

SUMMARY

In the pectoral fins of teleost fish a great variety of functions can be distinguished. Two of them are described: labriform propulsion and braking. The anatomical adaptations to these functions are described and the bending mechanism of fin rays is discussed.

Labriform swimming (Chapter II)

Coris formosa, propelling itself by means of the pectoral fins in the labriform mode, was filmed with a high-speed cinecamera. The movements of the pectoral fins were analysed. The fin beat cycle can be divided into three phases:

1. downstroke; the fin moves downward and then forward, or it moves first forward and then downward.
2. upstroke; the fin turns to a more or less vertical position, facing backward with a slightly hollow surface, and moves backward and also upward.
3. intermediate phase; the fin is pressed against the body wall and is turned slightly forward before it starts the downstroke again.

The complete cycle takes 0.3 to 0.5 s.

For each film frame the body velocity was calculated. The effects of each phase of the fin beat are variable, but downstrokes generally cause deceleration and upstrokes acceleration. The intermediate phase sometimes shows accelerations, possibly caused by a jet of water squirted out from the space between the fin and the body wall.

The drag of the body and the net propulsive forces of the pectoral fins are estimated. The drag coefficient of the body, calculated from film sequences of the coasting fish, is about twice the theoretical value for a rigid body of revolution.

The discrepancy is discussed between the observed fin shapes during the up- and downstrokes and the simplified representation of the fin as a flat plate.

The role of the pectoral fins in braking of three fast-swimming species
(Chapter III)

Braking of mackerel, cod and saithe was analysed from high-speed cinefilms. The body is curved, the pectoral fins are extended to a varying degree. In cod and saithe the dorsal and anal fins are curved. The role of the pelvic fins could not be studied, because they were not visible in the available film sequences.

The velocities and deceleration rates were calculated for each film frame. The maximum possible contribution to the braking force by the pectoral fins is discussed for the moments of highest deceleration. The pectoral fins, if fully extended perpendicular to the body and held vertical, cannot contribute more than about 30% of the braking force. The body and extended median fins, if held straight, do not deliver more than about 15%.

The maximum power output of the abductor muscles during braking is discussed. It is argued, that it is probably not more than about 20 W kg^{-1} of muscle. The maximum velocity at which a fish can fully extend its pectoral fins in vertical position will be about $0.5 L^{-2/3} \text{ s}^{-1}$ ($L =$ body length). This is very low in comparison to the maximum attainable speeds of 10 to $15 L \text{ s}^{-1}$. It indicates that the pectorals can play a significant role in braking only at low speeds.

The drag coefficient of the braking fish was 8 to 36 times higher than for a coasting cod, 1.5 to 7 times higher than for a steady swimming cod, and of about the same magnitude as for a cod swimming in the 'kick' or 'burst' phase.

Anatomy of the pectoral fins (Chapters IV, V and part of III)

The anatomy of the pectoral fin of a cichlid fish, Sarotherodon niloticus, is described (Chapter IV). This species, using its pectoral fins for manoeuvring, has a highly versatile pectoral fin. The articulation of the rays and the insertion of the muscles on the rays is analysed. An important element in the ray articulation is the fibrocartilage pad. By means of this pad, covering the distal ends of the proximal radials, a common, longitudinal, axis of rotation (X-axis) is realized for all rays, except the first. Each individual ray articulates with the fibrocartilage pad around an axis (Y-axis) perpendicular to

the longitudinal X-axis. The first ray articulates directly with the scapula with a saddle-shaped joint which is also biaxial. Models are given to illustrate the principles of these joints.

The musculature of the pectoral fin is described. An analysis is made of the possible effects on the rays. It is demonstrated by means of simple models that the muscles can effect multidirectional movements of the rays. This means that not only abduction and adduction are brought about by the abductor and adductor muscles, but that also movements in the plane of the fin are effectuated. It is concluded that the deep part of the m.abductor superficialis produces opposite movements in different parts of the fin: posterior movements in the anterior part and anterior movements in the posterior part.

The pectoral fin anatomy of two labrid species, Coris formosa and C.julis, is described and compared with S.niloticus (Chapter V). In teleost species where the fins are used for special purposes, the adaptation of form to function of the pectoral fins is usually straightforward and clear. In the case of the above mentioned species, where the pectoral fins are predominantly used for labriform swimming and for manoeuvring, adaptations are not so evident. There are two explanations possible:

1. The different movement patterns originate entirely at a cybernetic level and the fin morphology can therefore be identical.
2. The different functions are related to small morphological differences which have been overlooked.

Detailed study of the anatomy of the three species shows that the differences between the two Coris species are smaller than between S.niloticus and the two Coris species. The pectoral fin anatomy of the three species differs in small details, part of which can be related to differences in fin movement patterns. The cybernetic origin of these differences predominates, complemented only by minute morphological details.

The morphology of the pectoral fin in three species using the pectoral fins for braking, (mackerel, cod and saithe) shows aspects limiting the individual movements of the rays relative to each other (Chapter III). There is a firm connection between the proximal parts of the rays and the fibrocartilage pad, especially in mackerel. In cod and

saithe each lateral hemitrichium bears a lamella pointing posteriorly between the hemitrichia of the following ray. The insertion of the muscles on the rays tends to have a collective character by the sheet of connective tissue between the tendons; besides, the muscles are hardly divided in separate heads to individual rays. Also, the movability of the proximal radials is restricted.

In mackerel ligaments are present blocking the abduction beyond a certain limit.

The ratio of the weight of the abductor and the adductor muscles is about 2 in mackerel and about 1 in cod and saithe, but the ratio of the weight of the abductor muscles to body weight is not significantly greater in mackerel than in cod and saithe.

Fin ray structure and bending properties (Chapter VI)

The pectoral fins are supported by segmented or soft fin rays, except the first ray. Each ray is composed of two half-rays or hemitrichia, on each side of the fin. A hemitrichium consists of one basal element of varying length and many small segments of approximately equal lengths. In cross section each segment of a hemitrichium, or hemisegment, shows a curved or semilunar profile. The hemisegments of two opposite hemitrichia are situated just vis-a-vis. The distance between opposite hemisegments decreases from the basis to the tip of the ray. The intermediate space is filled with large cells embedded in a web of collagenous fibres. Segmented rays are the main constituent in teleost fins.

The opposing hemitrichia of a ray of the pectoral fins and the tailfin of Sarotherodon niloticus are connected by transverse collagenous fibres with a serpentine, curly appearance. Experimentally applied shift of the hemitrichia of isolated tailfin rays relative to one another causes bending of the ray over its entire length. The degree of curvature at any position along the ray is proportional to the applied shift, indicating that the serpentines have elastic properties. The degree of curvature reaches a maximum at any location along the ray

pectoral fins. It is demonstrated, that in saithe the mechanism serves in regulating the angle of attack of the tailfin.