

Animal Locomotion in Water: Adaptations and Mechanics.

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Introduction.

We live on a planet with a wrong name. It is called earth but it should be named water because the water surface is much larger than the surface of the dry land. Life on earth began in the water and even now, after 10^9 years of evolution, a vast number of animal species is purely aquatic. In nonaquatic animals individual life depends on the swimming performance of sperm cells in an aqueous environment. Therefore we expect to find a rich variety of adaptations enabling animals to move about in water. These adaptations will be directed by the physical properties of water. Small animals moving at a slow speed experience viscosity as the dominant property of the water. Large fast animals use the density and inertia to propel themselves. The Reynolds (Re) number conveniently expresses the relative importance of viscous over inertial forces in a dimensionless way:

$$Re = L U \rho / \eta \quad (1)$$

Where L is the size of the animal in the direction of movement in m, U the speed in m/s, ρ is the density (kg/m^3) and η the viscosity ($\text{Ns/m}^2 = \text{Pa s}$) of the water. The ratio of viscosity over density is called the kinematic viscosity. The reciprocal of the kinematic viscosity at 1 atm is 10 for fresh water at 20°C and $8.5 \cdot 10$ for sea water of 35 ‰ at 15°C . The Re number varies from smaller than 1 for protozoa to 10^8 for the blue whale (Fig. 1 and Table 1).

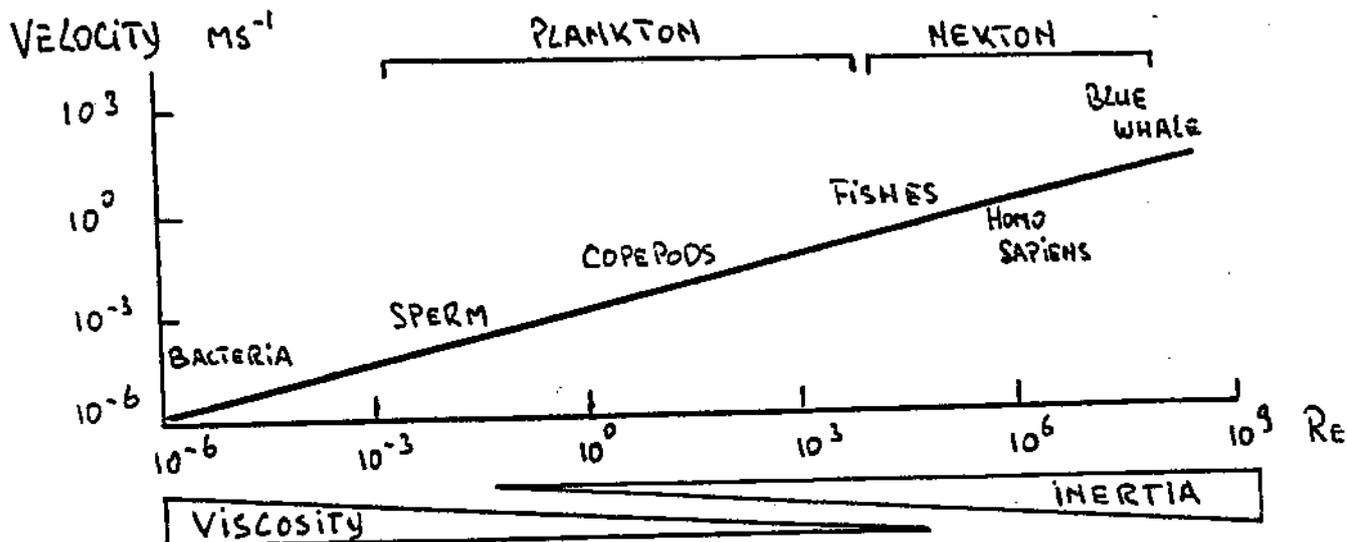


Fig. 1.

(Fig.1: The Re numbers of animals of the widest possible size range and swimming at their preferred speed of about one body-

length per second. The "animals" range from bacteria and flagellates under pure viscous regime to the largest of all living creatures the 33 m blue whale who uses the density of the water to propel itself. In oceanographic terms small animals with limited swimming capacity are called plankton and the large ones that can swim faster than the prevailing currents belong to nekton.)

Animals in the lower range are too small and not powerful enough to swim independent of the water currents and belong to the plankton. The main concern of these animals is how to control buoyancy. Many copepods (small crustaceans) for example move hundreds of meters up and down every day, feeding during the night in the upper layers and hiding in deep water in daytime.

At high Reynolds numbers, powerful swimmers are usually larger than plankton and travel independent of the water movements. Fish, whales, dolphins and squid belong to this group of animals called nekton. Some adaptations and mechanics of buoyancy control of nekton are different from those of plankton and will be discussed in relation to buoyancy control of terrestrial animals including man.

Fish swimming movements are usually undulatory. The whole body or parts of it are laterally flattened and the undulations move in a direction opposite to the swimming direction. The undulating parts are in propulsive interaction with the water. The fastest swimmers use high frequent undulations of the body to move a lunate tail. The body is not laterally flattened but round on transection and only the tail acts as a propeller. Adaptations of the fastest swimmer, the swordfish, will be described.

TABLE 1.

	Velocity m/s	Length m	Re number
Blue whale	10	30	$3 * 10^8$
Tuna	10	3	$3 * 10^7$
Human	1.7	1.8	$3 * 10^6$
Mackerel	3.3	0.3	$1 * 10^6$
Herring			
adult	1	0.2	$2 * 10^5$
larvae	0.5	0.1	$5 * 10^4$
	0.16	0.04	$6 * 10^3$
	0.06	0.02	$1 * 10^3$
	0.02	0.01	$2 * 10^2$
Copepods	0.002	0.001	2
Sea urchin sperm	0.0002	0.00015	$3 * 10^{-2}$

Sinking speed of viscosity dominated plankton

Plankton consists of small unicellular algae, of herbivorous animals feeding on the algae and of slightly larger predatory animals. The algae use light for the production of organic matter and the animals in the food chain all depend directly

or indirectly on this food source. Fig. 2 shows an example of a common alga and of its most important grazer, a copepod.

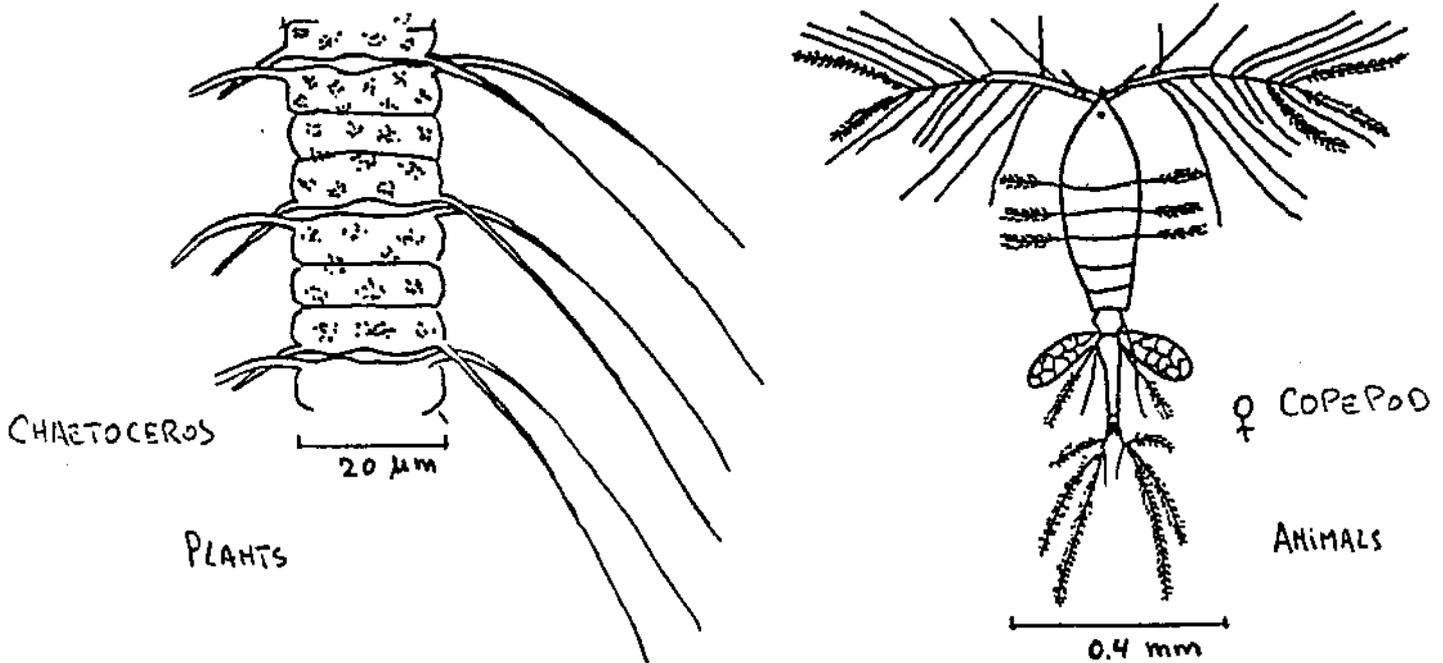


Fig. 2.: Plankton: Plants and animals without sufficient power of locomotion to move independent of the water currents.

Light is confined to the upper layers of water. So it is of ultimate importance for all these organisms to avoid sinking into deep and dark water. They must either swim in upward direction or avoid sinking altogether by controlling buoyancy.

A sphere in Fig. 3 represents a planktonic organism with radius R and underwater weight W :

$$W = \frac{4}{3} \pi R^3 (\rho_a - \rho_w) g \quad (N) \quad (2)$$

SINKING SPEED
DETERMINES LIFE TIME.

STOKES LAW: DRAG $D = 6 \pi R V \eta$
($Re < 1$)

UNDERWATER WEIGHT:
 $W = \frac{4}{3} \pi R^3 (\bar{\rho} - \rho_w) g$

SINKING AT STEADY SPEED IF $D = W$
 $6 \pi R V \eta = \frac{4}{3} \pi R^3 (\bar{\rho} - \rho_w) g$

WE FIND: $V = \frac{2}{9} R^2 g (\bar{\rho} - \rho_w) \eta^{-1}$



D : DRAG
 V : VELOCITY
 η : VISCOSITY
 R : RADIUS
 $\bar{\rho}$: DENSITY
 ρ_w : DENSITY OF WATER
 g : ACCELERATION DUE TO GRAVITY

Fig. 3: Forces on a sphere representing a planktonic organism

The factor in parentheses is the difference between the density of the animal (ρ_a) and the density of water (ρ_w). The acceleration due to gravity is indicated by g . Sinking will cause a drag force D_1 in a direction opposite to W . For Re numbers smaller than 1, Stokes's law predicts:

$$D_1 = 6 \pi R U \eta \quad (N) \quad (3)$$

Where U represents the sinking speed. The sphere will sink at a steady speed if D_1 equals W . We use (2) and (3) to find the expression for the sinking speed:

$$U = 2/9 R^2 g (\rho_a - \rho_w) / \eta \quad (m/s) \quad (4)$$

The options for an organism to keep U as small as possible can be directly deduced from this equation. The organism should be as small as possible, should try to reach the same density as water and should live in water with high viscosity and density. Water of the highest salinity near 0 °C has the highest viscosity and density (Fig. 4a and 4b) and offers the best floating conditions.

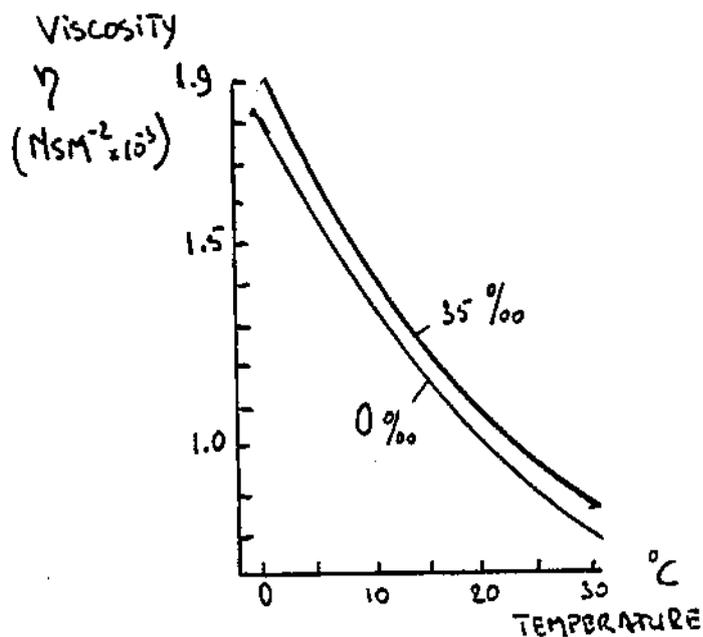


Fig. 4a.

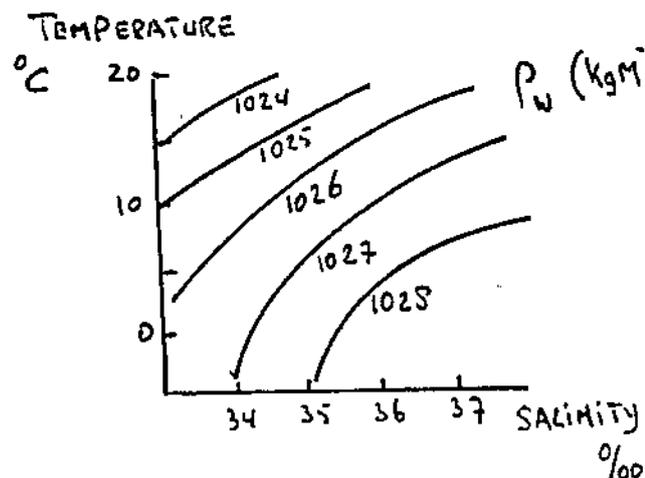


Fig. 4b.

Fig. 4a: The relation between viscosity and temperature of water of two extreme salinities.

Fig. 4b: Isopleths for constant densities in relation to temperature and salinity.

Reproduction and the avoidance of predation require that an animal reaches a fair size. This contradicts with the adaptations to counteract sinking. Several examples of the solutions to this apparent contradiction of different planktonic animals are depicted in Fig. 5.

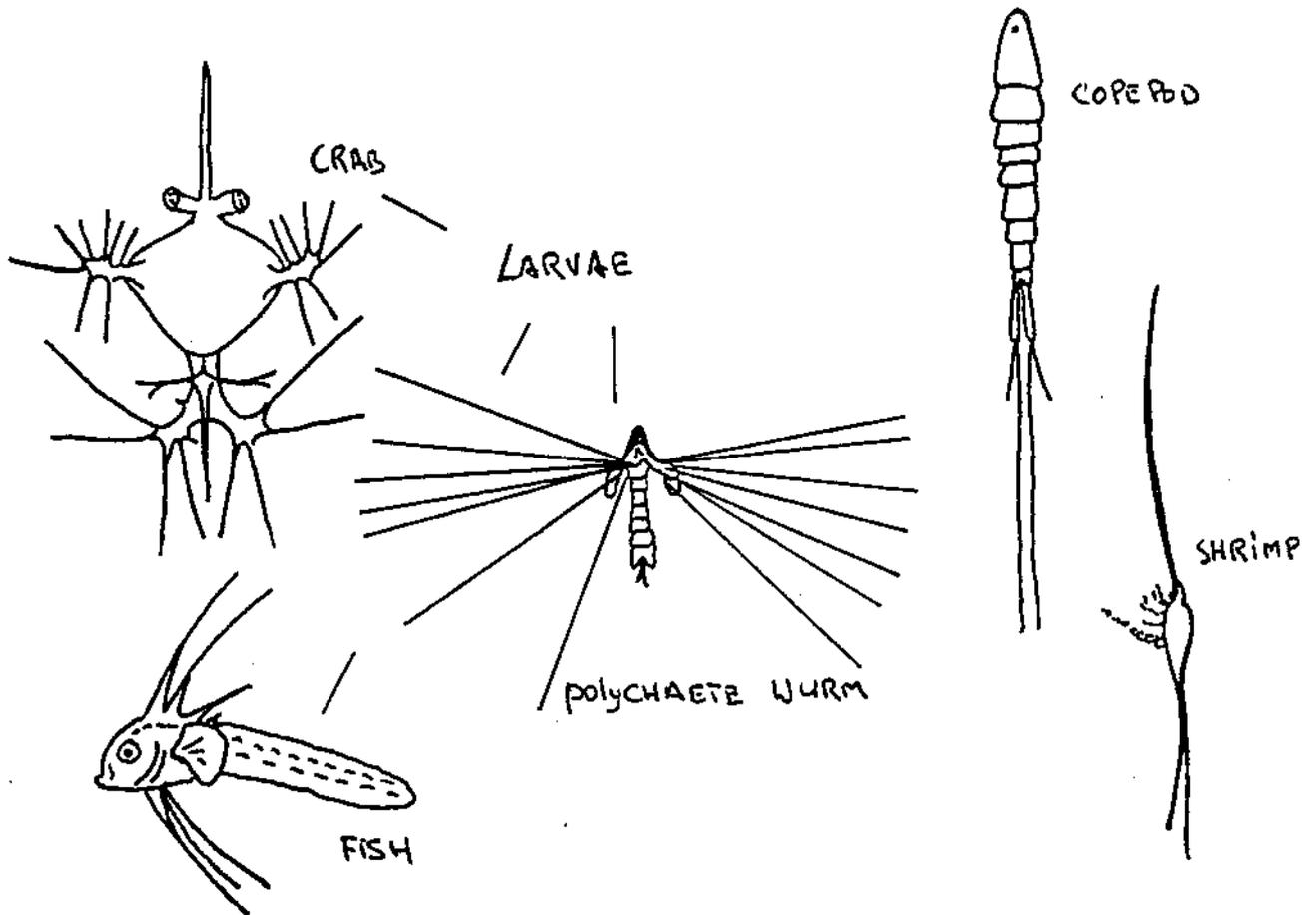


Fig. 5: Body shapes of plankton adapted to obtain large size and low sinking speed.

Long spines make animals less attractive to predators and keep the density close to that of water because the space between the spines is filled with water. Buoyancy aids are commonly used among planktonic organisms. Jelly fish use water to this end. Their water content is close to 99% of the body weight which is high compared with 90% for the average planktonic animal. The human water content varies between about 90 % for babies to 58 % for elderly people.

Oil has a lower density than water and it reduces the sinking rate of many species. The volume and hence the buoyancy provided by gas filled bladders changes with depth.

This serious disadvantage probably explains why gas bladders are rare among planktonic organisms.

Inertia dominated nekton

Animals belonging to nekton typically have spindle shaped streamlined bodies (Fig. 6).

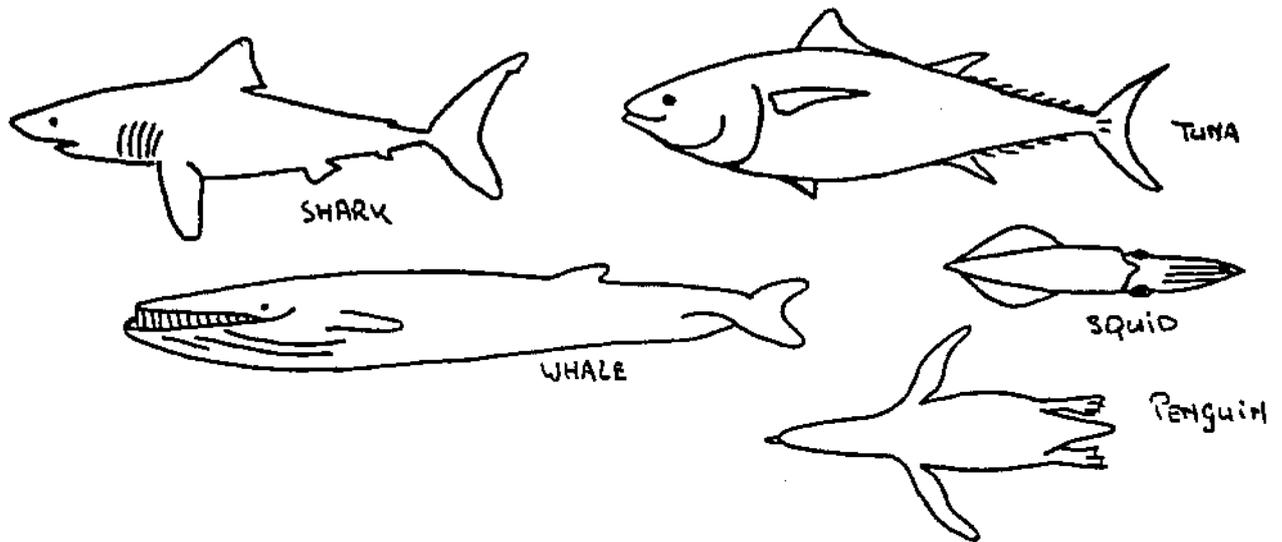


Fig. 6: Typical examples of the streamlined body shapes of nekton.

Such a body has a rounded front end, the largest thickness at about one third of the body length and a pointed rear part. The vast difference in body shapes between plankton and nekton is directly related to differences in the interactions between the animals and water. The drag on a body at high Re numbers (D_h) is equal to:

$$D_h = \frac{1}{2} \rho A_w U^2 c_d \quad (N) \quad (5)$$

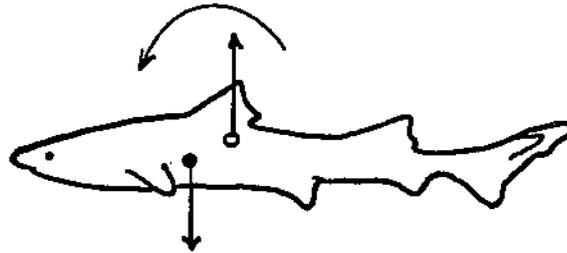
A_w is the wetted surface area and C_d a dimensionless drag coefficient. Two of the differences between equations 3 and 5 are striking: 1. D_h is proportional to the density and D_l to the viscosity.

2. D_h is proportional to the velocity squared and D_l to the velocity.

The last point implies for the fast swimmers that if they want to double their speed they have to generate about four times as much force and about eight times as much energy. (It is necessary to use the word "about" twice here because the drag coefficient, C_d , differs with the Re number and so changes with speed. At Re numbers up to a about 10^5 the flow around a streamlined body will be laminar and C_d is proportional to $Re^{-0.5}$ and to $U^{-0.5}$ (D_h proportional to $U^{1.5}$). Under turbulent flow conditions at high Re numbers, C_d is proportional to $Re^{-0.2}$ and consequently to $U^{-0.2}$. The drag D_h is in this case proportional to $U^{1.8}$.)

Drag on a streamlined body depends also highly on the ratio between thickness and length. Extremely thin bodies could offer low drag conditions, but animals need a certain volume for a variety of reasons and the optimum solution is the shape giving the lowest drag for the highest content. Flow tank experiments have shown that this optimum is reached if the ratio of thickness over length is about 0.22. Table 2 shows that the body shapes of the largest fast swimmers are very close to this optimum and that the eel for example has not the ideal shape for fast low drag swimming.

The hydrostatic equilibrium. The resting shark in Fig. 7a is principally unstable because the centre of buoyancy (Cb) and centre of mass (Cm) are not in the same position along the body.



O : CENTRE OF BUOYANCY

● : CENTRE OF GRAVITY

Fig. 7a: Vertical forces and turning moment on a resting shark.

The resultant of all the forces due to Archimedes principle (A) acts on Cb in upward direction. The weight of the animal (W) equals mass times the gravitational acceleration and this force acts in downward direction on Cm.

TABLE 2.

Thickness over Length ratios (D/L) of streamlined bodies:

	D/L
Optimal streamlined body (lowest drag with largest volume):	0.22
Nekton:	
Blue whale	0.21
Dolphins	0.25
Tuna	0.28
Cod	0.16
Mackerel	0.14
Eel	0.05

These two forces tend to rotate the body anti-clockwise until they act along the same line and Cb is exactly above Cm. The difference in magnitude between A and W determines whether the fish sinks to the bottom or rises to the surface in the head-down equilibrium posture shown in Fig 7b.

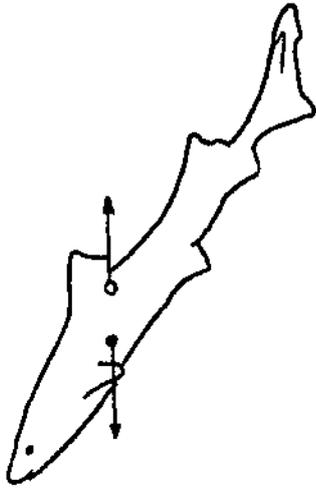


Fig. 7b: Equilibrium position and opposing forces on the body of a floating shark.

This difference depends on the density of the animal with respect to the density of the water. Fish use gas filled swimbladders and sharks oily livers to lower their density and to improve buoyancy. The density of the spermaceti oil in the bulging head of Sperm whales changes with temperature. Sperm whales dive more than thousand meters deep and need good buoyancy control which should not be affected by the water pressure. They use the surrounding water to cool the oil down which increases their density and gain buoyancy by rising the temperature with intensified blood flow through the spermaceti organ.

Most nonaquatic vertebrates tend to float in static equilibrium at the surface with a small part of the head just above the surface and the hind parts deeper down in oblique position (Fig. 7c).

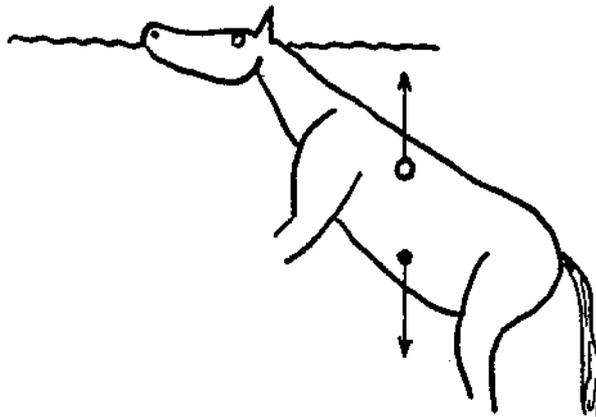


Fig. 7c: Static equilibrium of a non-aquatic animal in water.

The nostrils are usually situated on the top of the emerging part of the head. Humans are exceptional in this respect, mainly because of their strongly reduced snout length. The human equilibrium position is rather awkward since nose and mouth remain submerged making breathing impossible (Fig 7d).

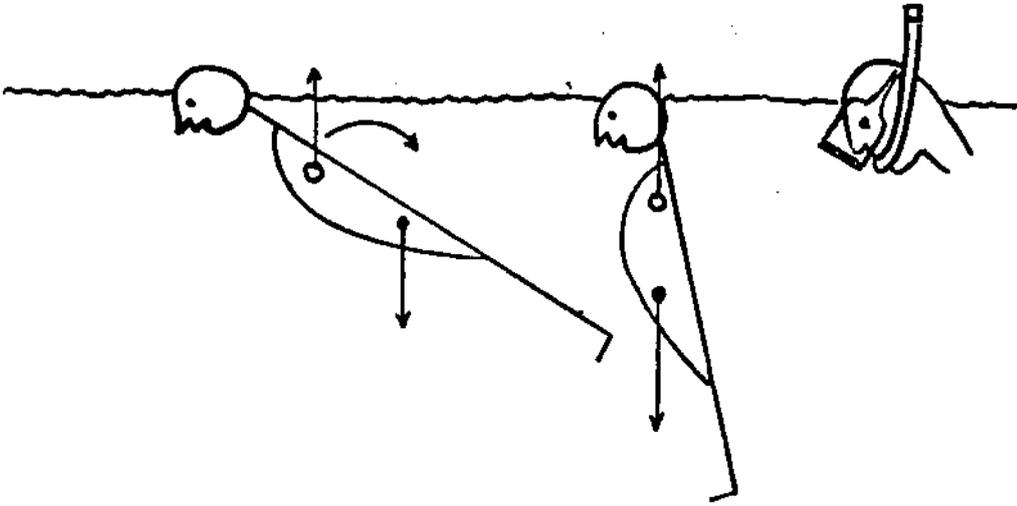


Fig. 7d: Rotation and stable equilibrium of a passive human body (fitted with mask and snorkel) in water.

If a human turns on his back and actively bends the head backwards, a new equilibrium, where nose and mouth emerge, will establish (Fig 7e).

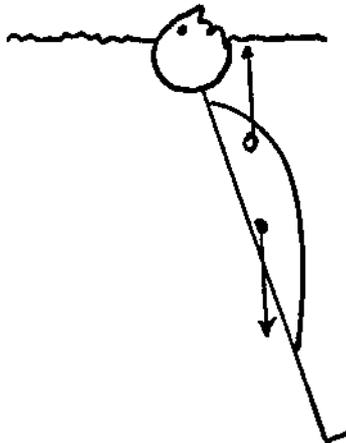


Fig. 7e: Unstable human equilibrium position, with active backward bending of the head.

This exercise however requires continuous muscle activity and consequently energy. The use of mask and snorkel overcomes this problem. It requires some practice to use these but this effort could be very rewarding in many cases where handicapped people have difficulties to find a position of static equilibrium in the water. (Lifejackets can greatly improve static equilibrium, because they add buoyancy above the centre of gravity.)

Forces on a swimming fish.

Resultant forces on a swimming animal (Fig. 8) are more complicated, compared to the resting situation.

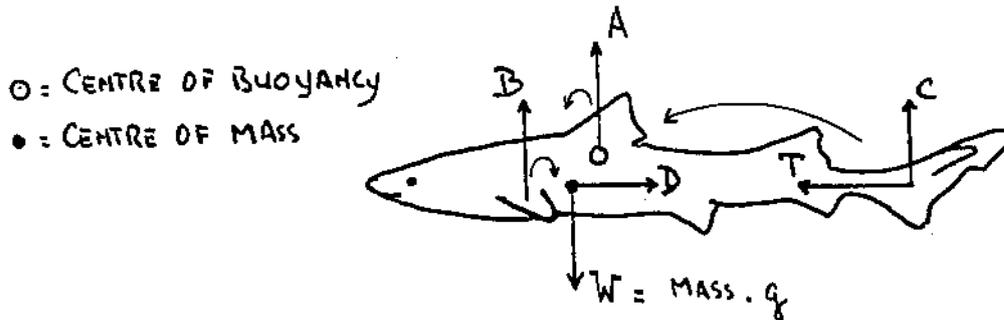


Fig. 8: Forces and moments on a swimming shark.

Horizontal forces T and D in the median plane are the resultants of thrust and drag, both acting along a horizontal line through the centre of mass. The rear part of the body generates the thrust with lateral movements of the tail. The dorsoventral asymmetry of the tail blade however generates also a force C in upward direction and a side force S in a direction opposite to the direction of movement. The extended pectoral fins of the shark act as the wings of an aircraft: they make a slight angle with the horizontal plane and generate an upward force B . The equilibrium conditions are:

$$\begin{aligned} T &= D \\ A + B + C &= W \\ Aa + Bb &= Cc \end{aligned}$$

a, b and c are the perpendicular distances between the lines of action of the forces A, B and C and the line of action of W .

Fish swimming dynamics

Dynamics of fish swimming are complicated and not yet fully understood. To avoid undue complexity, we will confine the survey of the existing knowledge to steady swimming at uniform speeds, although it is good to realize that free ranging fish usually do not swim steadily. To obtain steady conditions, fish were trained to swim back and forth between two feeding points by association of underwater flashing lights with the appearance of food, in a 14 m long tank. Pictures of top views of passing fish, taken with a high speed cine camera in fixed position above the tank, were analysed frame by frame. Fig. 9 exemplifies the results of the analysis of the swimming movements of a 0.42 m cod swimming at a uniform speed U of 0.7 m/s. The film was taken at 200 frames/s, the outlines of the fish on each frame were digitised and fed into a computer. One quarter of the total number of recorded outlines of a tail stroke from left to right is shown in Fig. 9. The outlines are spaced out to the right, the distance between two successive

frames represents a separation in time of 0.02s. The small circles indicate the same two fixed positions on the background, drawn with each frame.

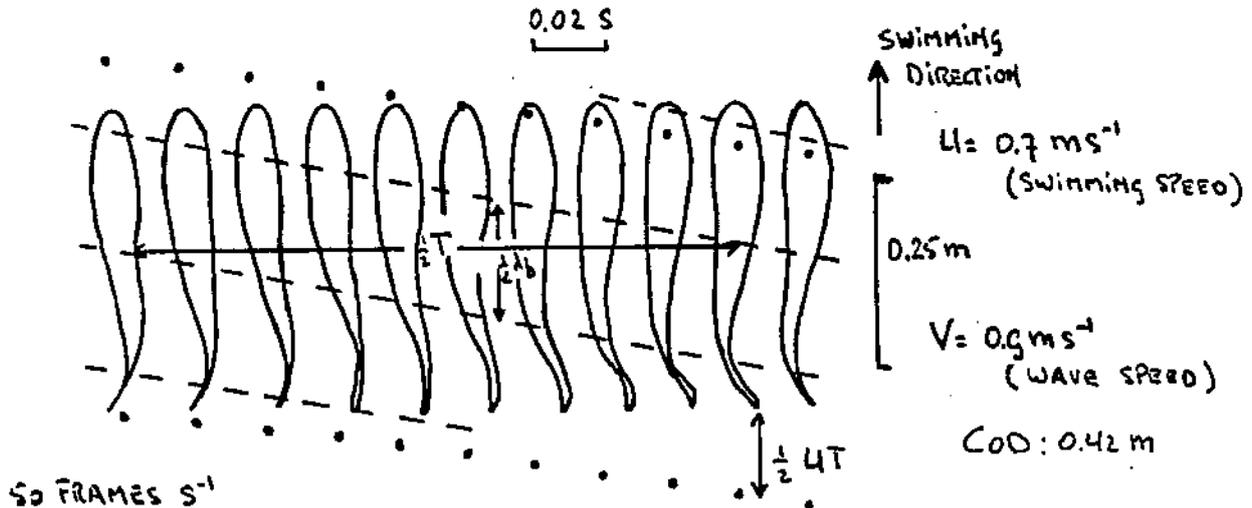


Fig. 9: Outlines of a swimming cod, drawn from the images of a high speed film.

Computer analysis of the frames shows that a wave of curvature runs down the body from head to tail. Wave crests on the left and right side of the body are indicated by the broken lines. The vertical distance between two successive lines represents half the wave length of the wave of curvature, The horizontal distance visualises half the wave period T and $\frac{1}{2}UT$ is the distance covered during this period. The speed of the propulsive wave backwards (V) is 0.9 m/s. The difference between U and V reflects the swimming efficiency. The amplitude is small near the head even smaller just behind the head and very large near the tail (Fig. 10a).

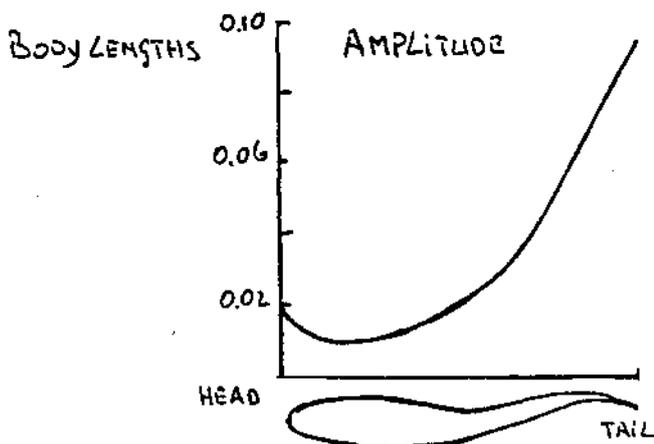


Fig. 10a:
The amplitude (expressed in bodylengths) of the lateral undulations of a swimming cod as a function of the position on the body between head and tail.

The wave of curvature travels in one period from head to tail, and one left-right tail beat is completed during the same time period (Fig. 10b).

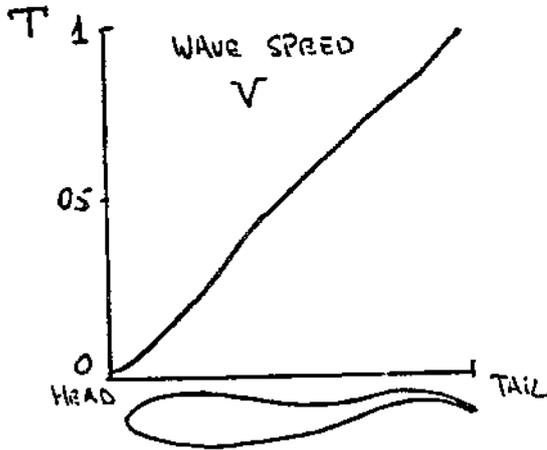


Fig. 10b:
The time (expressed in tail beat periods, T) used by the propulsive wave on the body of a cod, to travel from head to tail.

The interaction between fish and water.

How can a fish propel itself with a wave on the body?

From the point of view of the water, the interaction with the fish starts when the head of a swimming fish enters into undisturbed standing water. The undulating fish pushes the water aside and backwards and causes eddies. Reaction forces from the water push the fish forward. The interaction between a water particle and the fish comes to an end when the tail blade has passed and no more disturbance will be added. The tail blade action reflects the end result of the interaction. Therefore we will study the movements of the last piece of the tail blade in detail. Fig. 11a shows one outline of a swimming cod and four head and tail positions in an X-Z frame of reference.

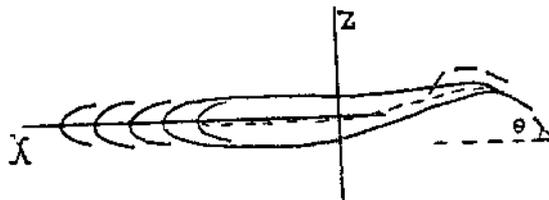
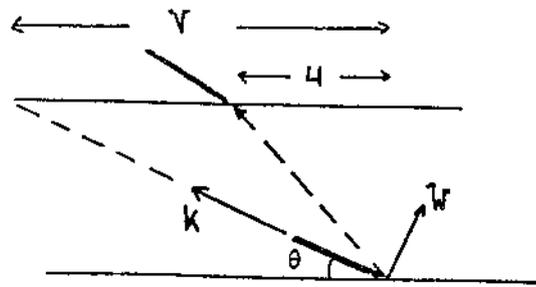


Fig. 11a: The outline, midline and successive head and tail positions of a swimming cod in a X-Z frame of reference. The X-axis is the mean path of motion and θ the angle between the tail blade and the X-axis.

The X-direction coincides with the swimming direction and the angle between the tail blade and the X-axis is called θ . We focus on two successive tail positions in Fig. 11b.



M_2 : AFFECTED MASS OF WATER / UNIT LENGTH

$$= \pi \rho_w \left(\frac{s}{2}\right)^2 \quad (\text{kg m}^{-1})$$

$K.M$: AFFECTED MASS / UNIT TIME (kg s^{-1})

$W.K.M$: PROPULSIVE FORCE IN W DIRECTION
($\text{kg ms}^{-2} = \text{N}$)

Fig. 11b: Two successive tail positions from 11a. The components of the instantaneous velocity of the tail tip are indicated.

The tail tip has moved in the time between the two frames from one position to the next as a result of the lateral movement and the difference in magnitude between the forward velocity U and the wave velocity V . The dashed arrow is the instantaneous velocity vector of the end of the tail blade. This vector is resolved into components k tangential to the tail blade and w perpendicular to it. We assume that the tail movement in the k direction causes little disturbance in the water. Vector w , however, imparts its velocity to all the water which passes through a circle drawn round the end of the tail. Fig. 11c shows this so called virtual mass of water per unit fish length in lateral and dorsal view.

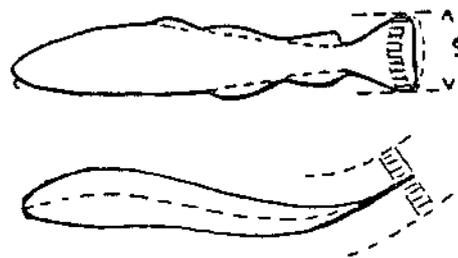


Fig. 11c: Lateral and dorsal view of a swimming cod, illustrating the virtual mass of water per unit length at the end of the tail blade.

The area of the circle is $\pi s^2/4$ where s is the span of the tail. The virtual mass of water of density per unit length is

$m = \pi \rho s^2 / 4$ kg/m. The tail slips with velocity k m/s through the circle, affecting km kg water per second. The force exerted by the tail in the direction w equals wkm N and this is the rate at which momentum is imparted to the water. The reaction from the water pushes the tail in the direction opposite to w according to Newton's second law, but part of the force in the w direction gives kinetic energy to the water and is lost. This part is $\frac{1}{2}mw^2$ and the net propulsive instantaneous force on the tail blade in the $-w$ direction is $(wkm - \frac{1}{2}mw^2)$ N. The resulting component in the swimming direction is $(wkm - \frac{1}{2}mw^2)\sin\theta$ N.

Fish swimming muscles

Structure and function of fish swimming muscles differ substantially from those of the locomotory muscles of other vertebrates. The body of a fish between head and tail is divided into two lateral halves by the vertical septum supported by the vertebral column and the dorsal and ventral spines (Fig. 12).

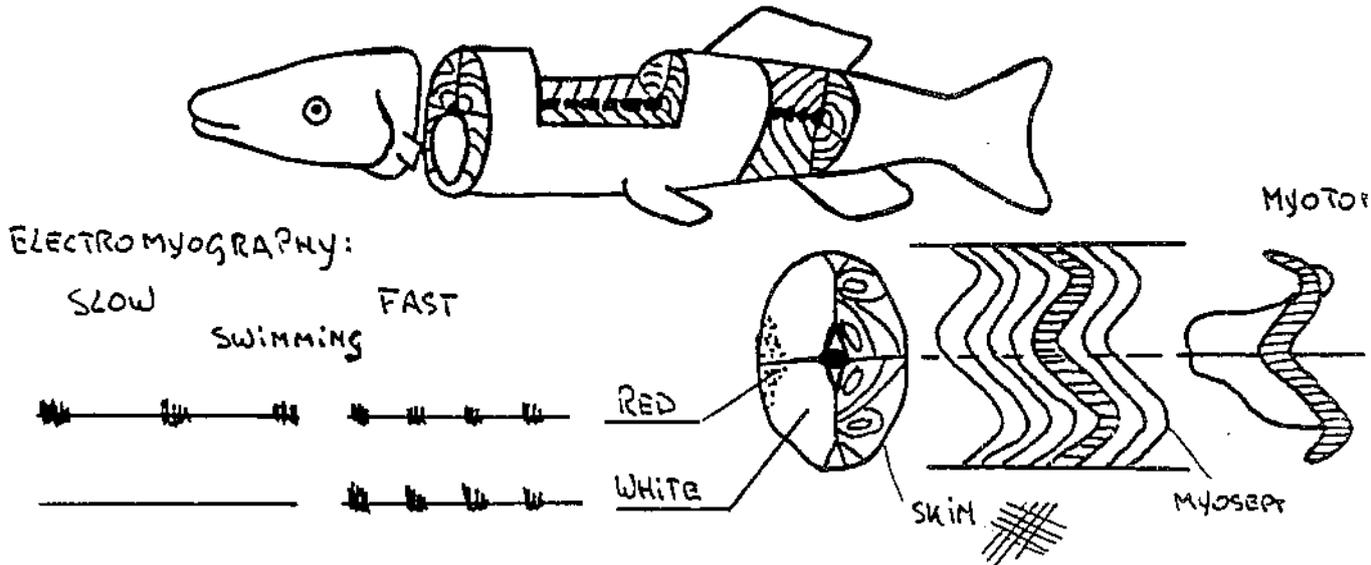


Fig. 12: Form and function of the lateral swimming muscles of a generalised fish.

The lateral muscles are the major part of the body mass in most fishes. The muscle fibres are short and packed into blocks called myotomes. These are stacked in a row between head and tail. The lengthwise direction of the muscle fibres in each myotome is approximately parallel to the body axis. Most fish show two distinct muscle fibre types: red fibres forming a thin layer on the outside of the myotome and white fibres filling the rest of it. Electromyography reveals that the red muscle is active during slow swimming at speeds below the maximum cruising speed of about 3 bodylengths/s. White muscle fibres become active above that speed.

Lateral fish muscles have no clear origin and insertion, they are tightly packed and wrapped in a strong skin with thick criss-cross layers of collagenous fibres. The relation between muscle activity and the wave of curvature running from head to tail on the body during swimming is not straight forward and difficult to understand. We saw that the wave of curvature uses about one tail beat period to run from head to tail. Muscle activity however travels much faster and takes only a small fraction of the time of one tail beat period to cover the same distance. In fast fishes the contraction near head and tail can be almost instantaneous. In air this type of muscle activity would bend the body into a C-shape. Water however interacts strongly with the moving body and this interaction causes the wave of curvature. In the laterally flattened tail region the water pushes strongly and lengthens the active muscle fibres causing an excentric contraction. The muscles just behind the head contract normally and in the region between head and tail the muscle contraction is isometrical.

A muscle with an origin and an insertion generates force during isotonic contraction by shortening while counteracting a force that tries to lengthen it. The volume of the muscle does not change and muscle becomes shorter and thicker. Fish lateral muscles use the latter effect and generate force by bulging and pushing against the tight skin. The angles between the collagenous criss-cross fibres in the skin are forced to change, widening the skin in dorso-ventral direction and shortening it longitudinally. (Both force generating methods can be demonstrated using the human biceps which has to be wrapped in tight cloth to feel the force generated by the bulging effect.)

Extreme speed adaptations

The swordfish (*Xiphias gladius*) is probably the fastest swimmer in the world and is extremely well adapted to minimize the energetic costs of high speed locomotion in water. The maximum speed of a 3 m long animal has never been measured accurately but is probably well above 100 km/hour where the Re-number for the whole body approaches 10^8 . Figure 13 shows some of its external features.

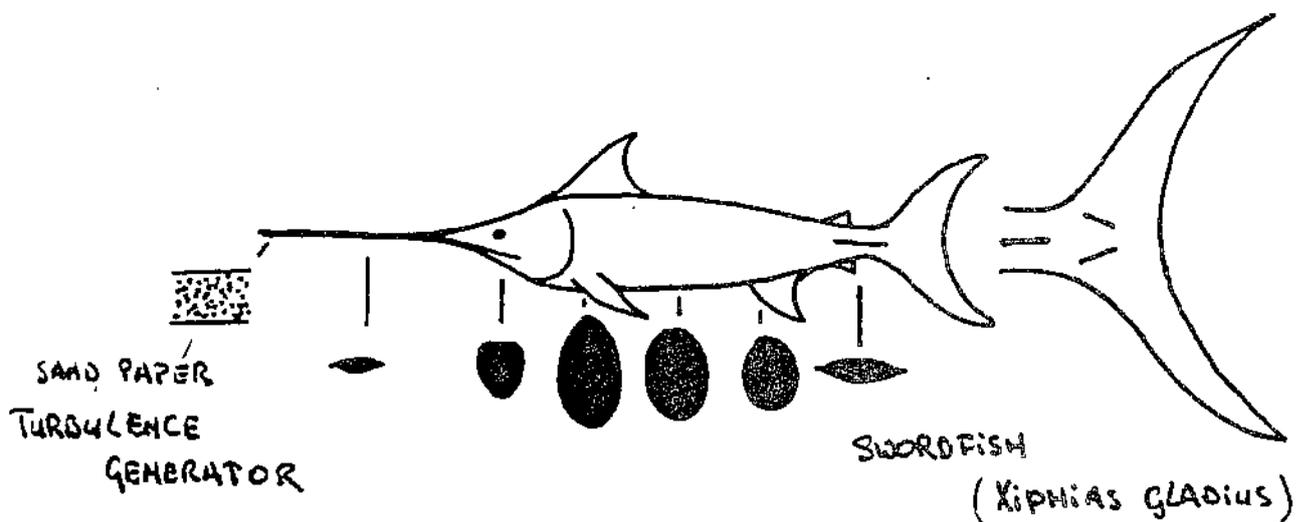


Fig. 13: Adaptations related to extremely high speed swimming of the swordfish, *Xiphias gladius*.

Its sword is a flat extension of the upper jaw. The lateral edges are sharp, but it has no offensive or defensive functions. The surface has the roughness of coarse sandpaper and it acts as a generator of micro-turbulence. The flow around a streamlined body at high Re-numbers is turbulent. The Re-number is proportional to the length of the body and consequently increases from front to rear along a streamlined body. At some point along the body laminar flow will change into turbulence and this transition causes a sudden drag increase. The swordfish avoids this enhanced drag effect by generating small scale turbulence in front of the body where the Re-number reaches its critical values early on due to the length of the sword. Micro-turbulence helps also to avoid drag penalties due to separation of the flow. The danger of flow separation occurs behind positions on a body where the shape in the direction of the flow suddenly changes. The abrupt increase of the volume of the head beyond the sword could easily cause separation at the thickest part of the body just behind the gill clefts. This fish is adapted to avoid this drag penalty by a concave instead of a convex shape of the head. The dorsal and the pectoral fins stick out in positions along the body beyond the point of greatest thickness, where the danger of separation is strongly reduced. The near elliptical shape of the body on transsection changes at the dorso-ventrally flattened caudal peduncle. Its function is to support and move the high lunate tail blade with as little interference with the water as possible. Ridges on the peduncle direct the water flow towards the centre of the tail blade to obtain optimal propulsion.

It is not the goal of the Halliwick method to make handicapped people swim as fast as a swordfish but we can learn from this example that relatively small specific adaptations could greatly improve the quality of the treatment by movements in water.