was  $35.55 \pm 4.52$  g, and length  $14.3 \pm 0.6$  cm ( $\bar{X} \pm 2$  s.e.). Fish were also dissected. Five fish were post-partum females, the remainder males. A tenth fish originally tested was rejected following dissection because of a heavy load of gill parasites. This fish also had the lowest 45 min  $U_{crit}$ .

Swimming speeds were converted to specific swimming speeds in  $L/sec$  to facilitate comparison with other species.

## RESULTS AND DISCUSSION

### *Pectoral-fin movements*

Pectoral-fin propulsion was in the labriform mode (Breder, 1926). Superficially the movements appeared like sculling movements, mediated by a propagated wave passing posteriorly (morphologically ventrally) over the fin in forward swimming. The length of the wave was long in relation to the length of the trailing edge of the fin (Harris, 1937).

In normal swimming the pectoral fins were used exclusively. The caudal fin was used at very low swimming speeds and at high speeds (described below).

Two patterns of pectoral-fin movements were observed, to be designated pectoral-

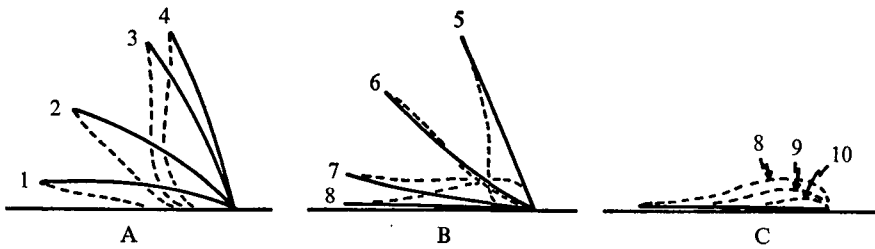


Fig. 1. Movements of the pectoral fin in pectoral-fin pattern *A*, as seen from the dorsal side, traced from successive frames of cine-film taken at 54 f.p.s. The fish was swimming at 17.5 cm/sec. Incident water flow is from right to left. The leading edge is shown as a solid line, and the trailing edge as a dotted line. Successive positions are numbered 1-10. (A) Abduction of the leading edge and commencement of abduction of the trailing edge. (B) Adduction of the leading edge and completion of abduction of the trailing edge. (C) Completion of adduction of the trailing edge and refractory phase of the leading edge.

fin pattern *A* and *B*. They differed only in kinematic detail related to the length of the wave propagated over the fin. In pectoral-fin pattern *A* the wavelength was approximately twice the length of the trailing edge. As a result, the movements of posterior fin-rays trailed behind those of anterior fin-rays with a phase difference of approximately  $\pi$ . In pectoral-fin pattern *B* a very much longer wave was propagated over the fin, such that the phase difference between posterior and anterior fin-ray movements was of the order of  $0.2\pi$ . As a result, locomotory movements in pectoral-fin pattern *B* were a simplification of those in pectoral-fin pattern *A*, with the fin tending to work more as a unit in the former case.

Mechanically, both patterns will therefore be similar, except that thrust forces will be distributed over a relatively longer period of time in pectoral-fin pattern *A* compared with *B*. Therefore, only pectoral-fin pattern *A* will be discussed in detail.

Details of fin movements in pectoral-fin pattern *A* as viewed from the dorsal side are shown in Fig. 1. Abduction commenced with the first complete fin-ray rotating outwards. It should be noted that this leading edge is anatomically the strongly thickened second fin-ray, the first being bound to it and specially modified for muscle attachment. Successive fin-rays decrease in thickness, and hence in flexibility, so that the fin is substantially stiffer anteriorly. This modified the configuration of the propagated wave to some extent so that the posterior portion of the fin superficially appeared to move like a flap attached to the remainder of the fin. This obviously disappeared in pectoral-fin pattern *B*.

As the propulsive wave passed over the fin, successive rays commenced abduction (Fig. 1 *A*). Because of the phase difference between the motion of anterior and posterior fin-rays, abduction was completed earlier anteriorly, and adduction commenced before abduction of posterior fin-rays was complete (Fig. 1 *B*). Similarly, following the completion of adduction of anterior fin-rays, adduction was completed by posterior fin-rays. Adduction of all portions of the fin was completed before the next fin stroke commenced. Consequently, each fin-ray moved intermittently, and for some portion of the fin-stroke was stationary. This phase of the fin-beat cycle will be called the refractory phase.

The leading edge of the fin did not simply rotate laterally, but there was also vertical

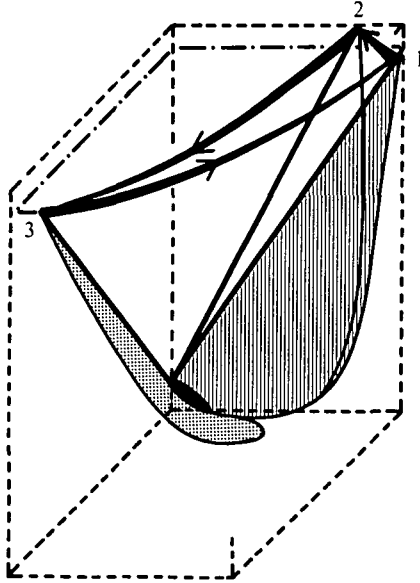


Fig. 2. Diagrammatic representation of horizontal rotation and lateral rotation of the leading edge of the pectoral fin during a complete stroke in pectoral-fin pattern *A*. The heavy arrows indicate the motion of the tip of trailing edge. The leading edge completes adduction in position 1 (the fin being shown by vertical shading) and rotates vertically against the body to position 2 during the leading-edge refractory phase. During abduction the leading edge rotates laterally and vertically to position 3 (the fin being shown stippled), and during adduction returns by lateral rotation to position 1.

rotation. This resulted mainly from the orientation of the fin-base, but also from vertical movements of the leading edge.

The fin-base was inclined ventrally at an angle of approximately  $35^\circ$  to the long axis of the body. Therefore, during abduction, the fin tended to rotate laterally forward, and vertically downward. Similarly, during adduction, the fin tended to move laterally backward, and vertically upward.

Vertical rotation of the leading edge itself occurred as part of the refractory phase and abduction (Fig. 2). At the end of adduction the leading edge was pressed against the body. During the refractory phase it rotated vertically upwards a small distance, while still being pressed against the body. As a result, abduction commenced with the leading edge elevated, and during abduction it rotated forward and downward. During adduction the leading edge simply rotated backwards about the fin-base, to reach a position in the original plane reached at the end of abduction. The behaviour of the leading edge amplified the forward and downward motion of the fin during abduction in addition to that due to the inclination of the fin-base. Asymmetries of this nature in different phases of pectoral fin-beat cycles were noted by Harris (1937).

#### *Forces generated by fin movements*

Forces generated by paired fins have been qualitatively discussed by Harris (1937), but most emphasis has been made on stationary fins acting as brakes and in controlling stability (Harris, 1936, 1937, 1938). However, the principles employed to describe these functions apply equally to moving fins (Breder & Edgerton, 1942).

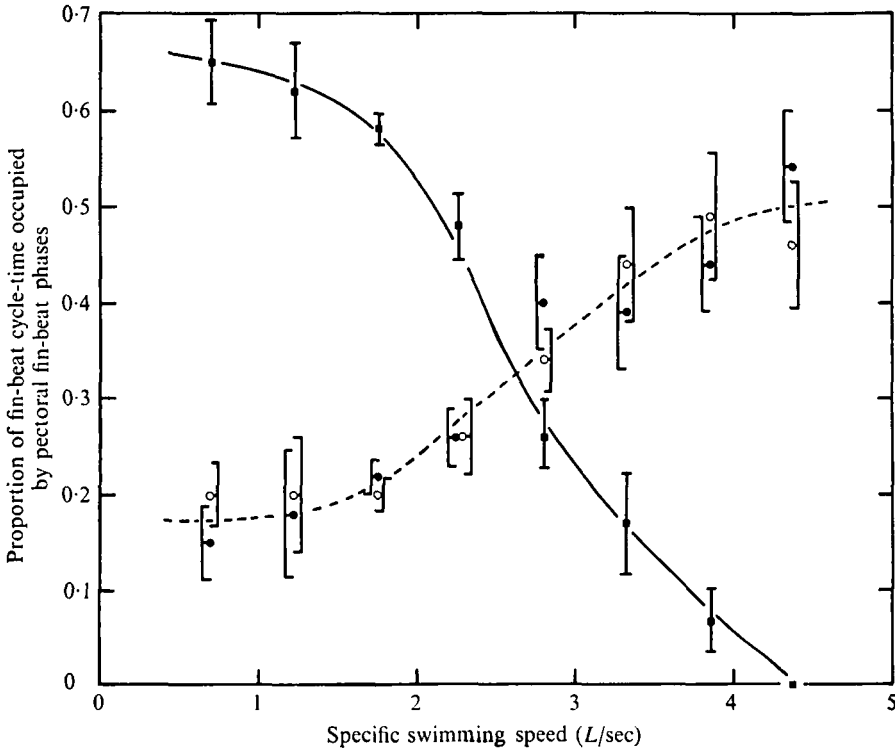


Fig. 3. The relationship between the proportion of time for a fin-beat cycle occupied by abduction, adduction and refractory phases, shown as a function of swimming speed. Vertical bars show  $\pm$  s.e. about mean values. Key: Abduction, solid circles; adduction, open circles; refractory phase, solid squares.

Therefore, any portion of the fin in pectoral-fin pattern *A*, and the whole fin in pectoral-fin pattern *B*, can be compared with a plane surface. During abduction this surface moves forward and downward against the incident flow, and at some positive angle to that flow. It will be realized that the normal force acting on the fin will thus be inclined backwards, and may be resolved into thrust and lift components. During adduction the fin moves backward and upward in the same direction as the incident flow and at some angle to that flow. The forces acting on the fin will have thrust and negative lift components. In this way thrust is generated throughout abduction and adduction phases in similar fashion to the generation of lift through most of the wing-beat cycle of many birds (see Gray, 1968).

The fish were also slightly negatively buoyant. Adduction negative lift forces plus a small gravitational force added to equal abduction lift forces, so that the mean axis of motion of the fish remained horizontal. Thus vertical forces cancelled out over a complete fin-cycle.

*The proportion of the pectoral fin-beat cycle occupied by various pectoral fin-beat phases*

Abduction, adduction and refractory phases occupied variable portions of the time required to complete a fin-beat cycle. The various proportions of time occupied by

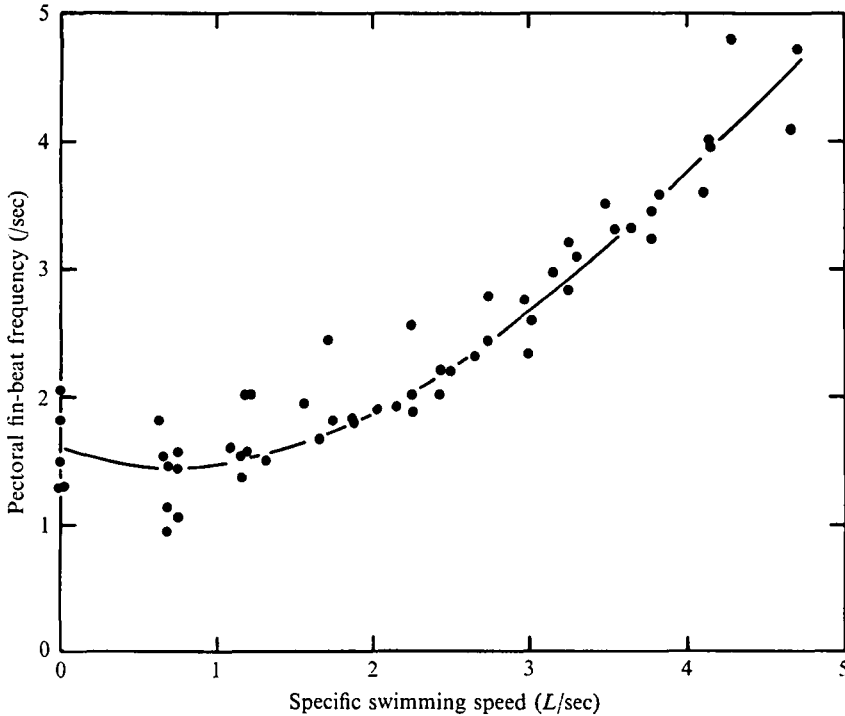


Fig. 4. The relationship between pectoral fin-beat frequency and swimming speed.

these phases were measured for the leading edge. It will be realized from the description of the kinematics that the relationships for this edge will apply equally to the remainder of the fin, and hence serve to characterize the motion of the fin in the same way that trailing-edge movements of the caudal fin characterize the body motion in caudal-fin swimming modes (Webb, 1971*a*, 1973).

The duration of the three phases was found to depend on swimming speed (Fig. 3). Abduction and adduction phases were of similar duration, but they occupied an increasing portion of time for any fin-beat cycle as swimming speed increased. As a result, the duration of the refractory phase decreased with increasing speed, reaching zero at the highest speeds obtained (4.38 L/sec).

#### *Pectoral fin-beat frequency and amplitude*

Pectoral fin-beat frequency was generally related to swimming speed when this exceeded 1 L/sec (Fig. 4). At lower swimming speeds frequency was fairly constant, although increasing slightly at zero speeds. As is well known, this latter effect results from continuous pectoral-fin movements as teleosts make stability and orientation control movements. No satisfactory linear transformation was found to adequately describe the relationship between frequency and swimming speed.

The amplitude of the pectoral fin-beat was measured in radians for the leading edge. Again, the motion of this edge characterizes the motion of the remainder of the fin. Relationships between amplitude and swimming speed were fairly complex (Fig. 5). Amplitude increased rapidly from approximately 1.09 to 1.28 radians at swimming

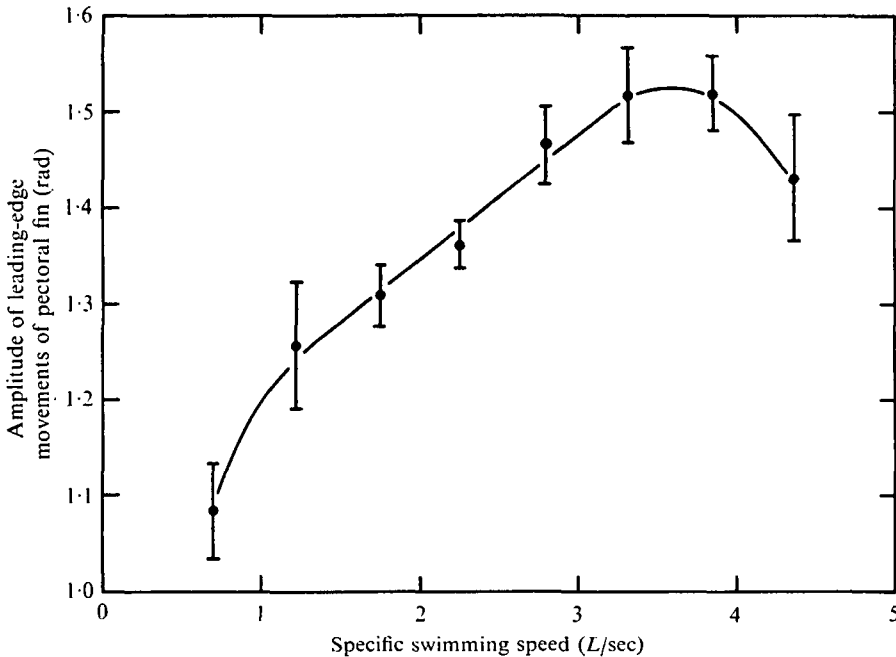


Fig. 5. Pectoral fin-beat amplitude, measured in radians for the leading edge, as a function of swimming speed. Vertical bars indicate  $\pm 2$  s.e. about mean amplitudes.

speeds between 0.5 and 1.5 L/sec, increasing at a lower rate to reach a maximum of 1.53 radians at 3.6 L/sec. Amplitude subsequently decreased to 1.43 radians at 4.38 L/sec.

*Relationships between frequency, amplitude, refractory phase  
and pectoral fin-beat patterns*

The movements of the pectoral fins in relation to swimming speed can be interpreted with reference to interactions between frequency, amplitude, refractory phase and pectoral-fin patterns *A* and *B*.

Bainbridge (1958) and Webb (1971a, 1973) have shown that frequency and amplitude of caudal-fin movements of fish swimming in the sub-carangiform mode are related to speed at steady swimming speeds. At higher speeds, and in other carangiform modes, amplitude is constant (Bainbridge, 1958; Hunter & Zweifel, 1971). Although neither frequency nor amplitude may necessarily be expressed as some linearized function of swimming speed, their product may be linearly related to swimming speed.

The present results for frequency and amplitude suggest the same may apply to pectoral-fin movements. Thus, in comparing Figs. 4 and 5, it can be seen that at speeds up to approximately 1.5 L/sec, frequency remains fairly constant while amplitude increases rapidly. At higher speeds both frequency and amplitude tend to increase more regularly with swimming speed. Therefore, the mean product of pectoral fin-beat frequency and amplitude was calculated and plotted as a function of swimming speed (Fig. 6). The relationship can be resolved into two straight lines. Initially frequency  $\times$  amplitude increased relatively slowly, but directly, with speed up to approximately

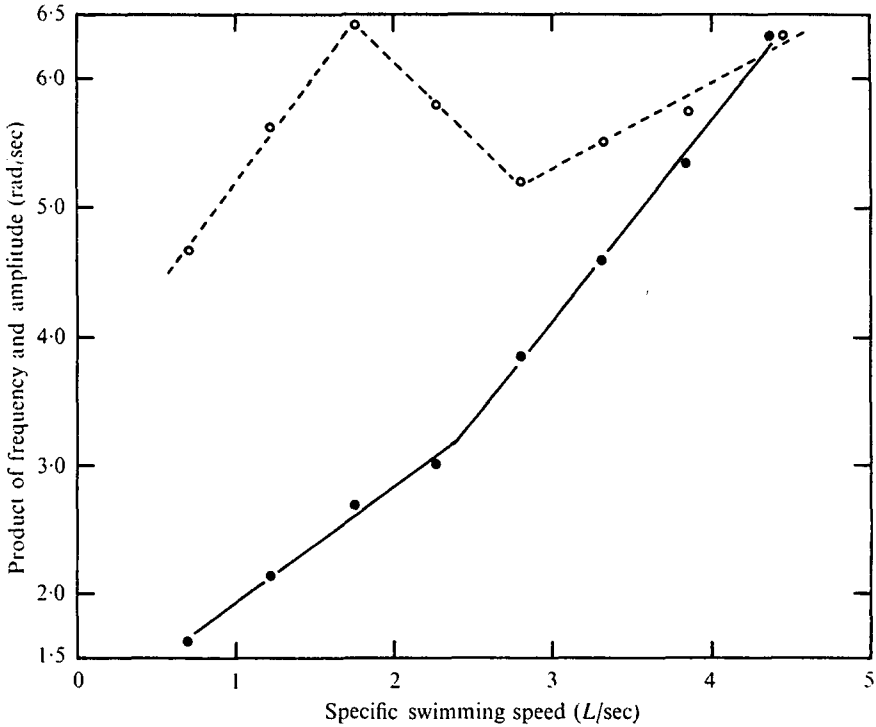


Fig. 6. The product of frequency and amplitude (solid line), and the product of corrected frequency and amplitude (dotted line) as functions of swimming speed. Further explanation is given in the text.

2.5 L/sec. Above this speed frequency  $\times$  amplitude increased more rapidly, but again directly, with swimming speed.

The relationship between frequency  $\times$  amplitude and swimming speed does not take into account the refractory phase. Because any portion of the fin is stationary for some period of time in the propulsive cycle, the velocity of fin movements will be higher than implied by measurements of frequency alone. Furthermore, the refractory phase is fairly constant up to a speed of approximately 2 L/sec, as is frequency. This suggests that the change in the slope of the relationship between frequency  $\times$  amplitude and swimming speed may result from the changing duration of the refractory period.

In order to test this possibility a corrected frequency may be calculated from the measured frequency multiplied by the portion of the pectoral fin-cycle occupied by propulsive movements and the product of corrected frequency and amplitude again plotted against swimming speed (Fig. 6).

This latter relationship was found to differ markedly from the relationship between frequency  $\times$  amplitude and swimming speed. Thus the relationship between corrected frequency  $\times$  amplitude and swimming speed could be resolved into three portions. Initially, corrected frequency  $\times$  amplitude increased rapidly to 6.4 at a speed of 1.8 L/sec. Between 1.8 and 2.8 L/sec, the product decreased to 5.2, and then increased above 2.8 L/sec but at a lower rate, to reach a second maximum of 6.2 at 4.38 L/sec.

Clearly, the various changes in slope cannot be explained simply in terms of frequency, amplitude and refractory-phase duration. However, it was found that up to,



Approximately 2.0 L/sec pectoral-fin movements were almost entirely of pectoral-fin pattern *A*. At swimming speeds greater than 2.8 L/sec pectoral-fin pattern *B* predominated. In the intermediate range individual fish would show a predominance of either of the two patterns, hence explaining the break in the relationship between corrected frequency  $\times$  amplitude and swimming speed.

The relationship between corrected frequency  $\times$  amplitude and swimming speed does not take into account the detailed kinematic differences between the two fin-patterns. The nature of pectoral-fin pattern *A* will mean that it takes relatively more time to complete a propulsive cycle compared with pectoral-fin pattern *B*, although both patterns may be characterized by the same parameters. However, it will be observed that maximum values of corrected frequency  $\times$  amplitude are similar, indicating a maximum speed of movement for any portion of the fin. Presumably, then, pectoral-fin pattern *B* is more effective at higher swimming speeds because the fin operates more as a unit and the fin can move at higher frequencies and hence at higher speeds. This would not be possible with pectoral-fin pattern *A* because of the time-factor involved in passing a shorter-length wave over the fin.

On this basis it can be seen that pectoral-fin pattern *A* is less suited to high-speed swimming, but does not give sufficient reason for there being two-speed-dependent kinematic variations in pectoral-fin movements. It would be expected that the fish could swim at lower speeds equally well by reducing frequency and amplitude of the fin-beat in pectoral-fin pattern *B*. This latter course would also be of some hydro-mechanical advantage, because the acceleration given to the water to increase its momentum in the generation of thrust would be greatly reduced with a concomitant increase in hydromechanical propulsion efficiency (Alexander, 1968).

However, the product of corrected frequency and amplitude also reflects the shortening-speed of the muscles. Reducing these kinematic parameters in pectoral-fin pattern *B* in order to swim at low speeds would also result in the locomotory muscles contracting at progressively lower shortening speeds. Hill (1950) has summarized the effects of shortening speed on muscle efficiency and power output. Muscle efficiency is optimal at a shortening speed of approximately 20% of its maximum shortening speed under a zero load. The efficiency curve is fairly flat in the optimum region, so that within the muscle shortening-speed range from 10–30% of the maximum, efficiency is only slightly affected by shortening-speed. Similarly, power output reaches maximum values between shortening-speeds of the order of 20–40% of the maximum shortening-speed. Once shortening-speeds move outside these optimum ranges, efficiency of contraction and power output decrease rapidly.

It is generally considered that muscles are designed to operate normally in some optimum speed range, and consequently there is more than one type of muscle fibre designed for different functions. Thus the bulk of the fish myotome is composed of fast muscles presumably designed for maximum power output at high levels of activity, while the remainder of the myotome is composed of slow muscle presumably designed to operate at optimum efficiency at slow, sustained levels of activity (see Alexander, 1967, 1968).

Against this background, the use of two types of kinematic patterns of pectoral-fin movements can be seen to be a mechanism that would permit a single muscle system to operate at optimum efficiencies and power outputs over a wider range of swimming

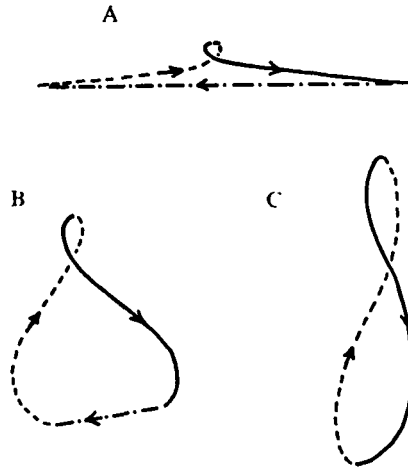


Fig. 7. Diagrammatic representation of the figure-8 motion of the body relative to a point moving at the mean speed of the fish. Movements of the body during the refractory phase are shown by the chain dotted line, during abduction by the dotted line, and during the adduction phase by the solid line. (A) shows the horizontally elongated figure-8 at low swimming speeds (less than about  $2 L/sec$ ) with pectoral-fin pattern A. (B) shows the motion of the body at about  $3 L/sec$  with pectoral-fin pattern B. (C) shows the motion of the body at speeds close to the maximum swimming speed as the duration of refractory phase becomes zero.

speeds than would otherwise be possible. Thus at lower swimming speeds pectoral-fin pattern *A* predominates but the product of corrected frequency and amplitude is as high, and reaches similar values to that product obtained at higher swimming speeds with pectoral-fin pattern *B*. In addition, the range of corrected frequency  $\times$  amplitude is fairly narrow. Consequently, muscle shortening speeds will also be confined to a fairly narrow band, following corrected frequency  $\times$  amplitude. It is to be assumed that this narrow band would coincide with optimum shortening-speeds of the muscle system. The use of the two variants of the basic pectoral-fin kinematic pattern can then be considered as a more subtle functional form of the dual muscle system.

#### *Resultant movements of the body*

Pectoral-fin movements are not only generate thrust, but also lift forces. Consequently the body tends to move up and down during normal forward swimming. In addition, thrust forces will be generated discontinuously because of the pattern of the fin-beat and the refractory phase. Thus between abduction and adduction, and during the refractory phase, no thrust will be generated. As a result the fish tends to accelerate during abduction and adduction, and to decelerate in between.

The net effect of these two motions was a complex figure-8 motion of any fixed point on the body, when viewed from a point moving at the incident velocity of the water. The form of the figure-8 was dependent on swimming speed (Fig. 7). At low swimming speeds, in pectoral-fin pattern *A*, the figure-8 was elongated horizontally (Fig. 7*A*), because of the relatively long refractory phase during which the fish drifted backwards (downstream) and downwards as the fish were slightly negatively buoyant. During abduction the fish surged forward and slightly upward, as a result of the thrust and lift forces generated during that phase. The fish drifted backwards slightly between

abduction and adduction, and then surged forward and downward as a result of thrust and negative lift forces generated by the adduction stroke. The vertical component of these movements was small presumably because of the phase difference in abduction and adduction along the length of the fin in this pectoral-fin pattern. Thus vertical forces would tend to cancel out to some extent along the fin, reducing the magnitude of the net vertical force.

As speed increased, and fish shifted to pectoral-fin pattern *B*, the figure-8 motion became more vertically orientated (Fig. 7*B*). This resulted from the decrease in the refractory phase reducing the horizontal displacement of the fish. In addition the vertical component of the body motion increased as a result of the change in fin-beat pattern, as vertical forces would no longer be partly balanced along the length of the fin.

At the highest swimming speeds the figure-8 motion of the body became further elongated vertically (Fig. 7*C*) as the refractory phase approached zero, and because vertical forces generated by the fins would increase with frequency and amplitude. At these high speeds the fish only drifted backwards very small distances between abduction and adduction phases.

The various figure-8 patterns are shown diagrammatically in Fig. 7. Accurate measurements of their magnitude was not possible because the movements were generally small, and magnification of film records to a size sufficient to permit accurate measurement was made at the cost of definition. However, in general, maximum horizontal movements were of the order of  $\pm 0.3$  mm, and maximum vertical movements were of the order of  $\pm 0.5$  mm.

#### *Caudal-fin movements*

The caudal-fin was used at very low speeds or zero speeds, and at high speeds. In still water the caudal web-fin was used in a scissor-like motion to balance the continuous pectoral-fin movements characteristic of teleosts. Pectoral-fin movements were of pectoral-fin pattern *A*, and were often asynchronous between fins.

Between swimming speeds of 0.5 and 3.4 *L*/sec, pectoral fins were used exclusively for locomotion as described above. The caudal fin was then furled, with the leading dorsal and ventral rays aligned horizontally with the base of the caudal peduncle. This minimized the area of the caudal fin when it was not used in locomotion, presumably to reduce drag.

Above approximately 3.4 *L*/sec, two patterns of caudal-fin movements were observed, which will be referred to as caudal-fin patterns *A* and *B*. Both types were carangiform (Breder, 1926).

Caudal-fin pattern *A* consisted of a train of approximately eight low-frequency, low-amplitude tail-beat cycles, following limited expansion of the caudal fin. Pectoral fins continued to be used normally. These caudal-fin movements had little observable effect on station holding which was still adequately achieved by the pectoral fins between caudal-fin movements.

Caudal-fin pattern *A* persisted up to 3.85 *L*/sec. Tail-beat trains occurred at a frequency of 0.3/sec, increasing slightly with time towards the end of the 45 min swimming period at 3.85 *L*/sec. (Fig. 8).

At the same time as the frequency of caudal-fin pattern *A* increased, caudal-fin

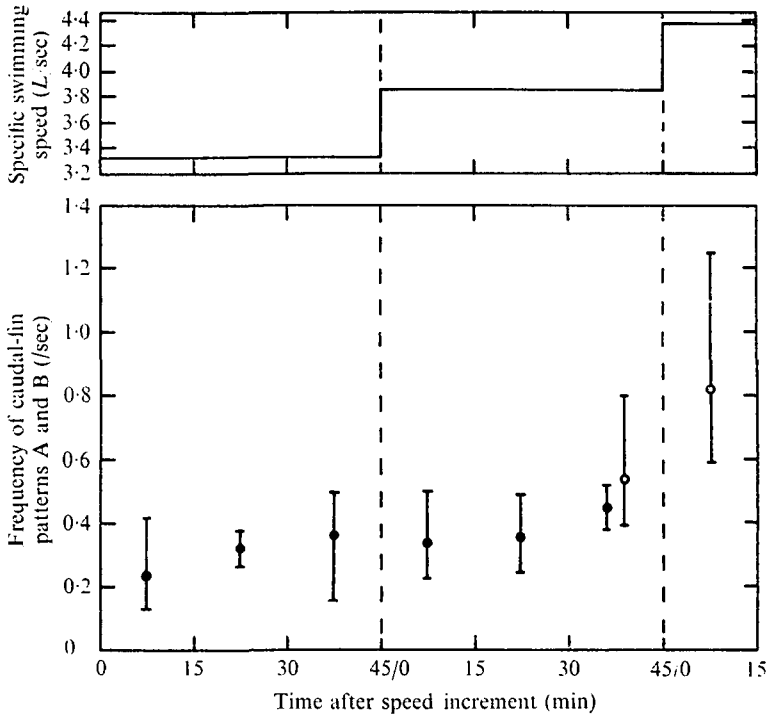


Fig. 8. The lower panel shows relationship between the frequency of caudal-fin patterns A (solid circles) and B (open circles) with increasing time after three-speed increments. Vertical bars show the range of frequencies of each pattern about the mean. Swimming speeds are shown in the upper panel.

pattern B appeared (Fig. 8). This always immediately preceded exhaustion of the fish. At the high swimming speeds involved the pectoral-fin movements were no longer sufficient to keep the fish on station. Since amplitude decreased at these speeds (Fig. 5), it appears that the fins were unable to move fast enough to generate sufficient thrust. As a result the fish tended to drift downstream.

The fish having drifted downstream, almost the full length of the fish-chamber, the caudal fin was fully expanded, and executed one to three propulsive strokes typical of those described by Weihs (1973) in the second phase of acceleration from rest. The pectoral fins were furled. As a result of the caudal-fin activity, the fish accelerated upstream, furled the tail, and recommenced pectoral-fin movements. Thus the caudal fin was used to supplement pectoral-fin locomotion at high swimming speeds, immediately prior to exhaustion.

#### *Critical swimming speed (45 min $U_{crit}$ )*

The 45 min  $U_{crit}$  was  $56.36 \pm 3.94$  cm/sec,  $3.94 \pm 0.26$  L/sec ( $\bar{X} \pm 2$  s.e.). Comparative performance data for other species (using body and caudal-fin movements in swimming) is most complete for the sockeye salmon, *Oncorhynchus nerka* (Brett & Glass, 1973), a fish that can sustain high levels of steady swimming. From Brett and Glass, the 60 min  $U_{crit}$  for 14.3 cm sockeye salmon at 15 °C would be 72.8 cm/sec, or 5.09 L/sec, that is, 22% higher than that for *Cymatogaster*. However, sockeye

Salmon have relatively high performance levels compared with many other salmonids or other species of fish. Beamish (1966) lists data for endurance of a wide variety of Atlantic species at various swimming speeds and temperatures. These data, and other data for salmonids (e.g. Bainbridge, 1962, 1963; Webb, 1971*a, b*, 1973), suggest that 45–60 min  $U_{crit}$  of the order of 3 L/sec are more typical for fish in the present size-range at their optimum temperatures.

Therefore, the 45 min  $U_{crit}$  for *Cymatogaster* using almost exclusively pectoral-fin propulsion compares very favourably with that of other fish swimming in body/caudal-fin modes.

#### SUMMARY

1. The kinematics of pectoral-fin propulsion have been measured for *Cymatogaster aggregata*, 14.3 cm in length, during an increasing-velocity performance test. Acclimation and test temperature was 15 °C, similar to the fishes' normal environmental temperature for the time of year of the tests.

2. Locomotion was in the labriform mode. Within this mode two pectoral-fin patterns were observed, differing only in the details of fin kinematics. These differences resulted from the length of the propagated wave passed over the fin. At low swimming speeds, up to about 2 L/sec, the wavelength was relatively short, approximately twice the length of the trailing edge of the fin. At higher speeds, a wave of very much longer wavelength was passed over the fin.

3. The pectoral fin-beat cycle was divisible into abduction, adduction and refractory phases. Abduction and adduction phases were of equal duration, and the proportion of time occupied by these phases increased with swimming speed. The duration of the refractory phase decreased with increasing speed.

4. The kinematics indicated that thrust was generated throughout abduction and adduction phases, together with lift forces that cancelled out over a complete cycle. As a result of lift forces and the refractory phase the body moved in a figure-8 motion relative to the flow.

5. Pectoral fin-beat frequency and amplitude increased with swimming speed, and the product of frequency  $\times$  amplitude was linearly related to swimming speed.

6. Interactions between pectoral fin-beat frequency, amplitude, refractory phase and kinematic patterns were interpreted as a mechanism to permit the propulsive muscles to operate at optimum efficiency and power output over a wider range of swimming speeds than would otherwise be possible.

7. Pectoral-fin propulsion was augmented by caudal-fin propulsion only at swimming speeds greater than 3.4 L/sec.

8. The mean 45 min critical swimming speed was 3.94 L/sec, and compares favourably with similar levels of activity for fish swimming by means of body and caudal-fin movements.

This work was completed during the tenure of a National Research Council of Canada postdoctorate fellowship. Facilities were provided by the Fisheries Research Board of Canada Pacific Biological Station at Nanaimo, and the courtesy of Dr J. R. Brett. I wish to record my thanks for their generous support. I am indebted to Dr J. R. Brett for his continued encouragement and stimulating comments, and to Dr H. Arai who having studied these fish for many years provided many useful comments during the course of the work.

## REFERENCES

- ALDERDICE, D. F., BRETT, J. R. & SUTHERLAND, D. B. (1971). Design of small holding tank for fish. *J. Fish Res. Bd Can.* **23**, 1447-50.
- ALEXANDER, R. MCN. (1967). *Functional Design in Fishes*. University Library Biological series. 160 pp. London: Hutchinson.
- ALEXANDER, R. MCN. (1968). *Animal Mechanics*. Biology Series. 346 pp. London: Sidgwick and Jackson.
- BAINBRIDGE, R. (1958). The swimming speed of fish as related to size and to the frequency and amplitude of the tail beat. *J. exp. Biol.* **35**, 109-33.
- BAINBRIDGE, R. (1962). Training, speed and stamina in trout. *J. exp. Biol.* **39**, 537-55.
- BAINBRIDGE, R. (1963). Caudal fin and body movements in the propulsion of some fish. *J. exp. Biol.* **40**, 23-46.
- BEAMISH, F. W. H. (1966). Swimming endurance of some Northwest Atlantic fishes. *J. Fish. Res. Bd Can.* **23**, 341-47.
- BONE, Q. (1966). On the function of the two types of myotomal muscle fibre in elasmobranch fish. *J. mar. biol. Ass. U.K.* **46**, 321-49.
- BREDER, C. M. (1926). The locomotion of fishes. *Zoologica N. Y.* **4**, 159-256.
- BREDER, C. M. & EDGERTON, H. E. (1942). An analysis of the locomotion of the seahorse, *Hippocampus*, by means of high speed cinematography. *Ann. N. Y. Acad. Sci.* **43**, 145-72.
- 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. & GLASS, N. R. (1973). Metabolic rates and critical swimming speeds of sockeye salmon (*Oncorhynchus nerka*) in relation to size and temperature. *J. Fish. Res. Bd Can.* **30**, 379-87.
- BRETT, J. R. & SUTHERLAND, D. B. (1965). Respiratory metabolism of pumpkinseed (*Lepomis gibbosus*) in relation to swimming speed. *J. Fish. Res. Bd Can.* **22**, 405-9.
- GRAY, J. (1968). *Animal Locomotion*. World Naturalist Series. London: Weidenfeld and Nicolson, 479 pp.
- HARRIS, J. E. (1936). The role of the fins in the equilibrium of the swimming fish. I. Wind-tunnel tests on a model of *Mustelus canis* (Mitchell). *J. exp. Biol.* **13**, 476-93.
- HARRIS, J. E. (1937). The mechanical significance of the position and movements of the paired fins in the teleostei. *Pap. Tortugas Lab.* **31**, 173-89.
- HARRIS, J. E. (1938). The role of the fins in the equilibrium of the swimming fish. II. The role of the pelvic fins. *J. exp. Biol.* **15**, 32-47.
- HARRIS, J. E. (1953). Fin patterns and the mode of life in fishes. In *Essays in Marine Biology* (ed. S. M. Marshall and P. Orr), pp. 17-28. Edinburgh: Oliver and Boyd.
- HILL, A. V. (1950). The dimensions of animals and their muscular dynamics. *Sci. Prog.* **38**, 209-30.
- HUNTER, J. R. & ZWEIFEL, J. R. (1971). Swimming speed, tail beat frequency, tail beat amplitude and size in jack mackerel, *Trachurus symmetricus*, and other fishes. *Fishery Bull. Fish Wildl. Serv. U.S.* **69**, 253-66.
- LIGHTHILL, M. J. (1969). Hydromechanics of aquatic animal propulsion. *Ann. Rev. Fluid Mech.* **1**, 413-46.
- LISSMANN, H. W. (1961). Zoology, locomotory adaptations and the problem of electric fish. In *The Cell and the Organism* (ed. J. A. Ramsay and V. B. Wigglesworth), pp. 301-317. Cambridge University Press.
- WEBB, P. W. (1971a). The swimming energetics of trout. I. Thrust and power output at cruising speeds. *J. exp. Biol.* **55**, 489-520.
- WEBB, P. W. (1971b). The swimming energetics of trout. II. Oxygen consumption and swimming efficiency. *J. exp. Biol.* **55**, 521-40.
- WEBB, P. W. (1973). Effects of partial caudal-fin amputation on the kinematics and metabolic rate of underyearling sockeye salmon (*Oncorhynchus nerka*) at steady swimming speeds. *J. exp. Biol.* **59**, 565-81.
- WEIHS, D. (1973). The mechanism of rapid starting of slender fish. *Biorheology* (in Press).