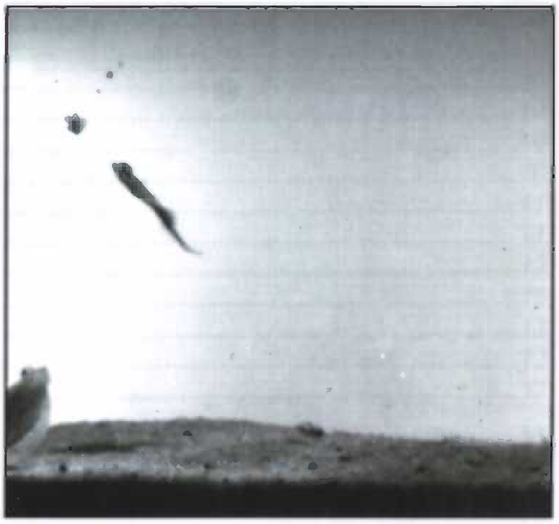
How Juvenile Flounders Swim

Body and fin kinematics of free swimming juvenile flounders



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1 Abstract

Flounders (*Platichthys flesus*) have a body geometry, which is adapted to a life on the sea bottom. When swimming the dorso-ventrally flattened body makes the flatfish to undulate its body vertical to the substratum. In addition the flounders use their dorsal and anal fin for propulsion as well, which stands in contrast to round fish. Due to the lack of a hydrostatic organ, flounders are heavier than water and need to produce lift while swimming. For this study, it was expected that flounders show significant differences in swimming kinematics compared to round fish. Comparison of the body and fin movements of the flounders was desirable to show a relation of the two propulsion systems.

Juvenile flounders were filmed in side view at 125 frames s^{-1} while swimming freely towards a food source. For analysing the wave characteristics of the undulatory movements, ten points on the upper body side, fifteen on the fin tip and fifteen points on the fin base were followed in time. Cubic splines were fitted through these points, to yield accurate estimates of the wave characteristics. The obtained lines indicate the movements of the body and the fin in space and time. Kinematic data were obtained following the methods of Videler and Wardle (1978).

Three film sequences showing upward swimming of three different juvenile flounders were analysed.

The following results were found:

- The last two third of the body of all flounders were active, having about 1 to 1.2 waves at once.
- The fins were undulating over the whole length, with 1.5 to 1.9 waves at one time.
- For the body the amplitude maximum was located at the tail.
- For the fin, the maximum amplitude was found half way to two third of the fin length.
- Differences were seen within and between the flounders in the tail beat amplitudes.
- An interpretation was given about a possible steering component of the tail beat direction.
- Wave speeds v varied quite strongly within and between the flounders. It indicated that the flounders have possibilities to alter their swimming style and are able to change quickly between wave speeds during swimming.
- Differences in swimming movements of flatfish compared to round fish were: a smaller wave length λ_b, stride length λ_s and swimming efficiency, which make flounders bad forward swimmers.
- The waves on the fins are not an artefact of the moving body, but the flounders appear to have two propulsing systems, the body and the fins.
- The fins are moving in phase with the body, enlarging the moving surface and the effect of the waving propulsion.
- Small differences in the movements are explained as complexity of the moving systems and can serve as steering components and stabilising factors.

2 Introduction

Many benthic fish have flattened bodies, which is an adaptation to their benthic life style. Their food sources are mainly located on the bottom and to save energy the flattened fish stay close to their food supply. Yet it is also easy to hide under the sediment for predators (Fonds et al, 1992). Most flattened groups are found among the pleuronectiform flatfishes, batoid rays and more ray like selachians (Webb, 2002). A big difference between flatfish and rays is the way in which they are flat. Rays lie on their ventral side and their large pectoral fins are propulsors. Flatfish instead have dorsoventrally flattened bodies, with the upper side being more vaulted than the flatter bottom side. While the appearance of flatfish compared to round fish is the same as they hatch, the body changes during the larval stage. The eyes of flatfish move to one side of the body and they come to lie on the other side. The larger dorsal fin and the smaller anal fin are now the sides of the fish and give it an asymmetrical body geometry (*see figure 1*). As the bodies of flattened fish are different from round fishes, their swimming behaviour is also different. Flatfish move their body vertical to the substratum, as opposed to the parallel swimming direction of round fishes.

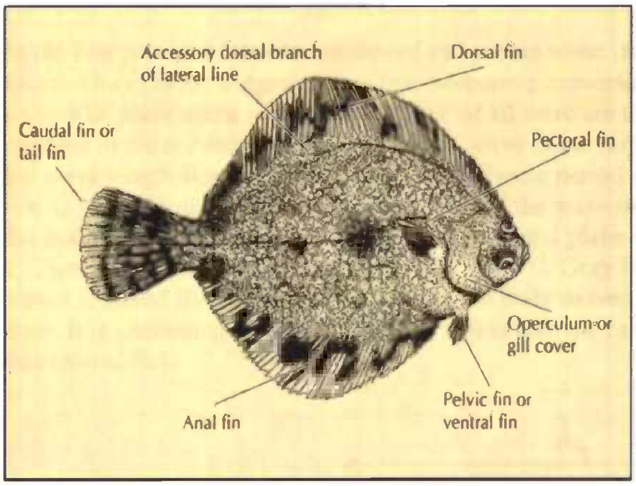


Figure 1. A schematic overview of the morphology of an adult flatfish.

Figure 2. A picture of a juvenile flounder.

Kinematic data on swimming movements are necessary to understand the means of propulsion by fish. A lot of research has been done already on the swimming kinematics of round fish (Gray, 1933; Videler and Wardle, 1978; Videler, 1993; Webb, 2002), but only recently the kinematics of flattened fish reached the interest. Rosenberger studied the swimming behaviour of various rays (2001), Pingguo He observed the swimming of winter flounders (2002) and Webb analysed the kinematics of adult plaice (2002). Due to their benthic lifestyle, adult flatfish will rarely show free swimming movements in the open water, instead of the juveniles which show them more often. However flatfish sometimes do have to swim in open water and the asymmetry and vertical movements to the substratum are expected to lead to a distinct way of swimming, which makes a kinematic analysis of the free swimming movements of a juvenile flatfish very interesting.
This report describes the results of a study of the swimming kinematics of juvenile flounders (*figure.2*). Flounders (*Platichthys flesus*) are common flatfish in the North and Wadden Sea and tend to be a good representation of flatfish in general. Juvenile flounders were preferred as experimental animals, because they are more agile and, compared to adult flounders, they are more likely to frequently show swimming in the open water.
Many research programs in fish locomotion were only focused on swimming by means of the body undulations (Videler, 1993) and some researches focused on fin propulsion (Blake, 1979, 1980; Walker and Westneat, 1997). However, flatfish not only use undulations of the body to create propulsion, but also the movements of their dorsal and anal fins. Therefore it really is necessary to study the body and fins at once. So far only a pilot study (Verspuy, 2001) has focused on the propulsion of fish by means of body undulations as well as fin propulsion. Verspuy analysed the swimming kinematics of juvenile plaice and suggested that the body and fin movements are in counter phase. This is a remarkable situation and it seems that the body and fin are competing with each other. To determine if the flounders also show a counter phase in the movements of the body and fin, both propulsion systems are analysed in their swimming kinematics in this study.

Apart from having asymmetrical bodies, flatfishes have another interesting feature. They have no swimming bladder, as most fishes have, and are therefore negatively buoyant. However, flatfishes frequently swim close to the bottom and therefore they make use of the ground effect. This ground effect allows a reduction of thrust requirements and increases the efficiency as result of interactions between the wake and the surface (Bainbridge, 1961; Webb, 1993, 2002). The ground effect has been studied in flatfishes (Webb , 2002), but also in other animals that move closely to the surface (Blake, 1983a,b; Webb, 1993) and the effect is already used in technical applications, e.g. for some vehicles. However this thrust reducing technique disappears when fish are swimming higher in the water column. As a result they need to produce lift. Most round fishes do have swimming bladders but not all of them. The mackerel (*Scomber scombrus*) for example has no swimming bladder and therefore needs to produce lift by continuous swimming (He and Wardle, 1986). The lift producing mechanisms are discussed by Magnuson (1970), in which the body attack and body tilt angle are involved. These two expressions almost mean the same, and refer to forward swimming under an angle. The body attack angle is the angle between the body axis and the direction of the water stream and the tilt angle is defined as the angle between the body axis and the horizontal. This behaviour of swimming under an angle was studied by) and they found larger body attack angles when Mackerel swam with lower speeds. At the preferred swimming speed they swam with zero attack angle so lift production only was generated by swimming. Some flatfishes also show a body angle while swimming forward. The winter flounder, for example, cannot produce enough lift by its asymmetrical body and has to swim under an angle at low speeds (He, 2002). It is interesting whether juvenile flounders also show these lift producing techniques.

In the first precise kinematic studies of swimming some important rules for the movements of round fish were found. Gray (1933) suggested that fish swimming movements could be understood as a combination of two wave-like phenomena (*see figure.3*). First of all there are the cyclic changes of the curved shape of the body. The changes in the curved shape show a lateral wave of curvature running down the body. Such a wave is defined as the wave length λ_b and has a velocity *v* and a wave period *T*. These parameters are connected by $v = \lambda_b * T^{-1}$. Furthermore, as a consequence of the wave of lateral curvature on the body, every single point of the body describes a sinusoidal track in a horizontal plane with forward speed U, stride length λ_s and wave period *T*. These parameters are connected by $U = \lambda_s * T^{-1}$. Gray found distinct differences between the two described waves in round fish. The wave speed *v* on the body moves faster backwards than the forward speed U of the fish does. It is interesting to find out whether this is also the case for flatfish or that the flatfish are even more distinct from round fish.

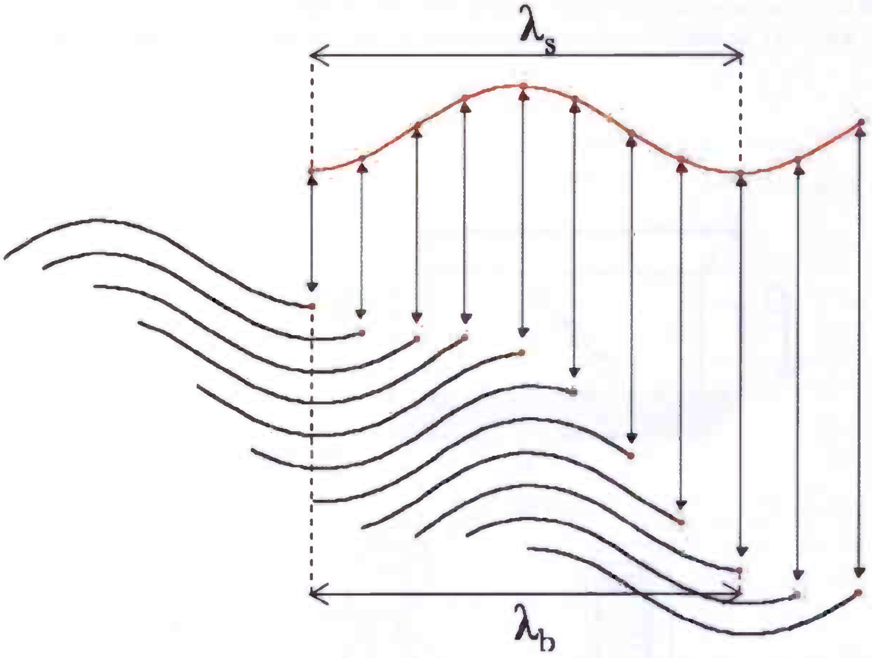


Figure 3. Schematic drawing representing the two wave-components used to describe the swimming movements of a fish. The black lines represent the lateral wave of curvature running down the body in successive time steps. The fish is swimming towards the left, and has been transposed upon the previous time step for clarity. The red line represents the sinusoidal track in space of the tail of the fish. The wave length λ_b is determined from the lateral waves and the stride length λ_s is determined from the sinusoidal track.

The aim of this study is to determine the swimming kinematics of juvenile flounders and to give an indication of the relation between the body and fin undulations. Besides, an attempt is made to explain the way of lift production by flounders. For the analysis two wave like phenomena (wave length λ_b resp. λ_f and stride length λ_s), which are present on the body and fin during swimming, are determined and the main kinematic parameters are calculated from them.

3 Materials and methods

3.1 Experimental animals

Five juvenile flounders (*Platichthys flesus*), with body sizes of 33 to 66 millimetres, were used to study the kinematics of free swimming movements. They were kept in an aquarium (45x15x30 cm) connected to a system with artificial sea water (S = 30‰) at 16°C. A filtering water system purified and aerated the water. Sand was put on the bottom, since flatfishes are known to be fragile against bacterial diseases if they are kept without sand. Juveniles were chosen as experimental animals, because they were expected to be more active compared to adult individuals. However, to enlarge the change of having the juvenile flounders swim in front of the camera, food was provided when filming happened.

3.2 Experimental set-up

Necessary illumination for the filming was provided by the use of three halogen spots of 50 watt power. Two lamps were placed oblique behind the aquarium, one at the right and one at the left side and a third lamp was mounted above the aquarium. To scatter the light and create an equally illuminating white background, a white transparent Perspex plate was placed at the backside of the aquarium (*see figure 4*).
A digital high speed camera (KODAK Motion Corder Analyser, SR series) was used for filming the flounders. It had a shutter time of 2 ms and was equipped with a zoom lens (50 mm Nikon Nikkor lens, f = 1:1.8). The camera was mounted on a perpendicular axis in front of the aquarium at a distance of approximately 1meter. Filming happened at 125 frames s^{-1} and was recorded endlessly into a ring buffer, which can hold 2184 frames. A monitor was connected to the camera, so all the recording was directly visible. As soon as a fish swam into the field of view (128 by 120 mm) a trigger was pushed by hand which stopped the recording from rewriting the ring buffer. This trigger was programmed in the middle of the recording, meaning that the 1092 pictures before the trigger signal was given and the following 1092 pictures with new frames where kept. After storage, the movie was analysed in the play back mode on its usability. Only film sequences were selected for further analysis in which the fish were filmed from their side. This means that the flounders had to swim perpendicular to the camera, with only the anal or dorsal fin visible. Other criteria were visibility of the fin and amount of wave cycles. When the film was accepted, only the images where the fish was visible in its whole body length were written to the hard disk of a connected computer and stored by frames as TIF-files.

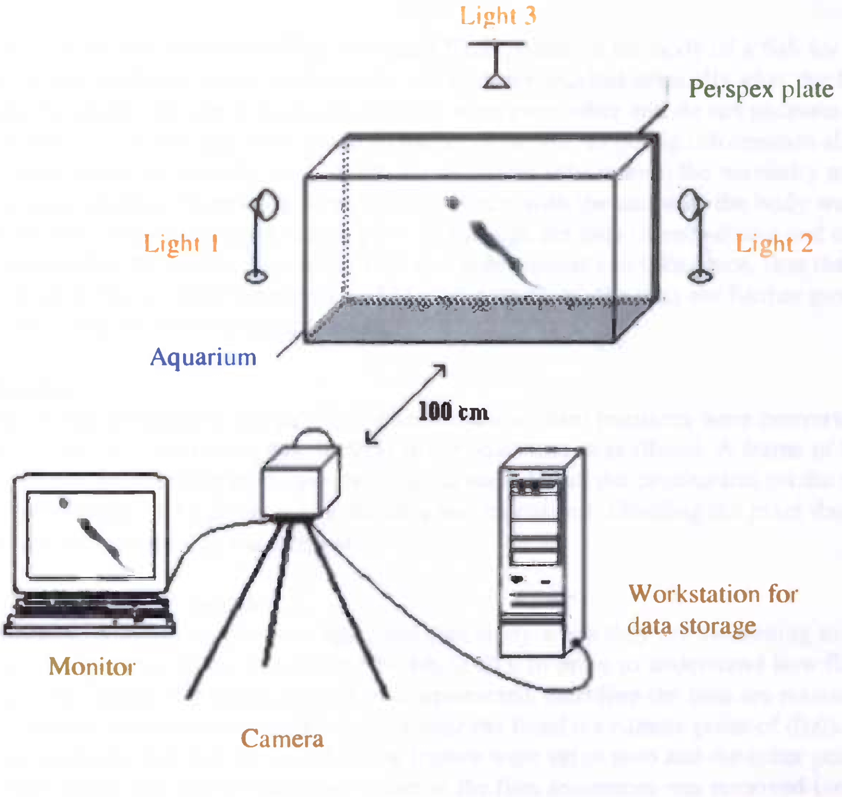


Figure 4. Schematic drawing of the experimental set-up. Explanations in text.

3.3 Picture processing

To get an indication about the movements of the body and fin waves in time, for each frame 40 points were selected on the fish with the mouse pointer (*see figure 5*). This was done by means of the computer program TimWin, which gives X- and Y-coordinates of the marked points. The coordinate values correspond to the pixel positions of each point in a frame. Ten of the points were marked on the upper body outline to create a line (shown in red), which represent the movements of the body. Four of these points were placed on conspicuous places; at the nose, behind the eyes, behind the stomach and at the tail tip. The other points were placed in between at about the same distance. To create a line, which describes the movement of the fin, two series of fifteen points each were made. The first series of points were marked at the end of the fin, also called the fin tip (shown in blue). These points describe the movement of the fin and body together. The second series were marked at the place where the fin is attached to the body, the fin base (shown in green). They were considered to represent the movements of the body at that very place. These points were placed according to the points of the fin tip. To separate the fin movements from the body movements, the values of the fin base were later subtracted from those of the fin tip. All the collected coordinates were saved in tables as text-files.

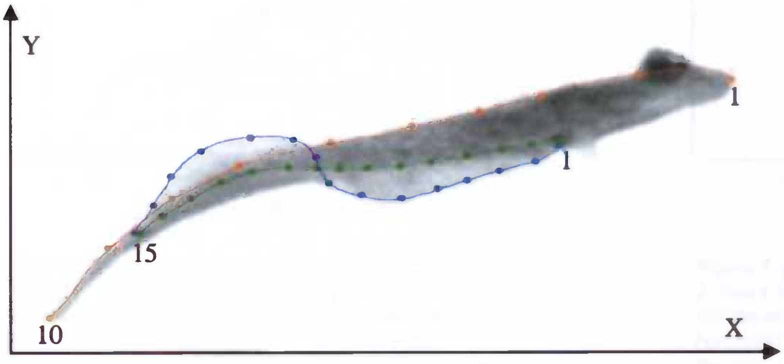


Figure 5. Picture of a juvenile flounder in side view. Depicted are the locations of the 40 points, used to create lines for description of the body and fin movements. The red line indicates the upper body outline, the blue line represents the fin tip and the green line stands for the fin base. Numbers indicate the count of points, starting at the nose and counting in caudal direction. For further explanation see text.

3.4 Data processing

The X- and Y-coordinates of the filmed frames were further processed in Microsoft Excel 97, Matlab 6.5, Sigmaplot 8.0 and Paint Shop Pro 7.

In contrast to Videler and Wardle (1978), who used fixed points on the body of a fish for analysing its movements, in this study the points on the body and fin were marked manually after the filming process. Consequently the points are not at the same distance from each other and do not necessarily represent exactly the same spot on the body or fin line from frame to frame. However, to obtain information about kinematic parameters fixed points on de body are needed. To attain this information the manually marked points should be placed at the same distance from each other, in compliance with the shape of the body wave. This is done with the program Matlab, which utilises a cubic spline fit through the data of each frame and calculates eleven new X- and Y-coordinates for the body movements. Before a cubic spline can take place, first the data should be rotated and translated with Excel. After the mentioned Matlab-processing the data are further processed in Excel and Sigmaplot, obtaining the kinematic parameters.

3.4.1 Calibration

The first step in data processing is a calibration in which the pixel positions were converted to millimetres. For this purpose a 1 cm by 1 cm raster, which stood in the aquarium, was filmed. A frame of this film was brought to Paint Shop Pro and by zooming in the pixels could be seen. Of all the centimetres on the raster, the pixels were counted and an average of 41 pixels per centimetre was calculated. Dividing the pixel data in Excel by 4.1, the data values were converted into millimetres.

3.4.2 Data translation and rotation

Flatfish always swim forward under an angle, and especially when they are swimming towards an aim, they have a large body tilt angle (*see figure 6*) (also see Webb, 2001). In order to understand how flatfish swim and to compare one with another the angles should be counteracted, therefore the data are rotated. Before rotation the data were translated, because rotation takes place over the fixed coordinate point of (0,0). All first coordinates (nose point of the body and first fin point) of the frames were set at zero and the other points in relation to the first point. This means that the forward movement in the film sequences was removed (*see figure 7*).

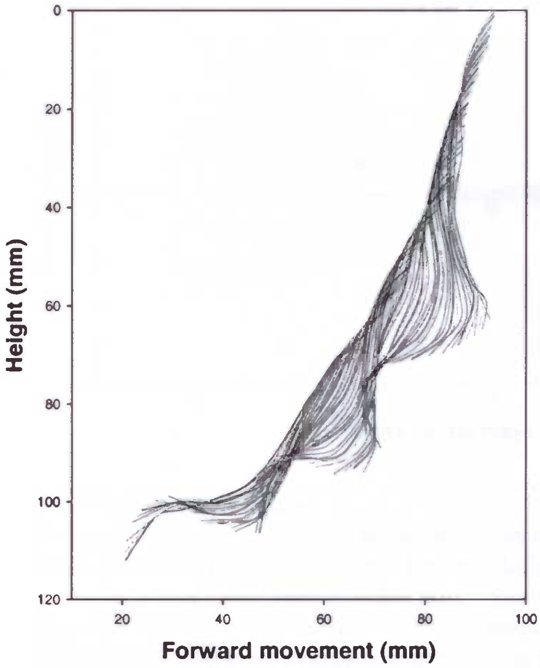


Figure 6. The swimming path and body motions of flounder 2 before data conversion. Every line represents the position of the body line in space at a particular frame. The fish is swimming upwards to the right, meaning that its head is positioned at the right top and its tail on the left end of the lines.

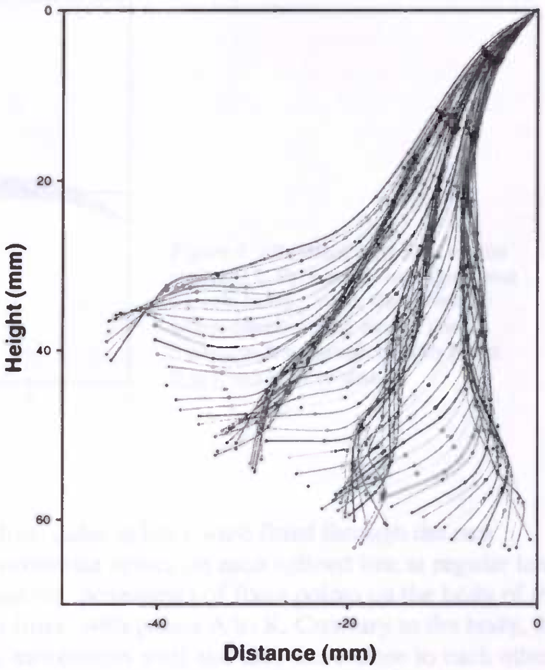


Figure 7. All translated body lines of film sequence 2. Every line represents the body in a single frame. For the next processing step the angle with the horizontal axis is calculated of every frame to rotate the data.

Further, the slope of the body was calculated over the still part of the body at every single frame, using the SLOPE function (of MS Excel®) over coordinate point 2 to 5 (after further data processing called B-E, *see* section 3.4.3). From this slope the rotation angle α was calculated and the translated coordinate data were rotated over α (*see figure 8 and 4.6*). The following formulas, as written in Excel, were used:

$$\alpha = \text{ATAN (SLOPE)} * 180 / \pi$$

$$X_{new} = X_{old} * \text{COS}(\alpha * \pi / 180) + Y_{old} * \text{SIN}(\alpha * \pi / 180)$$
$$Y_{new} = X_{old} * \text{SIN}(\alpha * \pi / 180) + Y_{old} * \text{COS}(\alpha * \pi / 180)$$

X_{new} and Y_{new} are the rotated coordinate values, while X_{old} and Y_{old} are the translated coordinate values. The angle between the mean direction of movement and the horizontal plane is described by α. For the fin new coordinates were created with α from the body. Because the upper body line was clearly visible, in contrast with the mid line of the flounder which was difficult to calculate, the axis of reference was calculated by a linear regression line through all body points B to E and set to zero.

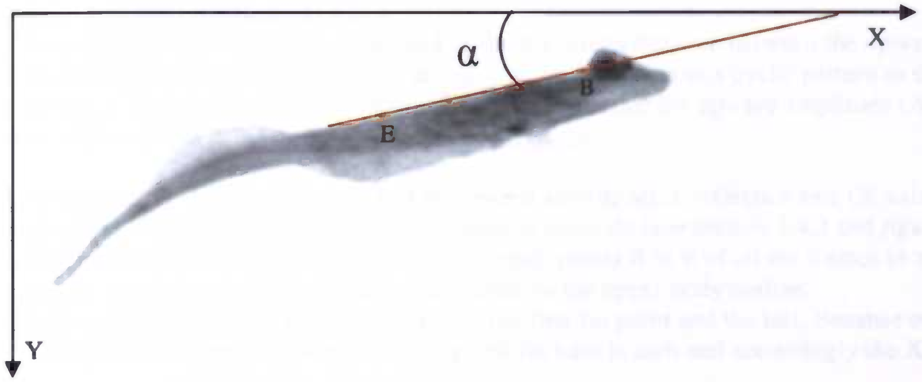


Figure 8. Picture of a swimming juvenile flounder chosen to depict the principle of data rotation for better explanation. For rotation of every body line the slope was measured through coordinate points B to E. From that slope the rotation angle α was calculated.

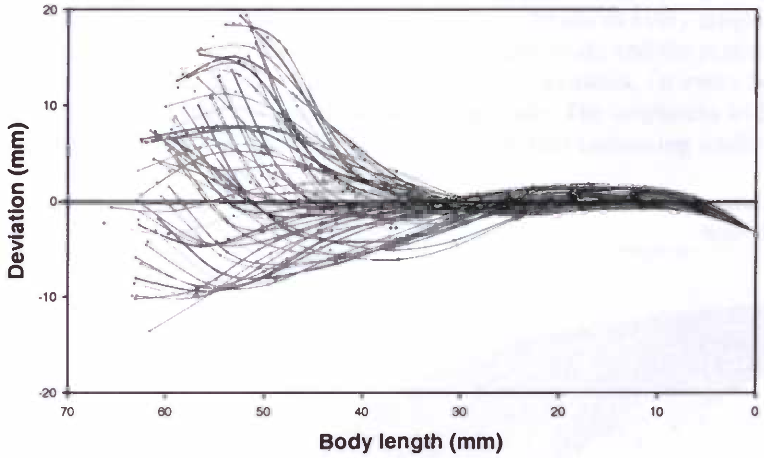


Figure 9. All rotated body lines of film sequence 2. Each body line origins from a single filming frame. The reference axis is determined by using a linear regression line through all body points B to E and is set to zero.

3.4.3 Cubic spline fitting

To create lines that match the shape of the upper body outline, cubic splines were fitted through the new coordinates of every single frame. By calculating eleven coordinate values on each splined line at regular length intervals, a new set of coordinates was created that represent the movements of fixed points on the body of the flounder. The resulting set of coordinates was called 'body lines' with points A to K. Contrary to the body, there were enough points on the relative small fin to describe its movements well and they were close to each other, considering that the points represent closely enough the same spot on the fin in every frame. This lead to the conclusion, that it was not necessary to fit a cubic spline through the fin points. The set coordinate data after rotation were called 'fin lines' with points 1 to 15.

3.5 Length of body and fin

The length of the body and fin were determined from the X-coordinates of the body and fin line data. From every line the last X-coordinate was subtracted from the first one, so for every frame a length appeared. To minimize errors the maximum length of frames was taken as the real length of the body of the flounders. Errors appeared because of waves on the body, which lead to an underestimation of the length. Body lines with maximum lengths hardly show any wave, meaning that the flounder's body is maximally stretched. For the fin the mean of the lengths were taken as being the fin length. The waves on the fin do not change the fin length, because the fin is attached to the body. To minimize errors made by selecting points on the fin edges, the mean length is taken from all frames.

3.6 Kinematic parameters

The handlings above are basic proceedings. Further operations of the data were done for every specific kinematic parameter, describing the swimming movements of the flounders. The used methods are almost the same as in Videler and Wardle (1978). For all these parameters, the length is given in mm and as proportion of body or fin length.

3.6.1 Amplitude maximum (A_{max})

The amplitude maximum A_{max} is defined as the maximum distance between the upward and downward tail or fin beat. Most points on the body and fin are moving up and down in a cyclic pattern as the fish is swimming (*see figure 10).* The most upward deviation of one wave is called the upward amplitude (A_{up}) and the most downward deviation in a beat is the downward amplitude (A_{down}).

To figure out the height of the up- and downward amplitudes, a reference axis (X-axis) was needed. The body respectively fin lines where turned and brought to coincide (*see* section 3.4.2 and *figure 9*). The needed axis of reference was calculated as the mean of coordinate points B to E of all the frames in a film. Accordingly, the up- and downward amplitudes are determined based on the upper body outline.
The X-axis of the fin line is the line between the first fin point and the last. Because on these points the fin meets the body, the difference between the fin tip and fin base is zero and accordingly the X-axis is also zero.

For the amplitude maximum the point on the body and the point on the fin were needed with the largest difference between the up- and downward amplitude. For that purpose a graph, showing the amplitude envelops of the body, fin line and fin tip, was made (*see figures 13, 23, 33*). An amplitude envelop describes the maximum upward and maximum downward amplitude of every single point over the whole sequence. The point on the body or fin with the maximum upward amplitude and the point on the body or fin with the maximum downward amplitude were taken for further measurements. Of every beat the amplitude was determined as the distance between the up- and downward amplitude. The amplitude with the largest value is the amplitude maximum (A_{max}) of the body or fin of the fish in that swimming track.

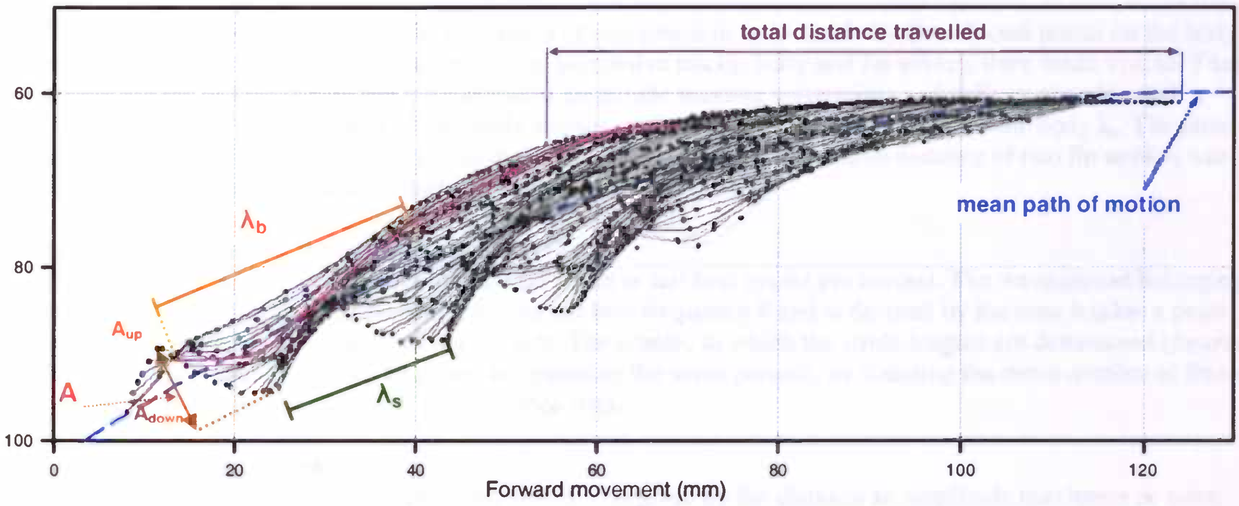


Figure 10. The swimming path and body motions of a flounder in one film sequence. Every line represents the position of the body in space at a particular frame (*example*: pink line). The blue dotted line shows the mean path of motion. The distance between the nose point of the first frame and the last one is the total distance travelled (purple arrow). The most important kinematic parameters are pointed out. These are the amplitude (A, red arrow), which is the length of the upward (A_{up}) and downward (A_{down}) tail beat together, the wave length (λ_b, yellow bar), which is the length of one wave on a body line and the stride length (λ_s, green bar), which is the travelled distance of one tail beat. See text for further explanation

3.6.2 Wave length of body and fin (λ_b resp. λ_f)

The wave length of the body λ_b respectively the fin λ_f are defined as the distance between two adjacent equal amplitude maxima on one body or fin line (*see figure 10*). Successive body and fin lines were shifted down over a defined distance, in order to see the individual amplitude maxima of the lines. All upward and all downward amplitudes of the successive frames were connected, which resulted in the appearance of several wave crests (*see figures 15, 25, 35 resp. 16, 26, 36*). The wave length of each frame with an amplitude maximum is determined from the distance between two positive or negative wave crests. The mean of these wave lengths per frame gave the wave length of the body or fin.

3.6.3 Stride length of body and fin (λ_s resp. λ_{sf})

The stride length of the body λ_s respectively the fin λ_{sf} are defined as the distance a fish swims in one beat cycle of body or fin (*see figure 10*). The stride lengths were calculated as the mean distance travelled between the appearance of two upward or downward amplitude maxima on one point of the body and fin (one tail beat resp. one fin beat). To obtain λ_s for body and λ_{sf} for fin, a graph was made showing the tracks in space of the points A to K and 1 to 15 (*see figures 17, 27, 37 resp. 18, 28, 38*). After replacing the forward movement of each track in the coordinate points, the beginning coordinate point of each track was subtracted from the following, in order to let the tracks coincide. The new obtained coordinates are set parallel along the X-axis. The amplitudes of each track are perpendicular to the X-axis, called the Y-axis. For example, the track of the tail, point K, was plotted in the figure by marking the position of the point every 0.008s. For better convenience, the tracks A to K and 1 to 15 are separated by a fixed distance on the Y-axis. Because the points were manually placed on the film frames, an error could have occurred by the amplitude data. Reduction of such errors was done with the five points differentiation formula of Lagrange followed by a five points running average. With these formulas, the amplitude data were smoothed and a wave-like track occurred in the graphs.

Five points differentiation formula of Lagrange:

$$dy/dt_{(\text{at } t=n)} = 100 * 0.008 * (2/3 * y_{(n-1)} - 1/12 * y_{(n-2)} + 2/3 * y_{(n+1)} - 1/12 * y_{(n+2)})$$

Five points running average (A at t = n):

$$A_{(n)} = 1/5 * (dy/dt_{(n-2)} + dy/dt_{(n1)} + dy/dt_{(n)} + dy/dt_{(n+1)} + dy/dt_{(n+2)})$$

In the formula of Lagrange 100 is a fixed value and 0.008 is the amount of seconds per frame. Further, the y-coordinate values of the nearest frames are taken with their own weight factor to calculate the new amplitude of that frame. With the five points running average the smoothing is completed.

The resulting graphs consist of wave-like tracks of movement in space made by the selected points on the body or fin. By connecting amplitude maxima on the successive tracks, body and fin strokes were made visible. These strokes are the distances between the successive amplitude maxima wave crests and indicate therefore half a stride length. The mean distance of two body strokes on the tail gave the stride length of the body λ_s. The same was done for the fin, except that from the entire wave showing tracks the mean distance of two fin strokes was taken to calculate a mean stride length λ_{sf}.

3.6.4 Wave frequency (F) and wave period (*T*)

The wave frequency F is defined as the number of fin or tail beat cycles per second. The wave period belonging to body T_b or fin T_f is the inverse of the fin and tail beat frequency F and is denoted by the time it takes a point on the fin or body to complete a full wave cycle. The graphs, in which the stride lengths are determined (*figures 17, 27, 37 resp. 18, 28, 38),* are also used to determine the wave periods, by counting the mean number of frames between two body or fin strokes of the smoothed data.

3.6.5 Wave speed (v_b and v_f)

The wave speed of the body v_b respectively the fin v_f is given by the distance an amplitude maximum or wave crest travelled over the body respectively fin per second. The values for v_b and v_f are calculated by plotting the position of the amplitude maxima on the body or fin against time and drawing linear regression lines through the plots (*see figures 19, 29, 39 resp. 20, 30, 40*). The slope of a regression line gives the average speed at which a wave travels down the body or fin. The mean of all complete wave crests on the frames of a film sequence was taken to figure out an average value for wave speeds.

3.6.6 Mean forward speed (U)

The mean forward speed U is given by the distance the flounder travelled per second. The distance was determined using the original coordinate points and subtracting the nose point of the first frame from the nose point of the last frame of a filming sequence. Because in all the films the fish swims upwards, a Pythagoras formula has used to determine the right horizontal coordinates.

Pythagoras formula:

$$z_{(n)} = \sqrt{}((x_{(n+1)} - x_{(n)})^2 + (y_{(n+1)} - y_{(n)})^2)$$

Per frame the travelled distance (z) was calculated to the next frame and the sum of all these distances was the total travelled distance in pixels. By dividing this value through 4.1, the distance in millimetres was given. The filming rate was 125 frames per second, meaning 0.008 seconds per frame. Multiplying the number of frames by 0.008 gave the total time of the film sequence. To calculate U, the distance was divided through the time the flounder travelled.

3.6.7 Swimming efficiency (U/*v*)

The ratio between U and *v* gives an indication about the swimming efficiency of the fish. This efficiency is a term pointing out the amount of force applied to the medium for propulsion that will actually result in propulsion. Division of the mean forward speed with the wave speed of the body, gives the efficiency of the body waves. In the same way, with the wave speed of the fin, the fin wave efficiency was given.

3.7 Body wave versus fin wave

Comparison of the body waves with the fin waves gives an indication about the relation between these two propulsion systems. From the amplitude envelop graphs (*see* section 3.6.1 and *figures 13, 23, 33*) points on the body and on the fin were selected which lie close to each other and showed waves. The amplitude tracks of the points were selected from the stride length graphs (*see* section 3.6.3 and *figures 17, 27, 37 and 18, 28, 38*) and were plotted together in a graph for every filming sequence (*see figures 50, 51 and 51*). The resulting graphs contain the movements of a body point and a fin point, which lay close to each other, in time and space.

4 Results

Three film sequences (1-3) of upward swimming juvenile flounders were analysed, using the described methods. Each of the three film sequences contains the swimming performance of a different individual. In all three sequences, the fish were swimming forward and ascending from the bottom towards a piece of food. Further was seen that the flounders used undulation of the body as well as of the dorsal respectively the anal fin for propulsion. In the following, for each of the three film sequences the resulting kinematic parameters are given separately. Each sequence is split up into sections where body and fin (fin line and fin tip) are described apart. For graphical reasons the figures of each sequence are placed at the end of their description. An overview of the gained values of the analysed kinematic parameters of the swimming motions of the three flounders is given in table 1 at the end of chapter 4.

4.1 Film sequence 1

In figure 11 the swimming path and body motions of a flounder recorded in film sequence 1 are shown. Every line represents the position of the body line in space at a particular frame. This sequence consists of 94 frames (time span of 0.744 seconds) in which the flounder was filmed from the ventral side, meaning that only the movements of the anal fin are recorded and analysed. The fish is swimming slightly upwards to the right, with a moderate body tilt angle in the beginning and a declining one towards the end. Movements of the tail are clearly visible and almost show a steady undulation. There are three complete body waves visible of the flounder with a body length of 62.8mm. In figure 12 the position of the anal fin line of every frame is plotted in space. It shows an almost regular wave pattern and because the fin is attached to the body it has a declining tilt angle, too. Three complete fin waves of the fin with a fin length of 37.3mm are visible.

4.1.1 Amplitudes

Body

The first part of the body, that is from the nose towards the stomach, hardly shows vertical movement, as depicted by the amplitude envelop of the body line (*see figure 13,* red line). The undulations begin behind the stomach, at about 40% of the total body length, and increase towards a maximum at the tail. Strikingly, the upward amplitudes A_{up} of the tail do not become positive. In figure 14 the amplitudes of the tail (red line) are set against the distance the flounder moves forward. It shows four upward amplitudes, with a mean value of -5.6mm. The three downward amplitudes A_{down} have a mean value of -14.6mm. The largest difference between an upward amplitude and a downward amplitude of one beat gives the maximum amplitude A_{max} of the flounder in sequence 1 and is 10.5mm.

Fin line

The amplitude envelop of the fin line, determined from the subtraction of the fin base from the fin tip (*see* also section 3.6.1), is shown in figure 13 by a blue line. It shows a small amplitude at the beginning of the fin towards one third of the total length of the fin. From that length, at point 5, the undulations begin and stop at the end of the fin. The location of the amplitude maxima on the fin differs from that of the body. Most times the upward amplitude A_{up} of the waves appear at approximately two third of its length, at point 10. The downward amplitude A_{down} of the waves appear most of the time at point 6, just after the beginning of the wave. Thus, the four upward amplitudes and the three downward ones, take place at two different locations on the fin. Therefore, in figure 14, the movements of both points are followed in time. Point 10 (blue line) has a larger amplitude and is repeatedly later with its maxima, than point 6 (green line). Also is seen that just after point 10 had its upward amplitude, the downward amplitude arise on the fin at point 6. The mean value of A_{up} is 5.5mm, and A_{down} has a mean value of -4.0mm. The maximum amplitude A_{max} is 10.2mm. Towards the end of the sequence it seems that the waves are travelling faster. This is good visible at the end of fin point 10 in which the downward amplitude at frame 88 is directly followed by an upward amplitude at frame 93 (*see figure 14*).

Fin tip

The amplitude envelop of the fin tip is visible in figure 13 as a green line. It shows an increasing amplitude range at the points towards the back, compared with the fin line, in which the fin base had been subtracted from the fin tip. Only at one point at the end of the fin, the upward amplitude is coming to the same height as the fin line. This wider amplitude range shows that the body wave influences the movements of the fin tip.

Body, fin line and fin tip

By plotting the amplitudes of the body line in the same graph with the amplitudes of the fin line, an indication is given about a possible relation between these two amplitudes (*figure 14*). In the figure is shown that both fin and body make three complete waves and that these three waves have a regular pattern. The tail point on the body and point 6 on the fin are showing the first upward amplitude A_{up} almost at the same time; the fin point 8 milliseconds (1 frame) earlier than the body. About 80ms (10 frames) later the upward amplitude of fin point 10 is seen. About 24ms (3 frames) after this upward amplitude A_{up}, the downward ones A_{down} appear, beginning with again an almost simultaneous one of the tail and fin point 6. Fin point 10 is delayed with about 80ms (10 frames). This pattern, of simultaneously maxima of the tail and fin point 6 and a delay of 80ms for fin point 10, repeats in the other two waves, starting with an upward amplitude A_{up} of fin point 6 about 36ms after the downward amplitude A_{down} of fin point 10 of the former wave.

4.1.2 Wave lengths

Body

When swimming, the flounder shows a wave on its body beginning behind its stomach and travelling towards the tail. The length of one wave on the body is determined on basis of figure 15, in which several frames are plotted underneath each other. On top of the figure frame 51 is depicted, which shows a maximal downward amplitude at the tail. Further down, at frame 66, an upward amplitude maximum of the tail is seen, and at the bottom of the figure, at frame 78, a second downward amplitude maximum arises. The frames in between show a replacement of some points in the upward or downward direction relative to the frame before. By connecting these upward moving points and downward moving points, wave crests are made visible. The wave crests from upward movements appearing in blue and the wave crests of the downward moving parts of the tail beat cycle are shown in green. These wave crests indicate the waves on the body which are travelling backwards. The length of such a wave is determined from the distance between two upward respectively downward moving parts of the tail beat cycles. This is shown on the example of frame 51 in figure 15. A mean value was calculated from all the wave lengths determined per frame. The mean wave length λ_b of the body was 31.6mm, meaning that one wave covers 50% of the total body length. Because the moving part of the body is about 60%, more than one wave (about 1.2 wave) appear at the same time on the body.

Fin

The length of the wave running down the fin is determined in the same way as done for the body. In figure 16 the fin lines of frame 50 to 79 are plotted below each other. On top of the figure the fin line of frame 50 is depicted, which shows a maximal downward amplitude at point 7. Further down, at frame 64, an upward amplitude maximum is shown for fin point 9, and at the bottom of the figure, at frame 79, a second downward amplitude maximum is shown. By connecting these upward moving points and downward moving points, wave crests are made visible. The wave crests from upward movements appearing in blue and the downward moving parts of the fin wave cycle are shown in green. These wave crests indicate the waves on the fin which are travelling backwards. The length of such a wave is determined from the distance between two upward respectively downward moving parts of the fin wave cycles. This is shown on the example of frame 50 in figure 16. A mean value was calculated from all the wave lengths per frame. The mean wave length λ_f of the fin was 21.6mm, meaning that one wave covers 61% of the total fin length. Because the whole fin is taking part in the swimming motions, more than one wave appears at the same time on the fin. Comparison of the wave length λ_f of the fin with the total body length gave 34% coverage of the total body length, which is less than the body wave coverage.

4.1.3 Stride lengths and wave periods

Body

Another wave which is analysed is the movement per body point in space and time, which is shown in figure 17. In this figure the body points are plotted separately and placed under each other for better clarity. The figure shows the vertical movements of each point at the distance the flounder is swimming forward. The frame numbers are put above the graph, in order to show the time period. Because a data smoothing had taken place, the first two frames and the last two frames are left out and are therefore not further analysed. Clearly visible are the waves from body points F to K, and as seen before, the almost still first part of the body. The upward and downward amplitude of the body points are connected, which results in the appearance of four complete body strokes. The dark blue lines are marking the upward amplitudes, while the green lines point out the downward ones. The body strokes change in width, because the amplitude maxima appear in some cases at the same time at different body points, as shown by the irregular wave crests.

The stride length λ_s is given by the displacement of the flounder in two body strokes, or one wave, and is shown in the figure for the first two body strokes of the tail. The mean stride length λ_s of the body is calculated by the mean of all sets of body strokes on the tail and has a value of 19.0mm. This corresponds to 30% of the total body length, meaning that in one beat the flounder is swimming forward about one third of its body length.

The wave period T_b of the body waves was calculated as the time it took to complete one wave, or two body strokes, shown in the figure by the bright blue line. As with the mean stride length λ_s, the mean wave period T_b is determined by the mean of the two waves the tail shows. Accordingly, the mean time the flounder completed one tail beat, is 0.22 seconds. The wave frequency F is the inverse of T, meaning that there are 4.5 tail beats per second.

Fin

In figure 18 the fin points are plotted separately and placed under each other for better clarity. The figure shows the vertical movements of each point at the distance the flounder is swimming forward. The frame numbers are put above the graph, in order to show the time period. Because a data smoothing had taken place, the first two frames and the last two frames are left out and are therefore not further analysed. Clearly visible waves appear from fin point 5 and end at fin point 13, so in contrast with the amplitude envelope in which all fin points show an amplitude, this graph shows a relatively unmoving first part of the fin. The upward and downward amplitudes of each fin point are connected with coloured lines showing four complete fin strokes. The dark blue lines are marking the upward amplitudes, while the green lines point out the downward ones. The fin strokes change in width, because the amplitude maxima appear in some cases at the same time at different body points, as shown by the irregular wave crest of the first positive amplitude maxima.

The stride length λ_{sf} of the fin is given by the displacement of the flounder in two fin strokes, or one fin wave, and is shown in the figure for the first two fin strokes of fin point 13. The mean stride length λ_{sf} of the fin is calculated by the mean of the individual stride lengths of all waves and has a value of 19.5mm. This corresponds to 52% of the total fin length and 31% of the body length, meaning that in one fin beat the flounder swims forward about one third of its body length.

The wave period T_f of the fin waves was calculated as the time it took to complete one wave, or two fin strokes, shown in the figure by the bright blue line. Like the mean stride length, the mean wave period is determined by the mean of the waves on all fin points. Accordingly, the mean time the flounder completed one fin beat, is 0.23 seconds. The wave frequency F is the inverse of T, meaning that there are 4.3 fin beats per second.

4.1.4 Wave speeds

Body

The speed v_b at which a wave travelled down the body was calculated using the same five wave crests along the body that described the body strokes (*see figure 17*). The time a wave crest passed through body points F to K is indicated in figure 19. A linear regression line was fitted through series of points of a wave crest. A steep slope indicates a fast wave and a gentle slope a slow wave. The speeds of each wave crest are depicted above the graph and the mean speed of these body wave crests has a value of 170mm per second. This is identical with 2.7 body lengths per second.

Fin

The same five wave crests along the fin that described the fin strokes (*see figure 18*), were used to calculate the wave speed v_f at which a wave travelled down the fin. The time a wave crest passed through fin points 5 to 13 is indicated in figure 20. A linear regression line was fitted through series of points of a wave crest. The slope of these linear regression lines represents the speed by which the waves travel down the fin. The speeds of each wave crest are depicted above the graph and the mean speed of these fin wave crests has a value of 119mm per second. This is identical with 3.2 fin lengths per second and 1.9 body lengths per second.

4.1.5 Mean forward speed

During 94 frames the fish travelled a distance of 65 millimetres. The total filming time was 0.744 seconds. The mean forward speed U was calculated as the distance divided by the filming time. This gave a speed of 87mm per second, identical with 1.4 body lengths per second.

4.1.6 Swimming efficiency

Body

The efficiency of the swimming technique employed by the body was calculated as the division of the mean forward speed by the mean speed of the body waves. This gave a value of 0.51. The higher this value, the more efficient the propelling technique is.

Fin

To calculate the efficiency of the fin propulsion the mean forward speed of the flounder was divided by the mean speed of the fin waves. A value of 0.73 was computed.

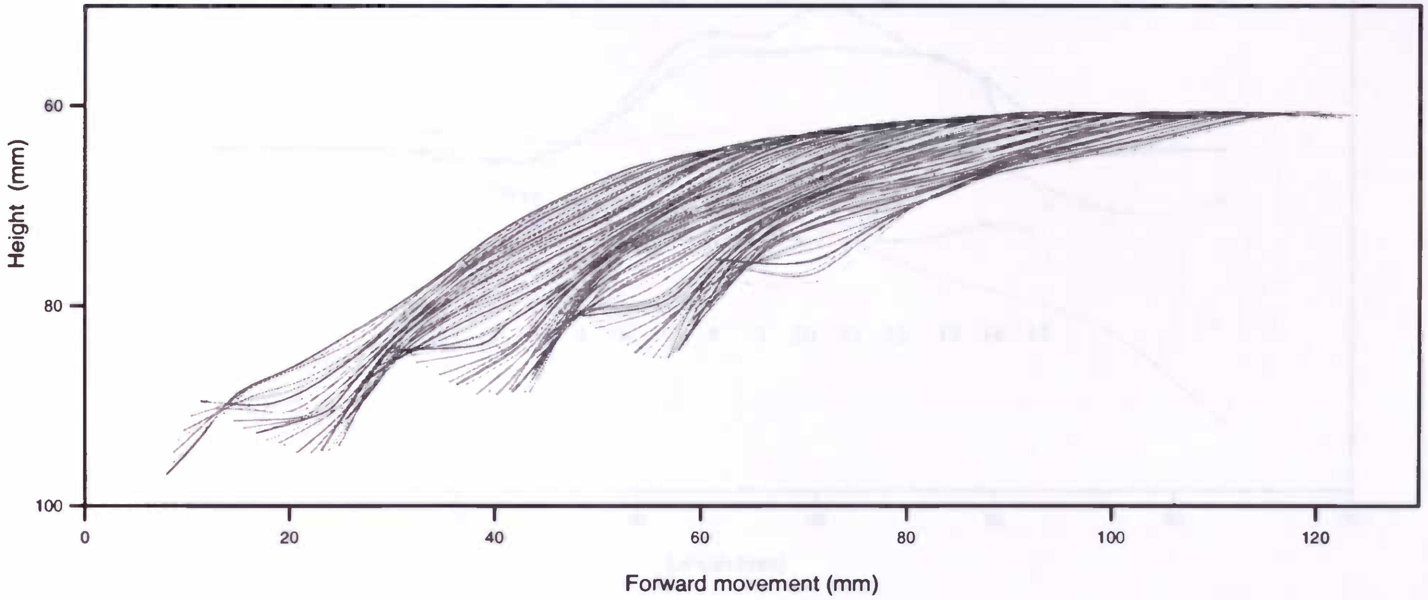


Figure 11. The swimming path and body motions of flounder 1. Every line is standing for the position of the body line in space at a particular frame. The fish is swimming to the right, meaning that his head is at the right side and his tail is on the left side of the lines.

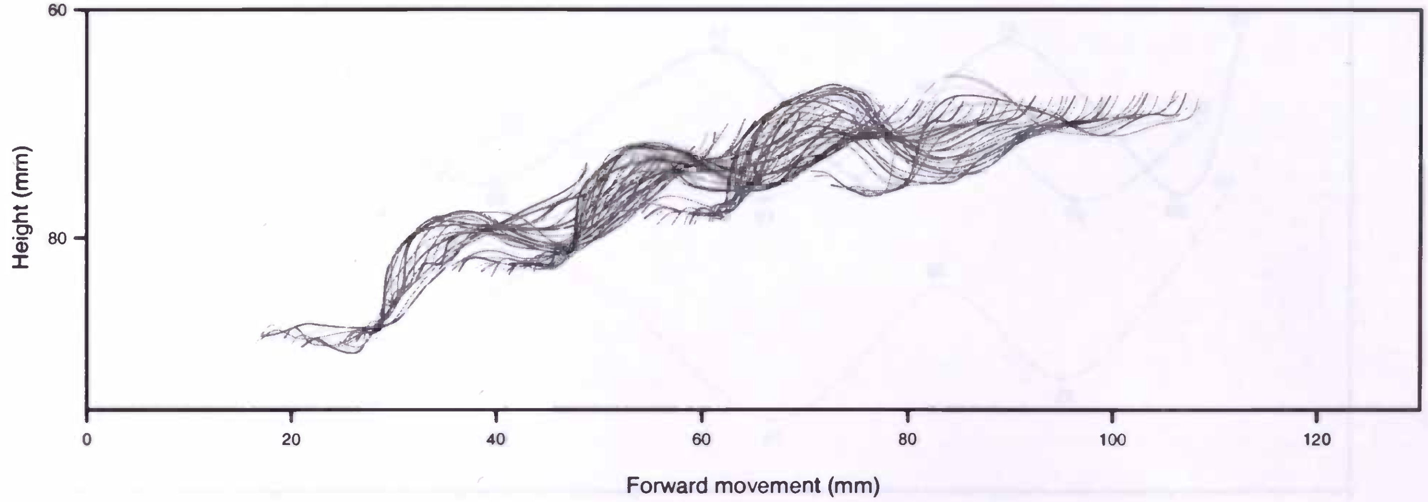


Figure 12. The movements of the fin of flounder 1. Every line is standing for the position of the edge of the fin in space at a particular frame. For the analysis of the fin, the fin base was subtracted from these lines. The beginning of the fin is at the right and the end is at the left side of the lines.

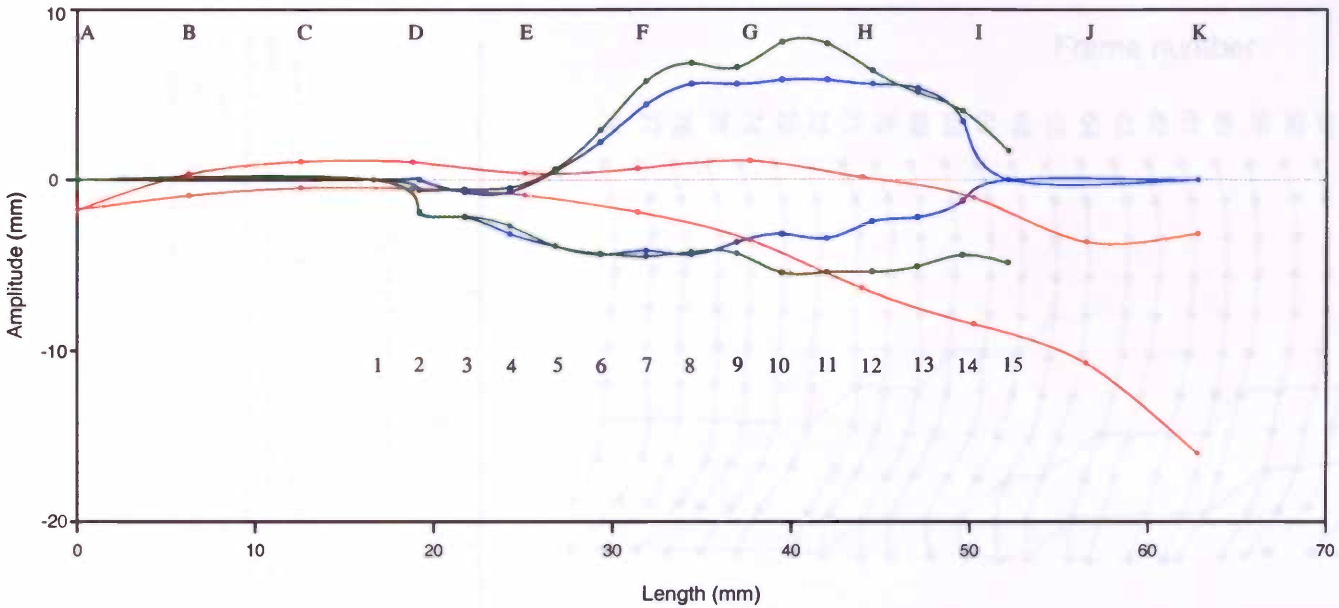


Figure 13. Amplitude envelopes of flounder 1, showing the most upward and downward amplitude maxima of the points on the body (red line), the fin (blue line) and the fin tip (green line). The nose of the flounder is at the left-hand side and the tail at the right-hand side. Letters at the top indicate the individual points on the body, A at the nose and K at the tail. Numbers indicate points on the fin, 1 at the start and 15 at the end of the fin. The reference axis for the body is a linear regression through body points B to E, and the reference axis for the fin lines is set as the line between the first fin point and the last, both fixed on the body.

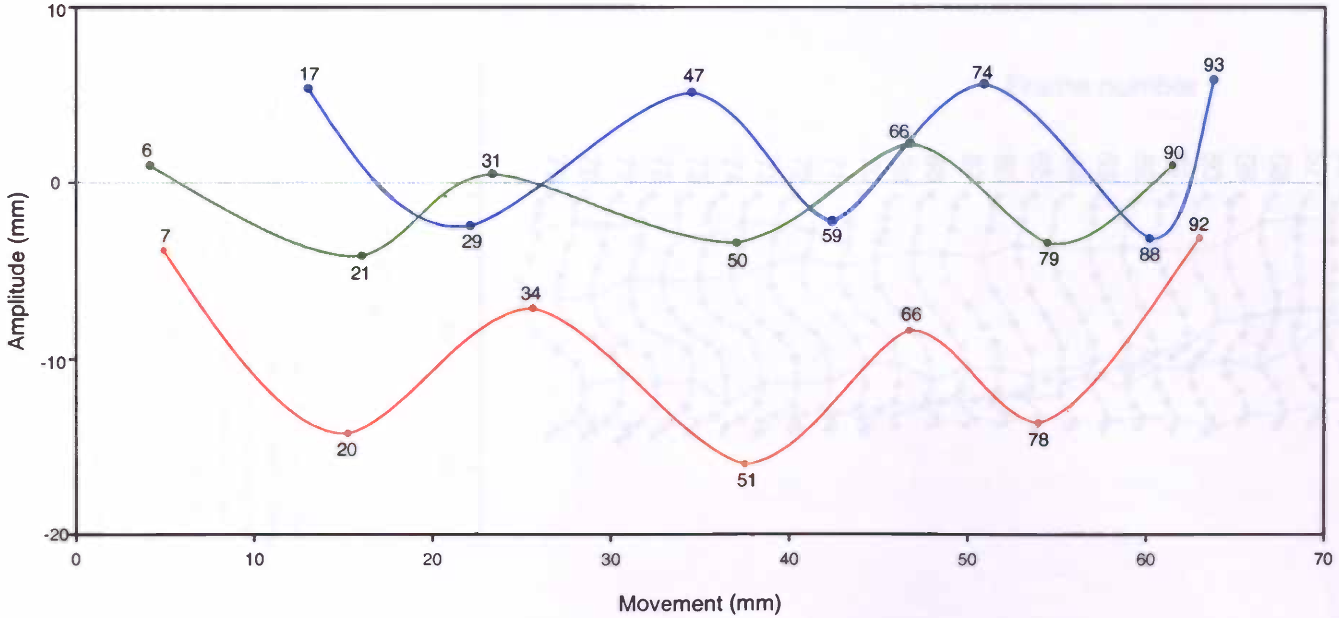


Figure 14. The upward and downward amplitude maxima of flounder 1 of the body (red line), of fin point 6 (green line) and of fin point 10 (blue line) set against the movement of the flounder. Numbers above the amplitude maxima indicate the frame number in which it appears. The reference axis for the body is a linear regression through body points B to E, and the reference axis for the fin lines is set as the line between the first fin point and the last, both fixed on the body. The movement of the flounder was set at zero on frame number 1.

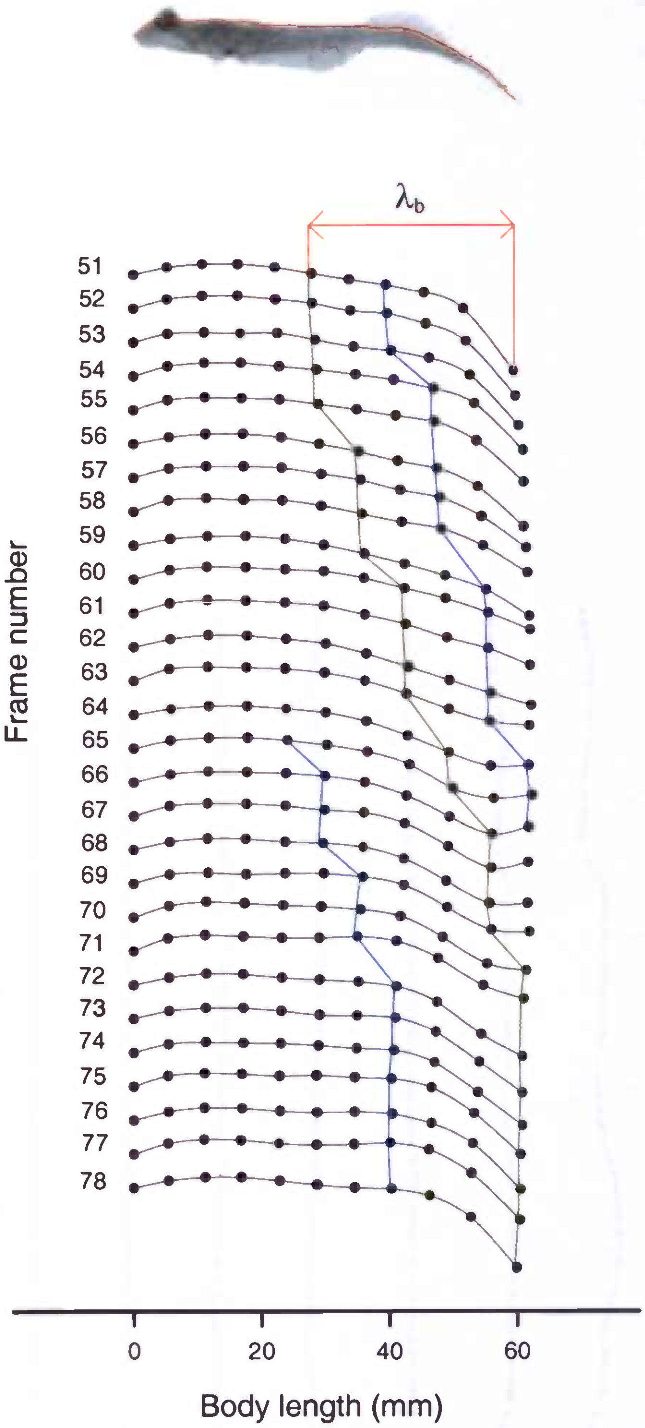


Figure 15. Body lines of flounder 1, taken from successive pictures of a film fragment. The body lines are shifted down over a defined distance to show wave crests running over the body. Head of the flounder is at the left-hand side and the tail at the right-hand side of the graph. The wave crests connecting the downward amplitude maxima are shown as a green line, and the upward amplitude maxima are connected with blue lines. The wave length λ_b of the body line of frame number 51 is shown by red lines but λ_b was calculated from the mean wave lengths of the frames with amplitude maxima.

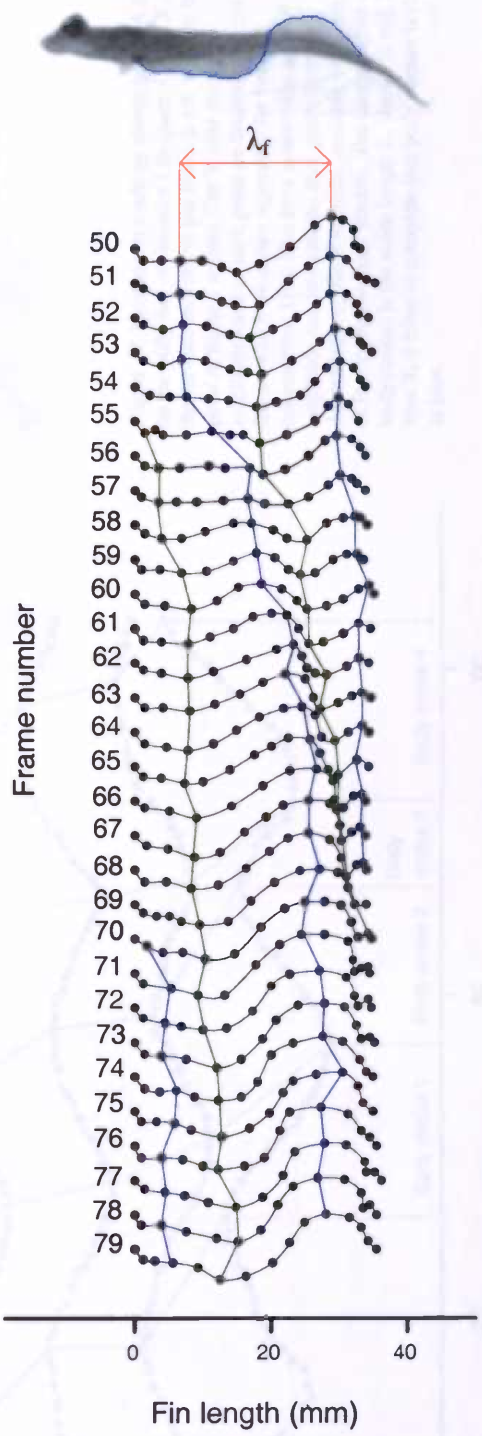
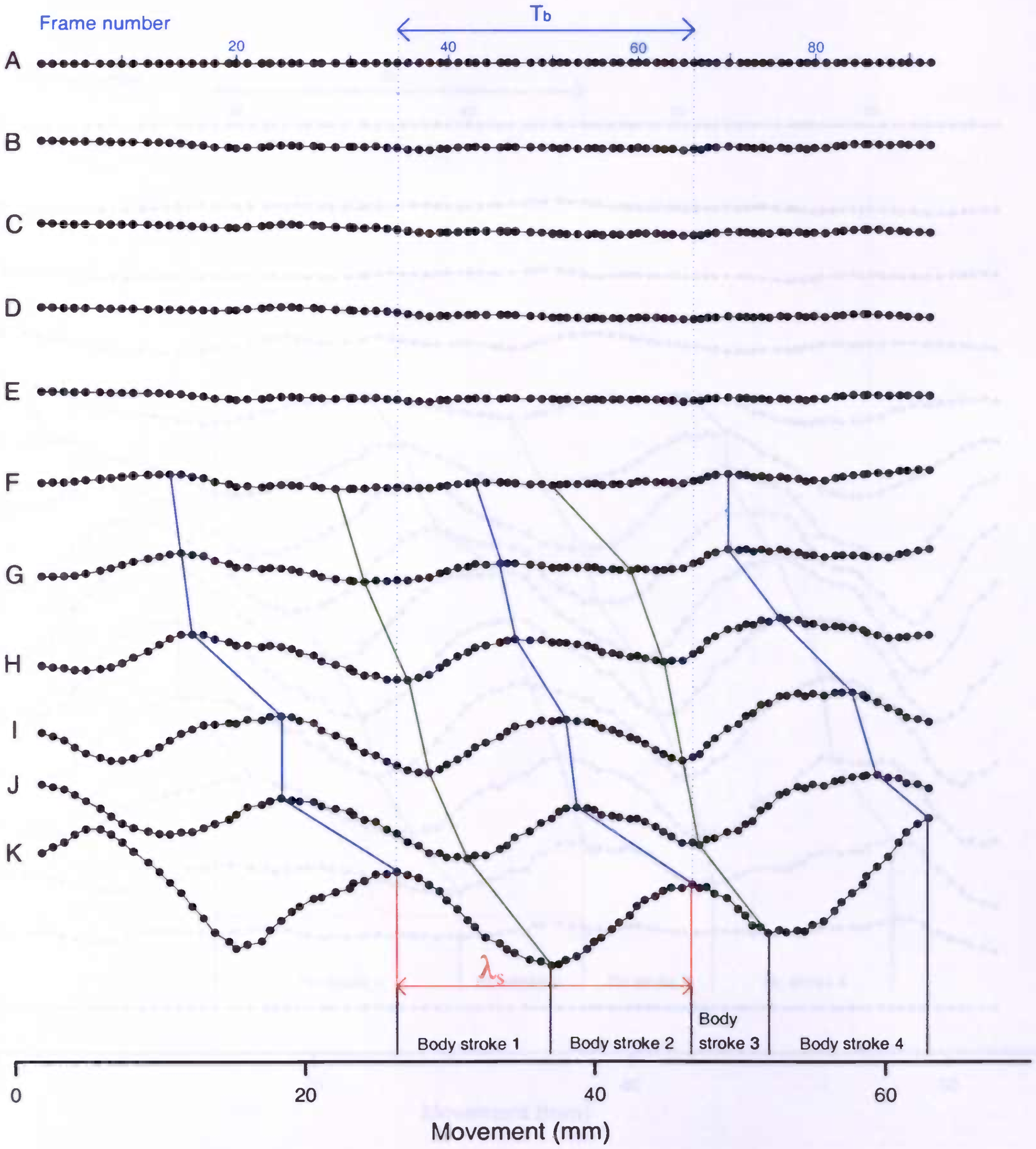


Figure 16. Fin lines of flounder 1, taken from successive pictures of a film fragment. The fin lines are shifted down over a defined distance to show wave crests running over the fin. Beginning of the fin is at the left-hand side and the end of the fin is at the right-hand side of the graph. The wave crests connecting the downward amplitude maxima are shown as green lines, and the upward ones as blue lines. The wave length λ_f of the fin line of frame 50 is shown by red lines but λ_f was calculated from the mean wave lengths of the frames with amplitude maxima.



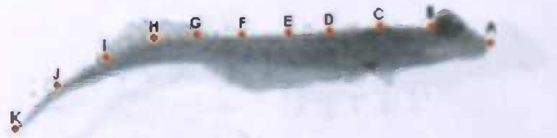
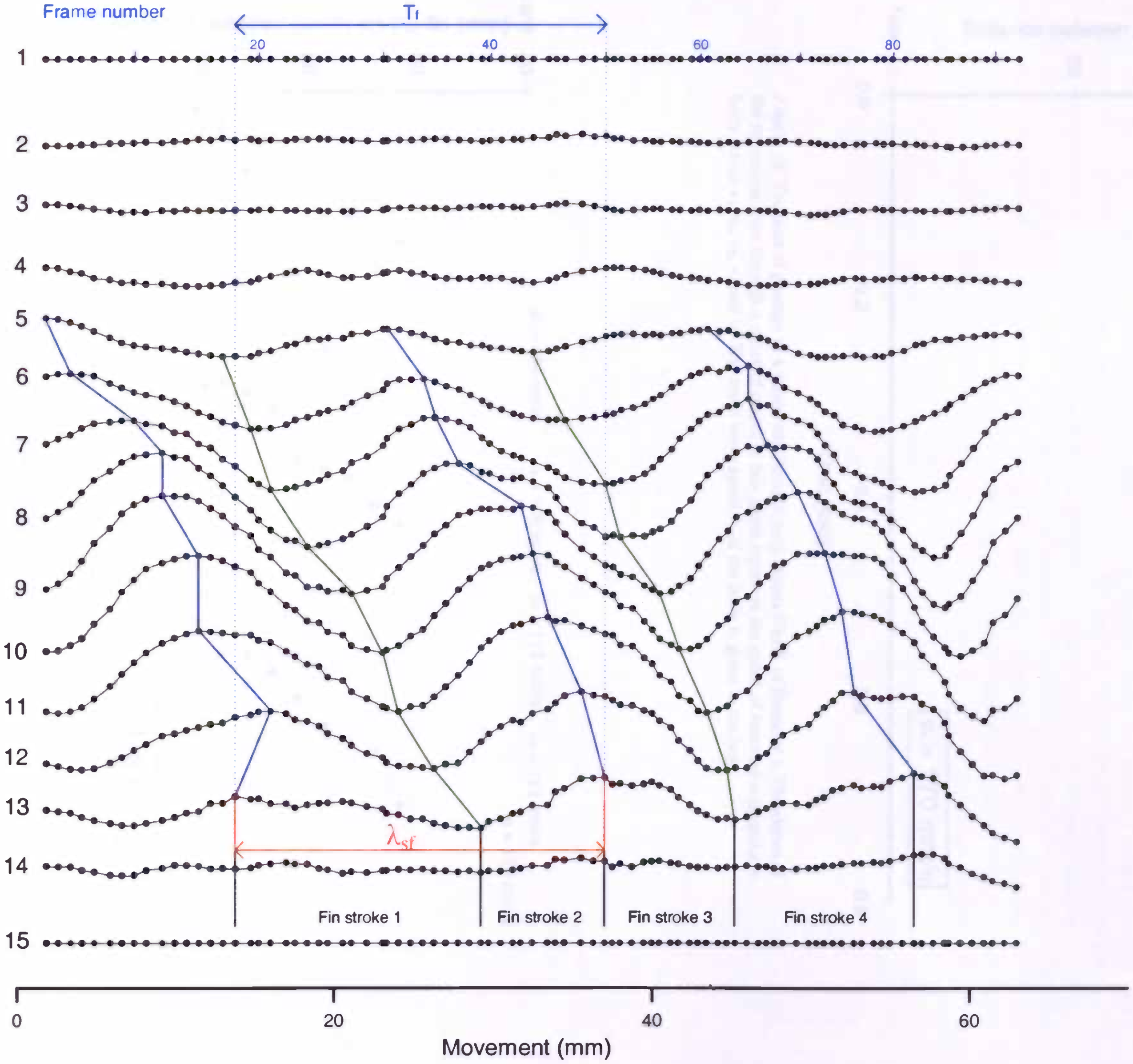


Figure 17. Movements made by eleven points A to K on the body line of flounder 1 in space. On the X-axis the forward movement per frame is set, with the tail point of frame 1 at zero. The Y-axis shows the amplitude track of each point on the body line per frame, which are drawn separately for better convenience. Dark blue lines connect the upward amplitude maxima and the dark green lines the downward amplitude maxima, resulting in the presence of four complete body strokes. The displacement of two body strokes is the stride length λ_s, shown in red. The time T_b it takes to complete two body strokes is shown in blue.



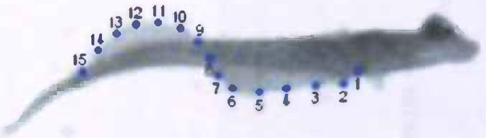


Figure 18. Movements made by fifteen points 1 to 15 on the fin line of flounder 1 in space. On the X-axis the forward movement per frame is set, with the end of the fin of frame 1 at zero. The Y-axis shows the amplitude track of each point on the fin line per frame, which are drawn separately for better convenience. Dark blue lines connect the upward amplitude maxima and the dark green lines the downward amplitude maxima, resulting in the presence of four complete fin strokes. The displacement of two fin strokes is the stride length λ_{sf}, shown in red. The time T_f it takes to complete two fin strokes is shown in blue.

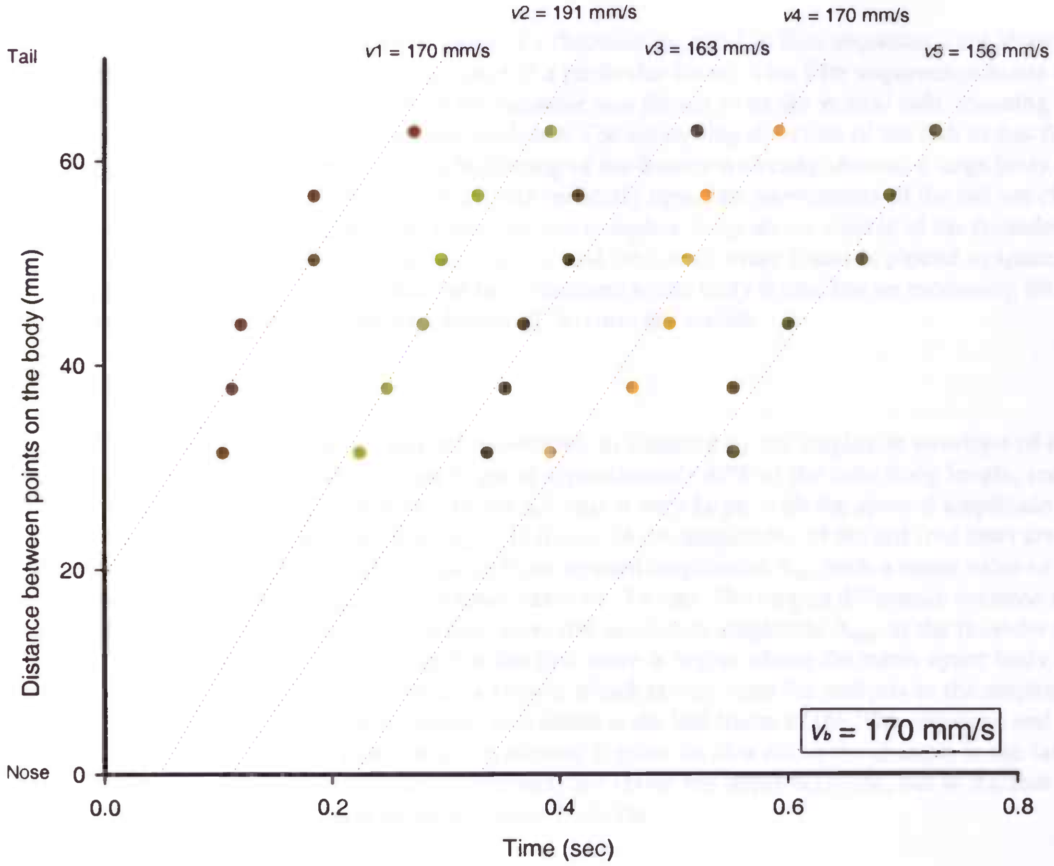


Figure 19. The time of passage of a wave crest through body points F to K of flounder 1. The slopes of the regression lines through a series of points in this graph represent the speed of successive propulsive body waves v_1, v_2, v_3, v_4 and v_5. The mean wave speed v_b of the body is given in the box.

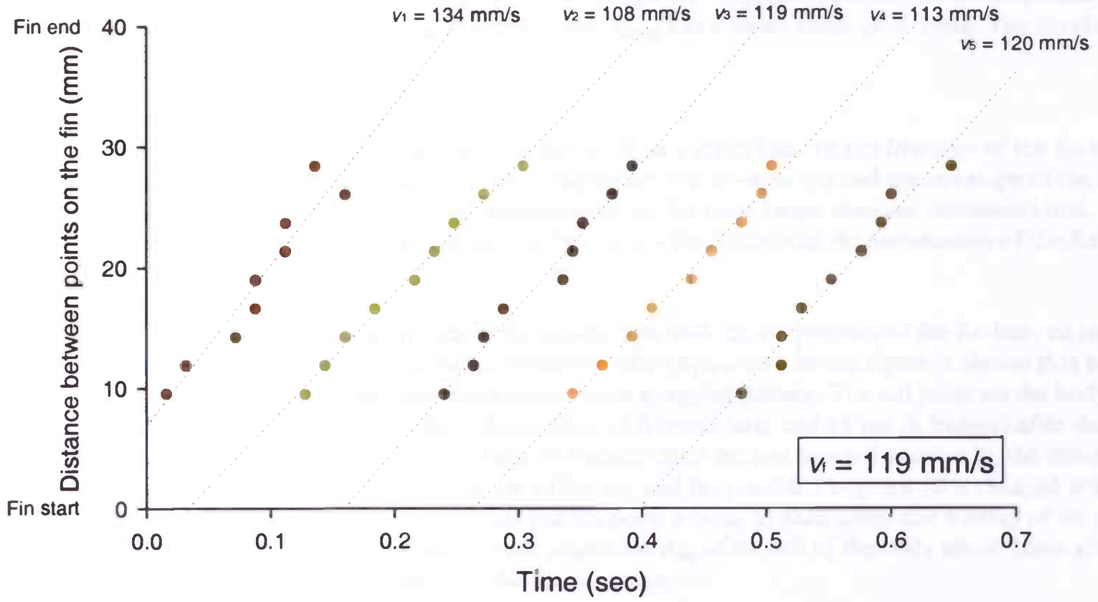


Figure 20. The time of passage of a wave crest through fin points 5 to 13 of flounder 1. The slopes of the regression lines through a series of points in this graph represent the speed of successive propulsive fin waves v_1, v_2, v_3, v_4 and v_5. The mean wave speed v_f of the fin is given in the box.

4.2 Film sequence 2

In figure 21 the swimming path and body motions of a flounder recorded in film sequence 2 are shown. Every line represents the position of the bodyline in space at a particular frame. This film sequence consists of 72 frames (time span of 0.568 seconds) in which the flounder was filmed from the ventral side, meaning that only the movements of the anal fin are recorded and analysed. The swimming direction of the fish in this film sequence was almost straight upwards. At the beginning of the frames it already showed a large body tilt angle, which increased at the end until the fish swam almost vertically upwards. Movements of the tail are clearly visible and show almost steady undulation. There are two complete body waves visible of the flounder with a body length of 66.3mm. In figure 22 the position of the anal fin line of every frame is plotted in space. It shows an almost regular wave pattern and because the fin is attached to the body it also has an increasing tilt angle. Two complete fin waves of the fin with a fin length of 36.1mm are visible.

4.2.1 Amplitudes

Body

The first half of the body hardly shows vertical movement, as depicted by the amplitude envelope of the body line (*see figure 23,* red line). The undulations begin at approximately 40% of the total body length, and increase towards a maximum at the tail. The deviation of the tail beat is very large, with the upward amplitude A_{up}, considerably higher than the downward one A_{down}. In figure 24 the amplitudes of the tail (red line) are set against the distance the flounder moves forward. It shows three upward amplitudes A_{up}, with a mean value of 14.1mm. The three downward amplitudes A_{down} have a mean value of -3.4mm. The largest difference between an upward amplitude and a downward amplitude of one beat gives the maximum amplitude A_{max} of the flounder in sequence 2 and is 20.7mm. The figure shows that the first wave is higher above the mean upper body line than the second wave. A third downward amplitude is shown, which is only used for analysis in the amplitude calculations. However, this downward amplitude maximum is the last frame of the film sequence and therefore not sure an amplitude maximum. By showing him anyway it gives an idea about the changes in the tail beat direction; at the beginning of the film all tail movements are above the upper bodyline, but as the fish swims further, the tail beat direction becomes under the upper bodyline.

Fin line

The amplitude envelope of the fin line, determined from the subtraction of the fin base from the fin tip (*see* also section 3.6.1), is shown in figure 23 by a blue line. In contrast with the body, the fin starts immediately with its undulations. The first point is the point which is tightened to the body, and therefore not movable. The second point shows already amplitude differences between the frames. The location of the amplitude maxima on the fin differs from that of the body. Like the fin of the flounder in film sequence 1, this flounder also has most upward amplitudes A_{up} on point 10 of the fin and most downward amplitudes A_{down} on fin point 6. In figure 24 the movements of both points are followed in time. Both points have about the same amplitude range, but fin point 6 (green line) is repeatedly earlier in time with its amplitude maxima and has lower amplitudes, than fin point 10 (blue line). Also is seen that just after fin point 10 had its upward amplitude, the downward amplitude arise of the fin at point 6. The mean value of A_{up} is 5.4mm, and A_{down} has a mean value of -4.8mm. The maximum amplitude A_{max} is 10.8mm.

Fin tip

The amplitude envelope of the fin tip is visible in figure 23 as a green line. At the first part of the fin the amplitude envelope of the fin line and fin tip are comparable, but towards the end the envelope of the fin tip increases. Just like the body line the upward amplitude of the fin tip is larger than the downward one. This comparable and wider amplitude range shows that the body wave influences the movements of the fin tip.

Body, fin line and fin tip

By plotting the amplitudes of the body line in the same graph with the amplitudes of the fin line, an indication is given about a possible relation between these two amplitudes (*figure 24*). In the figure is shown that both fin and body make two complete waves and that these waves have a regular pattern. The tail point on the body has the first upward amplitude A_{up}, with fin point 6 about 32ms (4 frames) later and 48 ms (6 frames) after the A_{up} of fin point 6 arises the A_{up} of fin point 10. About 24ms (3 frames) after the last upward amplitude, the downward ones A_{down} appear, beginning with a simultaneous one of the tail and fin point 6. Fin point 10 is delayed with about 72ms (9 frames). This pattern, of maxima of tail and fin point 6 close to each other and a delay of fin point 10, repeats in the other wave, starting with an upward amplitude A_{up} of the tail of the body about 16ms after the downward amplitude A_{down} of fin point 10 of the former wave.

4.2.2 Wave lengths

Body

When swimming, the flounder shows a wave on its body beginning behind its stomach and traveling towards the tail. The length of one wave on the body is determined on basis of figure 25, in which several frames are plotted underneath each other. On top of the figure frame 8 is depicted, which shows a maximal upward amplitude. Further down, at frame 21, a downward amplitude maximum arises, and at the bottom of the figure, at frame 32, a second upward amplitude maximum is shown. The frames in between show a replacement of some points in the upward or downward direction relative to the frame before. By connecting these upward moving points and downward moving points, wave crests are made visible. The wave crests from upward movements appearing in blue and the wave crests of the downward moving parts of the tail beat cycle are shown in green. These wave crests indicate the waves on the body which are travelling backwards. The length of such a wave is determined from the distance between two upward respectively downward moving parts of the tail beat cycles. This is shown on the example of frame 8 in figure 25. A mean value was calculated from all the wave lengths determined per frame. This gave a mean wave length λ_b of the body of 34.8mm, meaning that one wave covers 53% of the total body length. Because the moving part of the body is about 60%, there can be 1.1 wave present on the body at once.

Fin

The length of the wave running down the fin is determined in the same way as done for the body. In figure 26 the fin lines of frame 18 to 40 are plotted underneath each other. On top of the figure the fin line of frame 18 is depicted, which shows a maximal upward amplitude at point 10. Further down, at frame 21, a downward amplitude maximum is shown for fin point 7, and at the bottom of the figure, at frame 40, a second upward amplitude is shown. By connecting these upward moving points and downward moving points, wave crests are made visible. The wave crests from upward movements appearing in blue and the downward moving parts of the fin wave cycle are shown in green. These wave crests indicate the waves on the fin which are travelling backwards. The length of such a wave is determined from the distance between two upward respectively downward moving parts of the fin wave cycles. This is shown on the example of frame 18 in figure 26. A mean value was calculated from all the wave lengths per frame. The mean wave length λ_f of the fin was 21.0mm, meaning that one wave covers 66% of the total fin length. Because the whole fin is taking part in the swimming motions, more than one wave appears at the same time on the fin. Comparison of the wave length λ_f of the fin with the total body length gave 32% coverage of the total body length, which is less than the body wave coverage.

4.2.3 Stride lengths and wave periods

Body

The movement per body point in space and time is shown in figure 27. The body points are plotted separately and placed under each other for better clarity. The figure shows the vertical movements of each point at the distance the flounder is swimming forward. Frame numbers are put above the graph, in order to show the time period. Because a data smoothing had taken place, the first two frames and the last two frames are left out and are therefore not further analysed. The first body points show little and irregular amplitude differences, but from body point G to K waves are clearly visible. The upward and downward amplitude of the body points are connected, which results in the appearance of three complete body strokes. In the figure, dark blue lines mark the upward amplitudes, while the green lines point out the downward ones. The wave crests are as good as straight, so the waves run smoothly down the body. The stride length λ_s is given by the displacement of the flounder in two body strokes, or one wave, and is shown in the figure for the first two body strokes of the tail. The mean stride length λ_s of the body is calculated by the mean of all sets of body strokes on the tail and has a value of 24.4mm. This corresponds to 37% of the total body length, meaning that in one beat the flounder swims forward about 40 % of its total body length.
The wave period T_b of the body waves was calculated as the time it took to complete one wave, or two body strokes, shown in the figure by the bright blue line. As with the mean stride length λ_s, the mean wave period T_b is determined by the mean of all sets of body strokes on the tail. Accordingly, the mean time the flounder completed one tail beat, is 0.18 seconds. The wave frequency F is the inverse of T, meaning that there are 5.6 tail beats per second.

Fin

In figure 28 the fin points are plotted separately and placed under each other for better clarity. The figure shows the vertical movements of each point at the distance the flounder is swimming forward. The frame numbers are put above the graph, in order to show the time period. Because a data smoothing had taken place, the first two frames and the last two frames are left out and are therefore not further analysed. The waves are directly visible at fin point 2 and go on till fin point 13, a situation which was also seen in the amplitude envelope of the fin (*see* *figure 23*). The upward and downward amplitudes of each fin point are connected with coloured lines showing three complete fin strokes. Dark blue lines in figure 28 mark the upward amplitudes, while the green lines point out the downward ones. The first wave crest is very smooth, shifting the amplitude maxima in the beginning of the fin with 1 frame and with 2 frames more backwards of the fin. As a consequence, this wave runs regularly down the fin. The following wave crests, on the other hand, and especially the third one, are strange. This third wave crest shows a wave in which fin point 3 till 6 have their amplitude maxima at the same time. From fin point 10 till 12 this situation is seen again, followed by an amplitude maximum of fin point 13 which is back in time.

The stride length λ_{sf} of the fin is given by the displacement of the flounder in two fin strokes, or one fin wave, and is shown in the figure for the first two fin strokes of fin point 13. The mean stride length λ_{sf} of the fin is calculated by the mean of the individual stride lengths of all waves and has a value of 27.8mm. This corresponds to 77% of the total fin length and 42% of the body length, meaning that in one fin beat the flounder swims forward about half its body length.

The wave period T_f of the fin waves was calculated as the time it took to complete one wave, or two fin strokes, shown in the figure by the bright blue line. Like the mean stride length λ_{sf}, the mean wave period T_f is determined by the mean of the waves on all fin points. Accordingly, the mean time the flounder completed one fin beat, is 0.19 seconds. The wave frequency F is the inverse of T, meaning that there are 5.2 fin beats per second.

4.2.4 Wave speeds

Body

The speed v_b at which a wave travelled down the body was calculated using the same four wave crests along the body that described the body strokes (*see figure 27*). The time a wave crest passed through body points G to K is indicated in figure 29. A linear regression line was fitted through series of points of a wave crest. The slope of these linear regression lines represents the speed by which the waves travel down the body. A steep slope indicates a fast wave and a gentle slope a slow wave. The speeds of each wave crest are depicted above the graph and the mean speed of these body wave crests has a value of 496mm per second. This is identical with 7.5 body lengths per second. .

Fin

The four wave crests along the fin that described the fin strokes (*see figure 28*), were used to calculate the wave speed v_f at which a wave travelled down the fin. The time a wave crest passed through fin points 2 to 13 is indicated in figure 30. A linear regression line was fitted through series of points of a wave crest. The slope of these linear regression lines represents the speed by which the waves travel down the fin. The speeds of each wave crest are depicted above the graph and the mean speed of these fin wave crests has a value of 218mm per second. This is identical with 6.0 fin lengths per second and 3.3 body lengths per second.

4.2.5 Mean forward speed

During 72 frames the fish travelled a distance of 78 millimetres. The total filming time was 0.568 seconds. The mean forward speed U was calculated as the distance divided by the filming time. This gave a speed of 136mm per second, identical with 2.1 body lengths per second.

4.2.6 Swimming efficiency

Body

The efficiency of the swimming technique employed by the body was calculated as the division of the mean forward speed by the mean speed of the body waves. This gave a value of 0.27. The higher this value, the more efficient the propeller technique is.

Fin

To calculate the efficiency of the fin propulsion the mean forward speed of the flounder was divided by the mean speed of the fin waves. A value of 0.63 was computed.

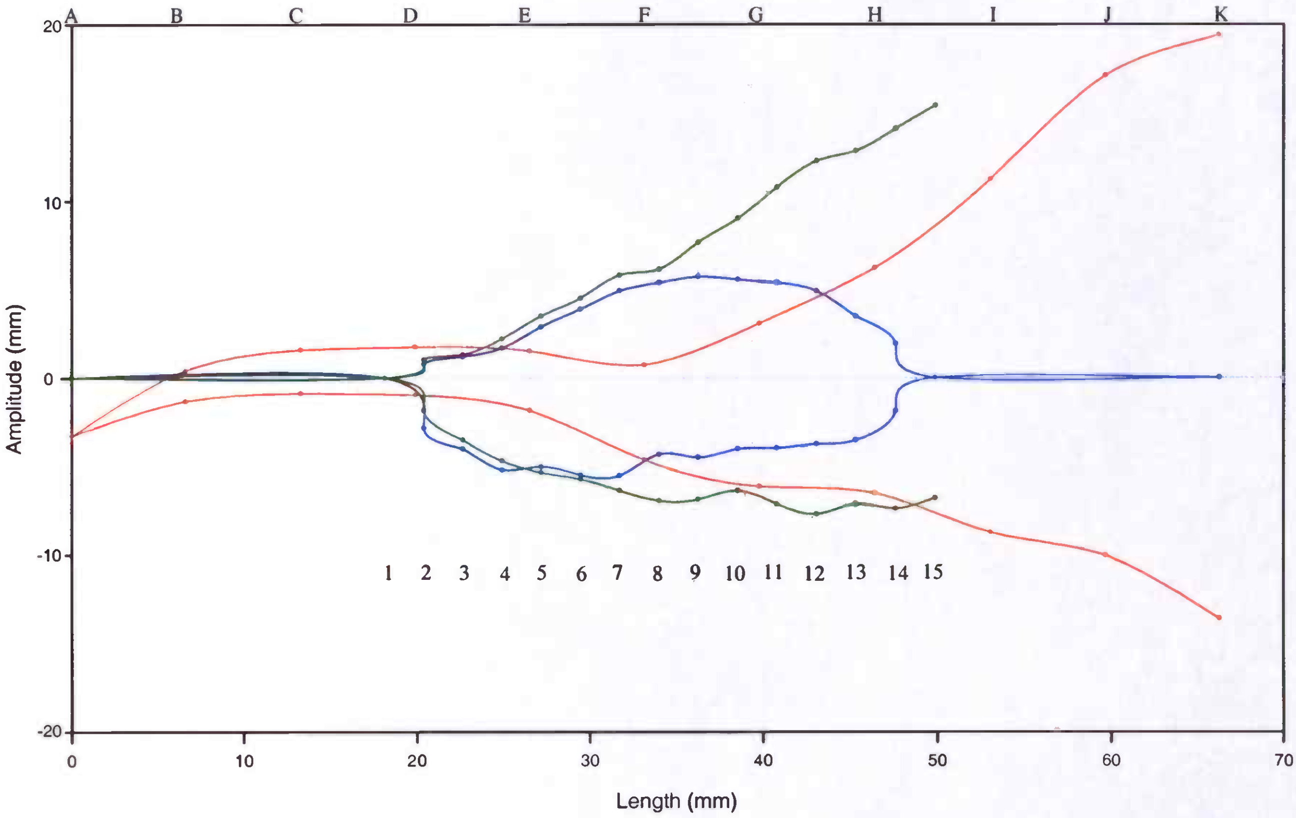


Figure 23. Amplitude envelopes of flounder 2, showing the most upward and downward amplitude maxima of the points on the body (red line), the fin (blue line) and the fin tip (green line). The nose of the flounder is at the left-hand side and the tail at the right-hand side. Letters at the top indicate the individual points on the body, A at the nose and K at the tail. Numbers indicate points on the fin, 1 at the start and 15 at the end of the fin. The reference axis for the body is a linear regression through body points B to E, and the reference axis for the fin lines is set as the line between the first fin point and the last, both fixed on the body.

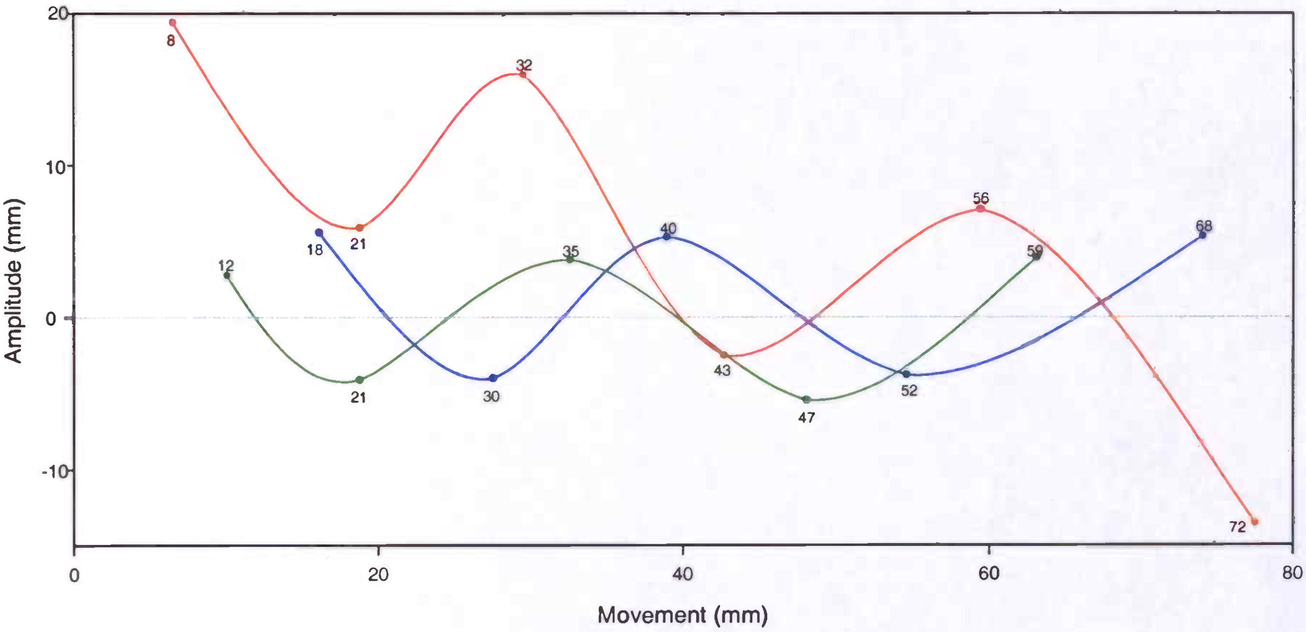


Figure 24. The upward and downward amplitude maxima of flounder 2 of the body (red line), of fin point 6 (green line) and of fin point 10 (blue line) set against the movement of the flounder. Numbers close to the amplitude maxima indicate the frame number in which it appears. The reference axis for the body is a linear regression through body points B to E, and the reference axis for the fin lines is set as the line between the first fin point and the last, both fixed on the body. The movement of the flounder was set at zero on frame number 1.

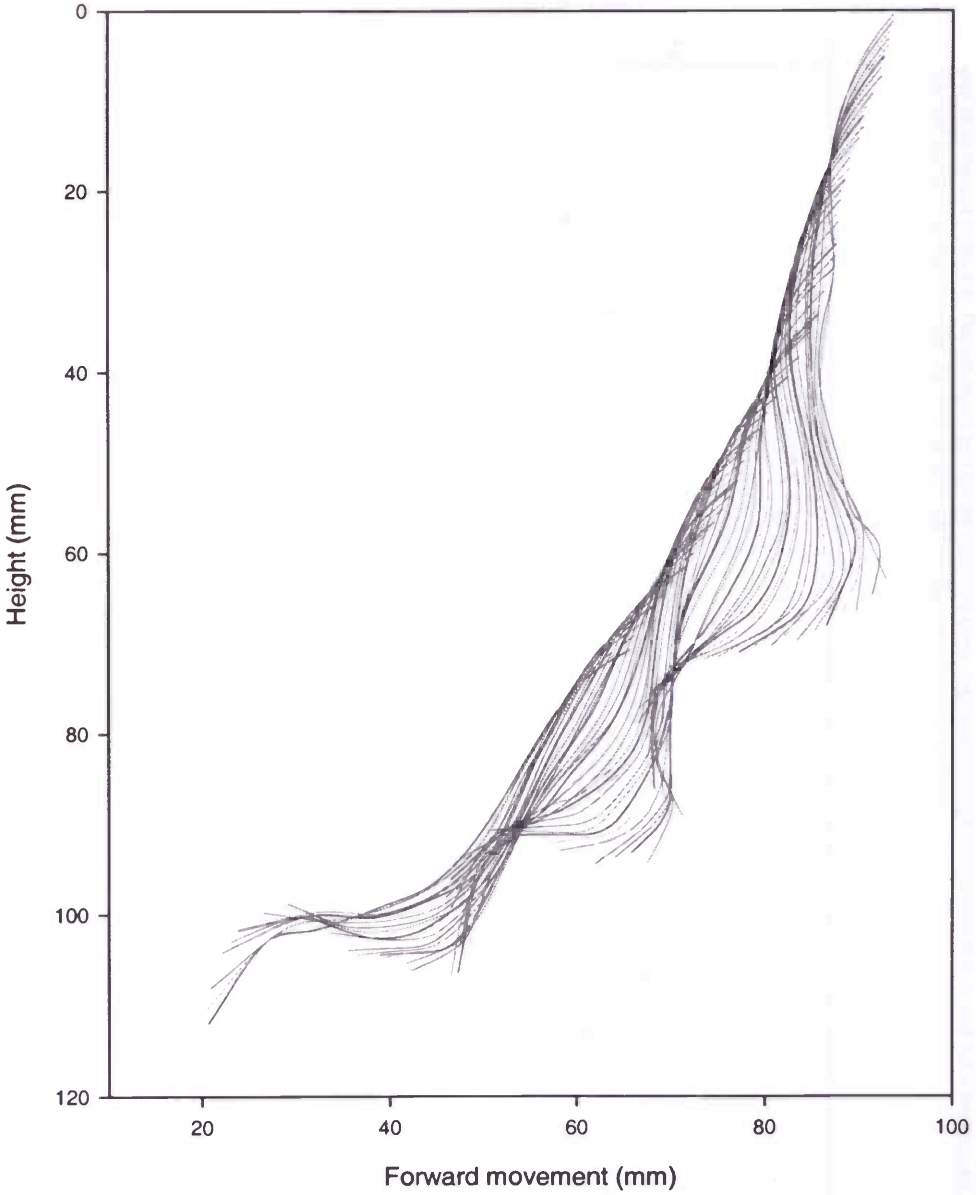


Figure 21. The swimming path and body motions of flounder 2. Every line represents the position of the body line in space at a particular frame. The fish is swimming upwards to the right, meaning that its head is at the right top and its tail is on the left end of the lines.

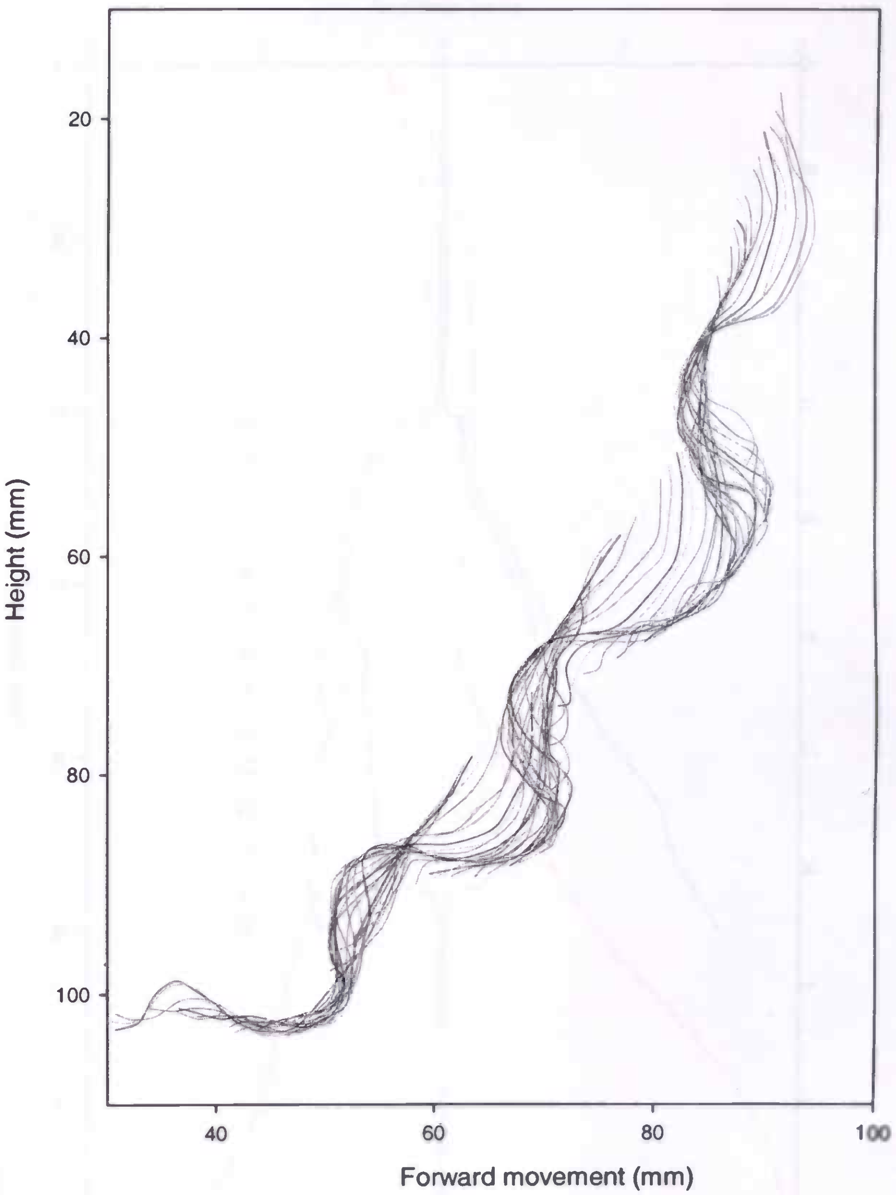


Figure 22. The movements of the fin of flounder 2. Every line represents the position of the edge of the fin in space at a particular frame. For the analysis of the fin, the fin base was subtracted from these lines. The beginning of the fin is at the right top and the end is at the left-hand side of the lines.

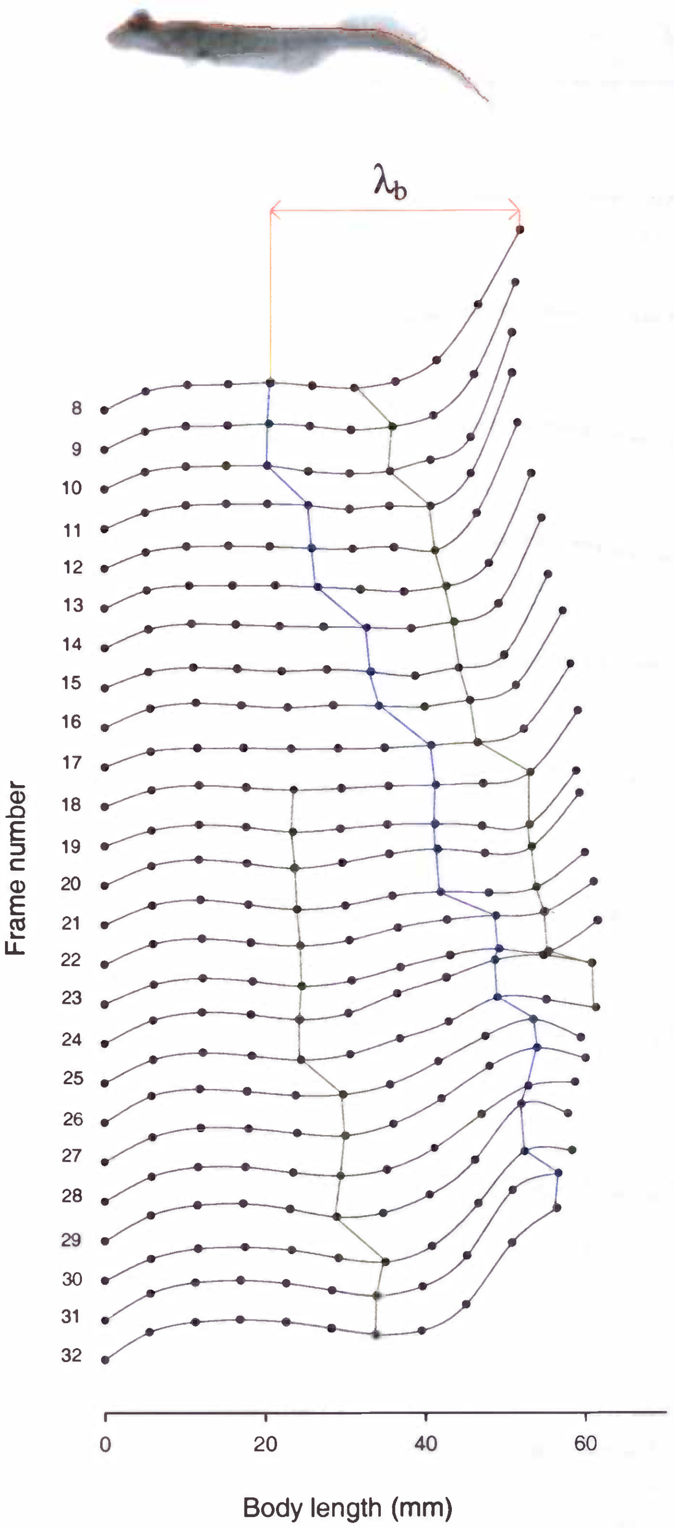


Figure 25. Body lines of flounder 2, taken from successive pictures of a film fragment. The body lines are shifted down over a defined distance to show wave crests running over the body. Head of the flounder is at the left-hand side and the tail at the right-hand side of the graph. The wave crests connecting the downward amplitude maxima are shown as a green line, and the upward amplitude maxima are connected with blue lines. The wave length λ_b of the body line of frame number 8 is shown by red lines but λ_b was calculated from the mean wave lengths of the frames with amplitude maxima.

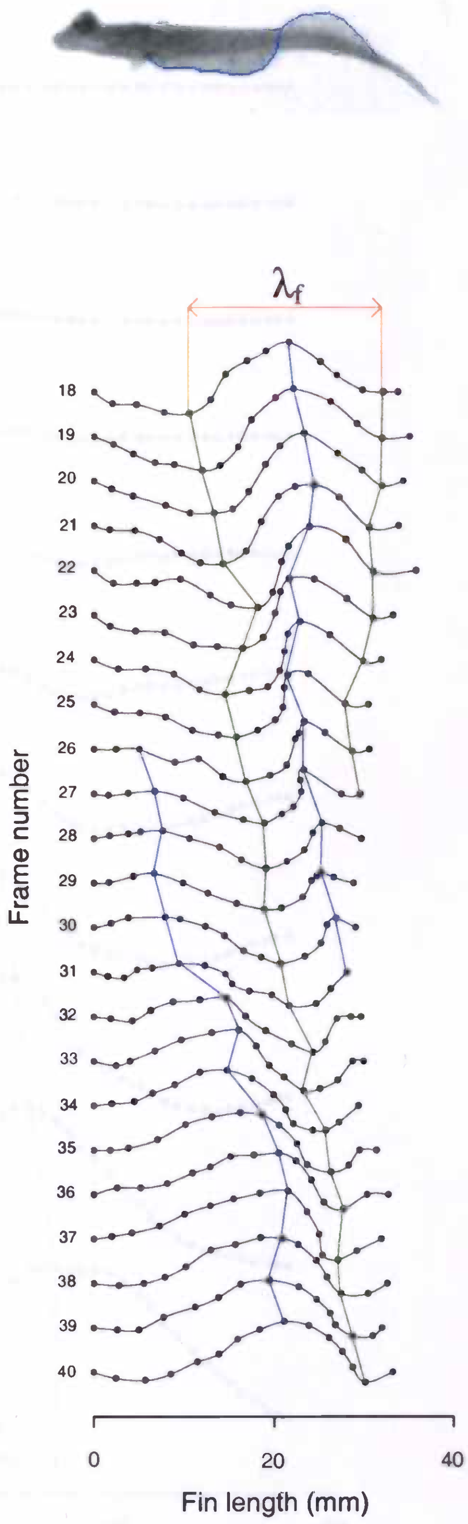


Figure 26. Fin lines of flounder 2, taken from successive pictures of a film fragment. The fin lines are shifted down over a defined distance to show wave crests running over the fin. Beginning of the fin is at the left-hand side and the end of the fin is at the right-hand side of the graph. The wave crests connecting the downward amplitude maxima are shown as green lines, and the upward ones as blue lines. The wave length λ_f of the fin line of frame 18 is shown by red lines but λ_f was calculated from the mean wave lengths of the frames with amplitude maxima.

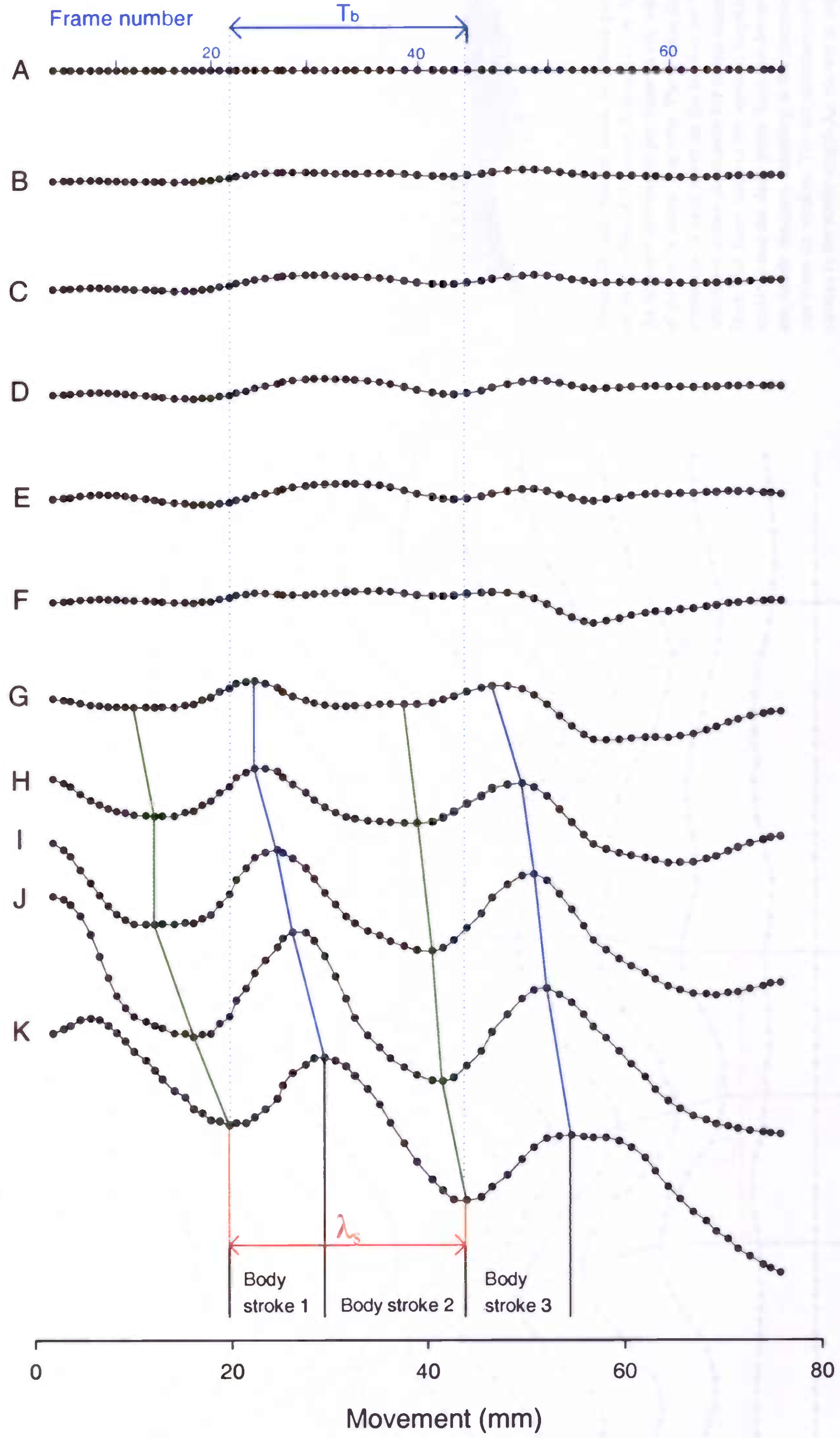
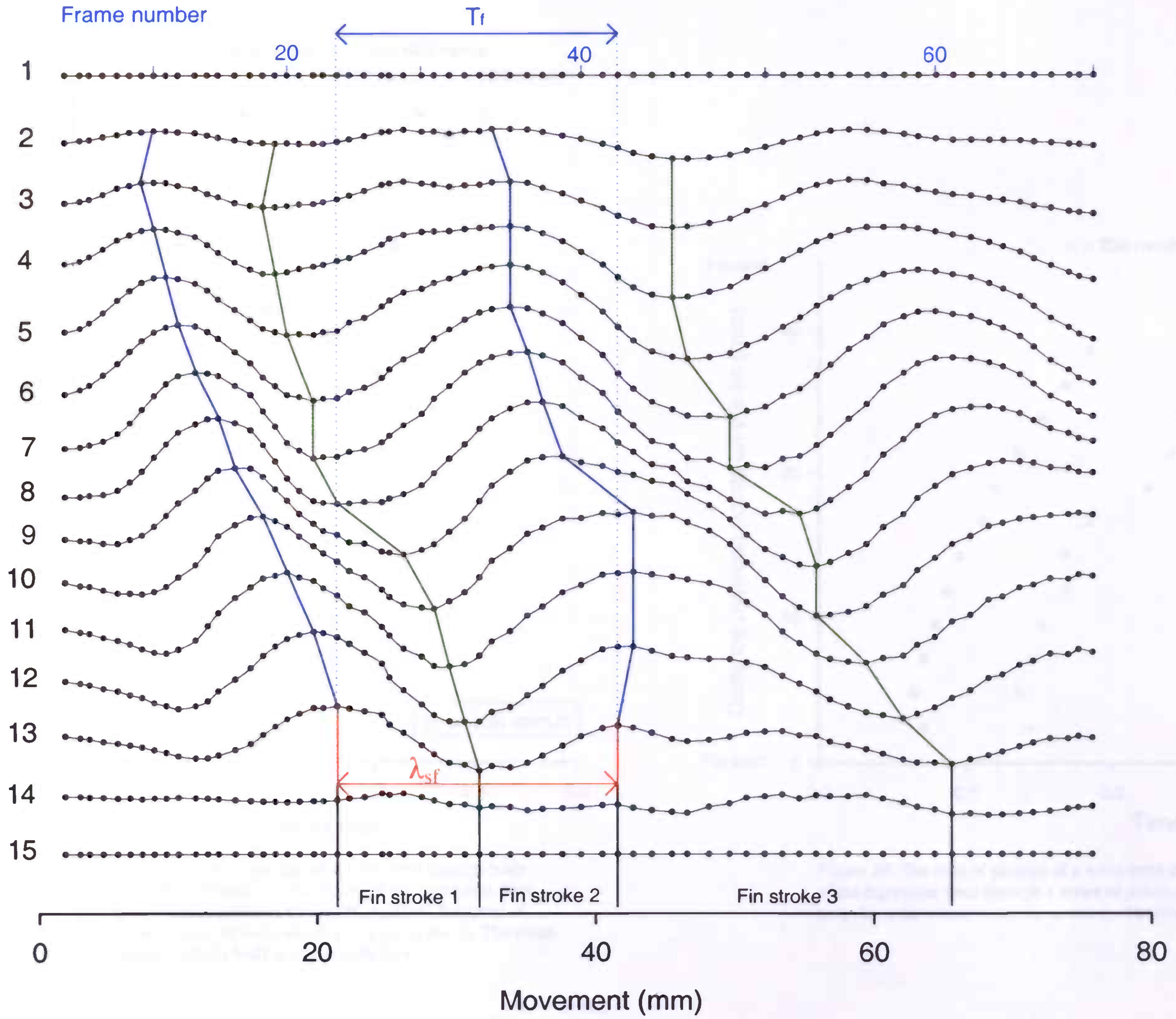


Figure 27. Movements made by eleven points A to K on the body line of flounder 2 in space. On the X-axis the forward movement per frame is set, with the tail point of frame 1 at zero. The Y-axis shows the amplitude of each point on the body line per frame, which are drawn separately for better convenience. Dark blue lines connect the upward amplitude maxima and the dark green lines the downward amplitude maxima, resulting in the presence of three complete body strokes. The displacement of two body strokes is the stride length λ_s, shown in red. The time T_b it takes to complete two body strokes is shown in blue.



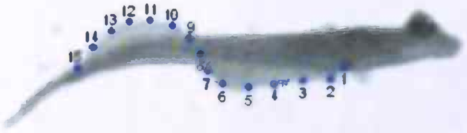


Figure 28. Movements made by fifteen points 1 to 15 on the fin line of flounder 2 in space. On the X-axis the forward movement per frame is set, with the end of the fin of frame 1 at zero. The Y-axis shows the amplitude of each point on the fin line per frame, which are drawn separately for better convenience. Dark blue lines connect the upward amplitude maxima and the dark green lines the downward amplitude maxima, resulting in the presence of three complete fin strokes. The displacement of two fin strokes is the stride length λ_{sf}, shown in red. The time T_f it takes to complete two fin strokes is shown in blue.

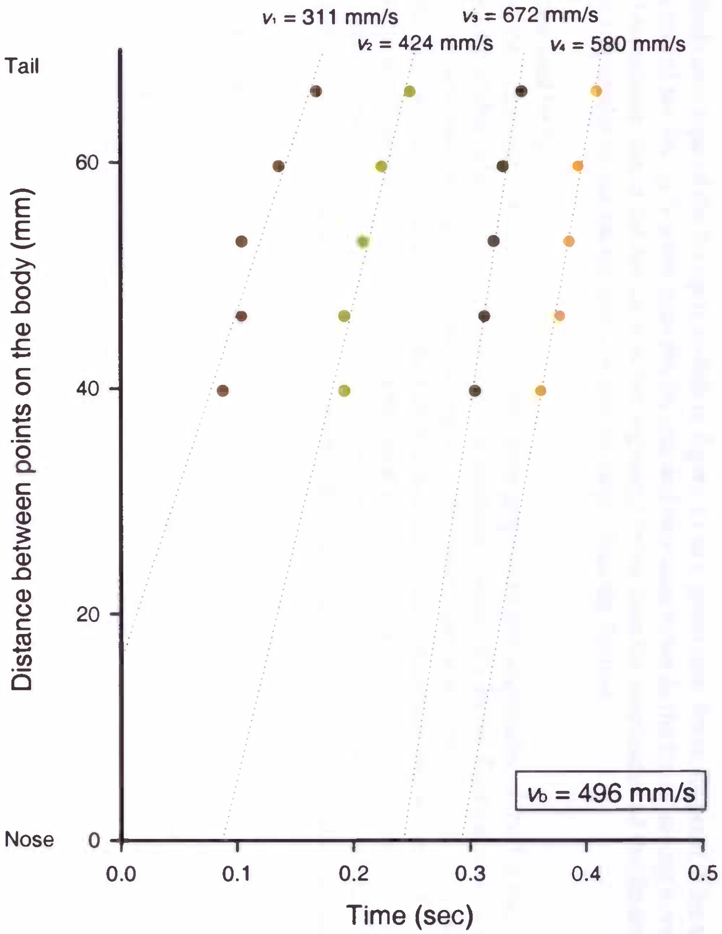


Figure 29. The time of passage of a wave crest through body points G to K of flounder 2. The slopes of the regression lines through a series of points in this graph represent the speed of successive propulsive body waves v_1, v_2, v_3, v_4 and v_5. The mean wave speed v_b of the body is given in the box.

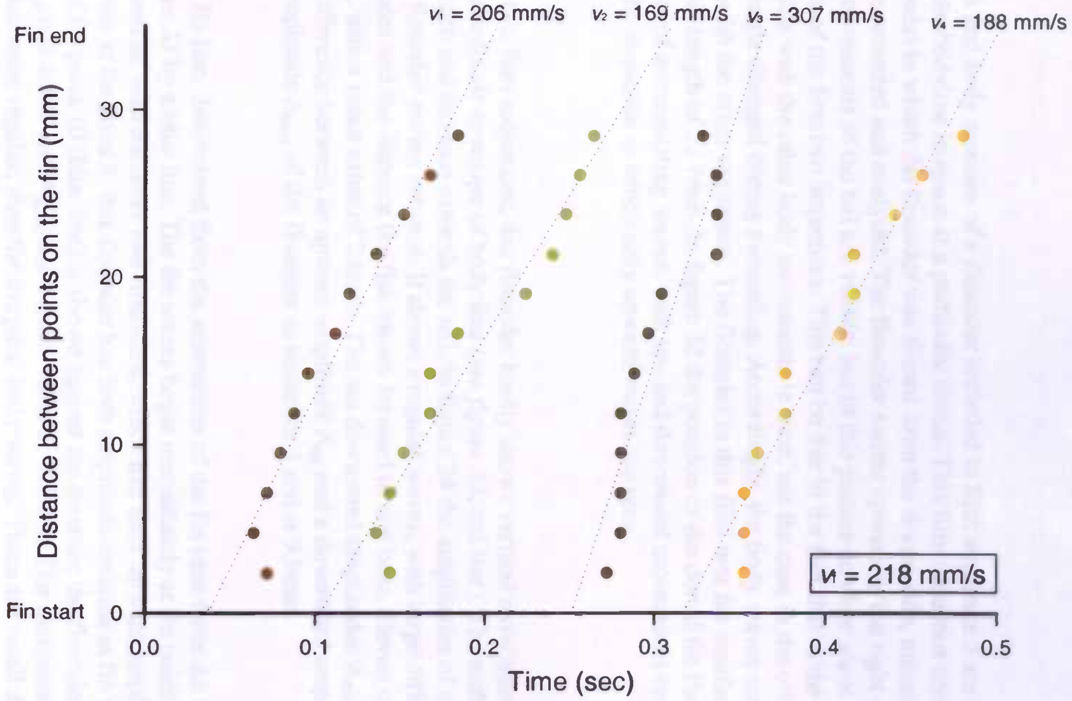


Figure 30. The time of passage of a wave crest through fin points 2 to 13 of flounder 2. The slopes of the regression lines through a series of points in this graph represent the speed of successive propulsive fin waves v_1, v_2, v_3, v_4 and v_5. The mean wave speed v_f of the fin is given in the box.

4.3 Film sequence 3

In figure 31 the swimming path and body motions of a flounder recorded in film sequence 3 are shown. Every line represents the position of the bodyline in space at a particular frame. This film sequence consists of 166 frames (time span of 1.32 seconds) in which the flounder was filmed from the dorsal side, meaning that only the movements of the dorsal fin are recorded and analysed. The flounder swims upward to the right under a body tilt angle around 45 degrees. The movements of the tail are visible, but in this picture no clear wave patterns can be seen, as shown by the flounders of the first two sequences. This can be due to the fact that in the figure (5.1.3) the tail movements are in one line with the other body movements in time, not the case in the other film sequences where the body tilt angle changed during swimming. Accordingly, the body waves can not be counted using figure 31, like was done with the other sequences. The flounder in this film was the smallest animal with a body length of 32.8mm and a fin length of 23.7mm. In figure 32 the position of the dorsal fin line of every frame is plotted in space. It shows a lot of accumulating waves, with up- and downward movements opposite to each other, except in the middle of the sequence in which only upward waves are seen.

4.3.1 Amplitudes

Body

Like the flounders in the other two film sequences, this flounder hardly shows vertical movement at the first part of its body, as depicted by the amplitude envelope of body line (*see figure 33*, red line). The undulations begin at about 50% of the total body length and increase towards the tail. In figure 34 the amplitudes of the tail (red line) are set against the distance the flounder moves forward. It shows irregular waves, with large differences in upward and downward amplitudes and the distance the fish swims forward in one beat. Eleven upward amplitudes A_{up} can be counted, with a mean value of 2.6mm. The ten downward amplitudes A_{down} have a mean value of -3.2mm. The largest difference between an upward amplitude A_{up} and a downward amplitude A_{down} of one beat gives the maximum amplitude A_{max} of the flounder in sequence 3 and is 9.9mm.

Fin line

The amplitude envelope of the fin line, determined from the subtraction of the fin base from the fin tip (*see* also section 3.6.1), is shown in figure 33 by a blue line. The fin waves begin immediately at fin point 2, but increase in height from fin point 5. In contrast with the other two flounders, which had their upward amplitudes at fin point 10 and their downward ones at fin point 6, this flounder has both amplitude maxima at fin point 10. In figure 34 the amplitude track of fin point 10 (blue line) is shown against the distance the flounder moves forward. The mean value of A_{up} is 2.4mm, and A_{down} has a mean value of -2.3mm. The maximum amplitude A_{max} is 5.9mm. The fin waves are more regular, than the irregular body waves. There are small differences in the height of the waves, but the speed of the waves does change, as seen in figure 34 between frames 88 till 102, where only one wave is present in a long distance. The body has at the same time such a long wave.

Fin tip

The amplitude envelope of the fin tip is visible in figure 33 as a green line. From fin point 2 the upward amplitude line of the fin tip is wider than the fin line and increases towards the back, having a wave in it. The downward amplitude line of the fin tip is in the beginning lower than the amplitudes of the fin line, but after fin point 5 the amplitudes of the fin tip increase and are larger than the fin line.

Body, fin line and fin tip

By plotting the amplitudes of the body line in the same graph with the amplitudes of the fin line, an indication is given about a possible relation between these two amplitudes (*figure 34*). In the figure is shown that the body makes ten complete waves, beginning and ending with an upward amplitude and that the fin makes eleven complete waves, beginning and ending with a downward amplitude. Generally, the waves of the fin and body have a pattern in which first the body has its amplitude maxima and a few frames later the fin. However, this is not the situation in all waves, as seen by frame 115 of the fin which has its amplitude maximum before the body it has, at frame 120. A wave later the pattern is re-established, by a shorter during wave of the body, than of the fin.

4.3.2 Wave lengths

Body

When swimming, the flounder shows a wave on its body beginning behind its stomach and travelling towards the tail. The length of one wave on the body is determined on basis of figure 35, in which several frames are plotted underneath each other. On top of the figure frame 9 is depicted, which shows a maximal upward amplitude. Further down, at frame 20, a downward amplitude maximum arises, and at the bottom of the figure, at frame 29, a second upward amplitude maximum is shown. The frames in between show a replacement of some points in the upward or downward direction relative to the frame before. By connecting these upward moving points and downward moving points, wave crests are made visible. The wave crests from upward movements appearing in blue and the wave crests of the downward moving parts of the tail beat cycle are shown in green. These wave crests indicate the waves on the body which are travelling backwards. The length of such a wave is determined from the distance between two upward respectively downward moving parts of the tail beat cycles. This is shown on the example of frame 9 in figure 35. A mean value was calculated from all the wave lengths determined per frame. This gave a mean wave length λ_b of the body of 15.2mm, meaning that one wave covers 46% of the total body length. Because the moving part of the body is about 50%, one wave is present at the body at once.

Fin

The length of the wave running down the fin is determined in the same way as done for the body. In figure 36 the fin lines of frame 15 to 31 are plotted underneath each other. On top of the figure the fin line of frame 15 is depicted, which shows a maximal upward amplitude at point 10. Further down, at frame 23, a downward amplitude maximum arises, and at the bottom of the figure, at frame 31, a second upward amplitude maximum is shown. By connecting these upward moving points and downward moving points, wave crests are made visible. The wave crests from upward movements appearing in blue and the downward moving parts of the fin wave cycle are shown in green. These wave crests indicate the waves on the fin which are travelling backwards. The length of such a wave is determined from the distance between two upward respectively downward moving parts of the fin wave cycles. This is shown on the example of frame 15 in figure 36. A mean value was calculated from all the wave lengths per frame. The mean wave length λ_f of the fin was 11.2mm, meaning that one wave covers 54% of the total fin length. Because the whole fin is taking part in the swimming motions, two waves appear at the same time on the fin. Comparison of the wave length λ_f of the fin with the body length, gave 34% coverage of one fin wave at the total body length, which is less than the body wave coverage.

4.3.3 Stride lengths and wave periods

Body

The movement per body point in space and time is shown in figure 37. The body points are plotted separately and placed under each other for better clarity. The figure shows the vertical movement of each point at the distance the flounder is swimming forward. Frame numbers are put above the graph, in order to show the time period. Because a data smoothing had taken place, the first two frames and the last two frames are left out and are therefore not further analysed. The first body points show little and irregular amplitude differences, but from body point E to K waves are visible. The upward and downward amplitude of the body points are connected, which results in the appearance of nineteen body strokes. In the figure, dark blue lines mark the upward amplitudes, while the green lines point out the downward ones.

The wave crests are most of the times straight, but some do have a kink in it. Further is seen that some wave crests have an amplitude maximum at different body points at the same moment, like with the upward wave crest 7, which has an amplitude maximum at body points E to I all in frame number 69. The wave crests are at different distances from each other, partly due to changing wave speeds.

The stride length λ_s is given by the displacement of the flounder in two body strokes, or one wave, and is shown in the figure for body strokes 3 and 4 of the tail. The mean stride length λ_s of the body is calculated by the mean of all sets of body strokes on the tail and has a value of 6.8mm. This corresponds to 21% of the total body length, meaning that in one beat the flounder swims forward about one fifth of its body length.

The wave period T_b of the body waves was calculated as the time it took to complete one wave, or two body strokes, shown in the figure by the bright blue line. As with the mean stride length λ_s, the mean wave period T_b is determined by the mean of all sets of body strokes on the tail. Accordingly, the mean time the flounder completed one tail beat, is 0.12 seconds. The wave frequency F is the inverse of T, meaning that there are 8.6 tail beats per second.

Fin

In figure 38 the fin points are plotted separately and placed under each other for better clarity. The figure shows the vertical movements of each point at the distance the flounder is swimming forward. The frame numbers are set above the graph, in order to show the time period. Because a data smoothing had taken place, the first two frames and the last two frames are left out and are therefore not further analysed. From fin point 2 there are some small waves visible, but large waves appear from fin point 5 to 14. The waves of fin point 2 to 4 do not fit in the latter waves, good visible in the first frames of the film, and are therefore not seen as real waves. In the amplitude envelope graph (*figure 33*) this fin point 5 was already seen as the part of the fin from where larger amplitudes were found. The upward and downward amplitudes of each fin point are connected, which results in the appearance of twenty complete fin strokes. Dark blue lines in figure 38 mark the upward amplitudes, while the green lines point out the downward ones.

The stride length λ_{sf} of the fin is given by the displacement of the flounder in two fin strokes, or one fin wave, and is shown in the figure for fin stroke 3 and 4 of fin point 14. The mean stride length λ_{sf} of the fin is calculated by the mean of the individual stride lengths of all waves and has a value of 6.7mm. This corresponds to 28% of the total fin length and 20% of the body length, meaning that in one fin beat the flounder swims forward one fifth its body length. This is comparable with one tail beat of the body, which has also a swimming movement of one fifth of the body length.

The wave period T_f of the fin waves was calculated as the time it took to complete one wave, or two fin strokes, shown in the figure by the bright blue line. Like the mean stride length λ_{sf}, the mean wave period T_f is determined by the mean of the waves on all fin points. Accordingly, the mean time the flounder completed one fin beat, is 0.11 seconds. The wave frequency F is the inverse of T, meaning that there are 8.9 fin beats per second.

4.3.4 Wave speeds

Body

The speed v_b at which a wave travelled down the body, was calculated using the wave crests along the body that described the body strokes (*see figure 37*). The time a wave crest passed through body points E to K is indicated in figure 39. A linear regression line was fitted through series of points of a wave crest. The slope of these linear regression lines represents the speed by which the waves travel down the body. A steep slope indicates a fast wave and a gentle slope a slow wave. The speeds of each wave crest are depicted above the graph and the mean speed of these body wave crests has a value of 444mm per second. This is identical with 13.5 body lengths per second.

Fin

The wave crests along the fin that described the fin strokes (*see figure 38*), were used to calculate the wave speed v_f at which a wave travelled down the fin. The time a wave crest passed through fin points 5 to 14 is indicated in figure 40. A linear regression line was fitted through series of points of a wave crest. The slope of these linear regression lines represents the speed by which the waves travel down the fin. The speeds of each wave crest are depicted above the graph and the mean speed of these fin wave crests has a value of 107mm per second. This is identical with 4.5 fin lengths per second and 3.2 body lengths per second.

4.3.5 Mean forward speed

During 166 frames the fish travelled a distance of 76 millimetres. Total filming time was 1.32 seconds. The mean forward speed U was calculated as the distance divided by the filming time. This gave a speed of 58mm per second, identical with 1.8 body lengths per second.

4.3.6 Swimming efficiency

Body

The efficiency of the swimming technique employed by the body was calculated as the division of the mean forward speed by the mean speed of the body waves. This gave a value of 0.13. The higher this value, the more efficient the propeller technique is.

Fin

To calculate the efficiency of the fin propulsion the mean forward speed of the flounder was divided by the mean speed of the fin waves. A value of 0.54 was computed.

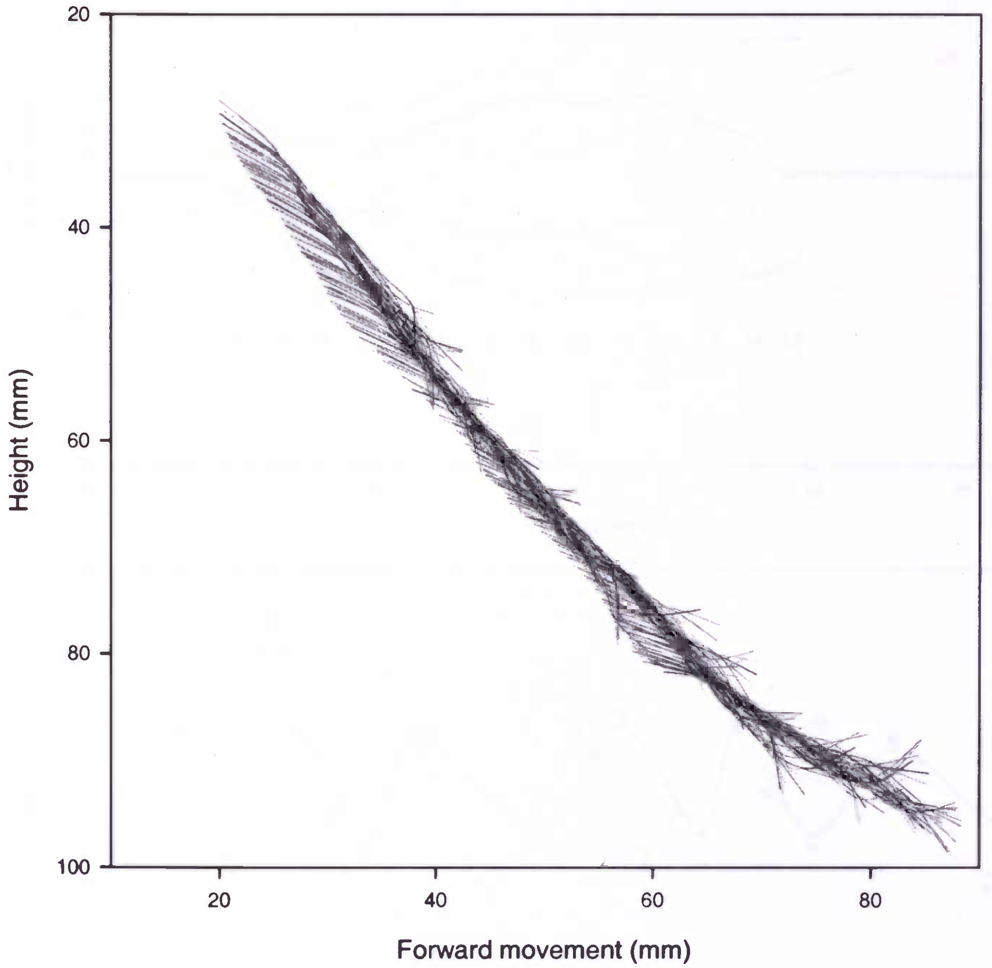


Figure 31. The swimming path and body motions of flounder 3. Every line represents the position of the body line in space at a particular frame. The fish is swimming to the left, meaning that its head is at the left-hand side and its tail is on the right-hand side of the lines.

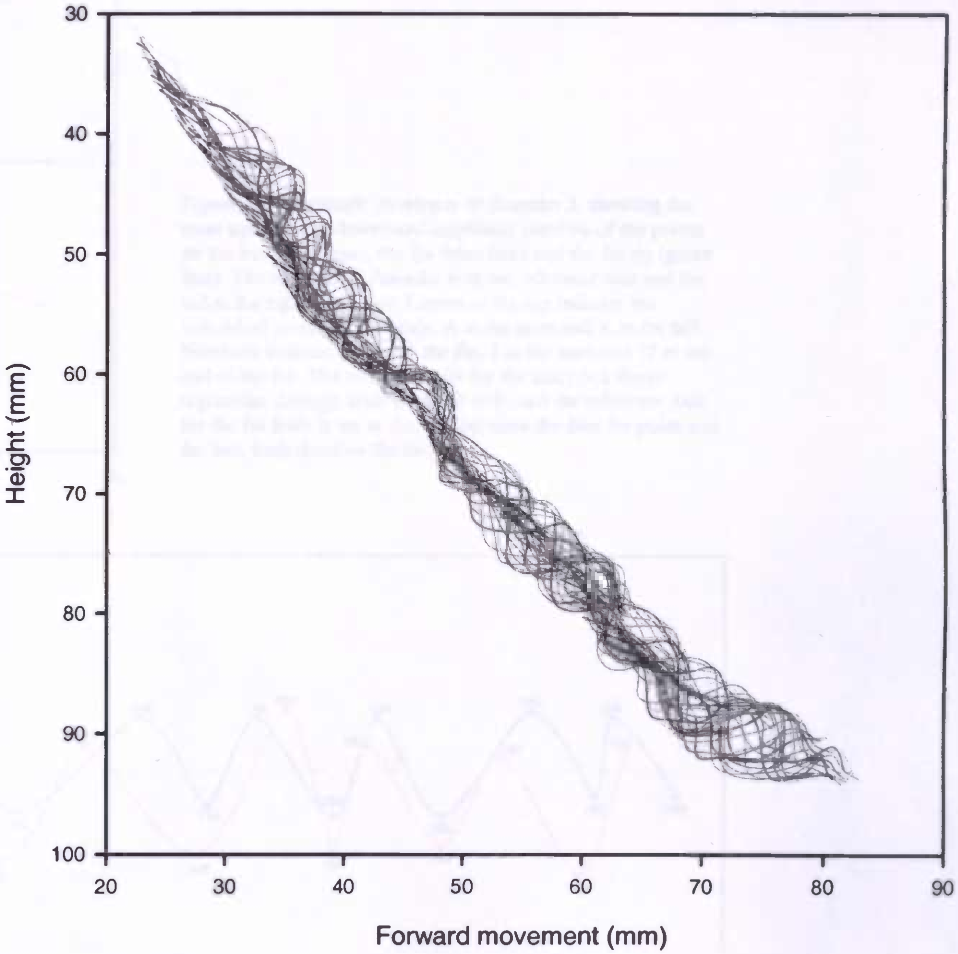


Figure 32. The movements of the fin of flounder 3. Every line represents the position of the edge of the fin in space at a particular frame. For the analysis of the fin, the fin base was subtracted from these lines. The beginning of the fin is at the left-hand side and the end is at the right-hand side of the lines.

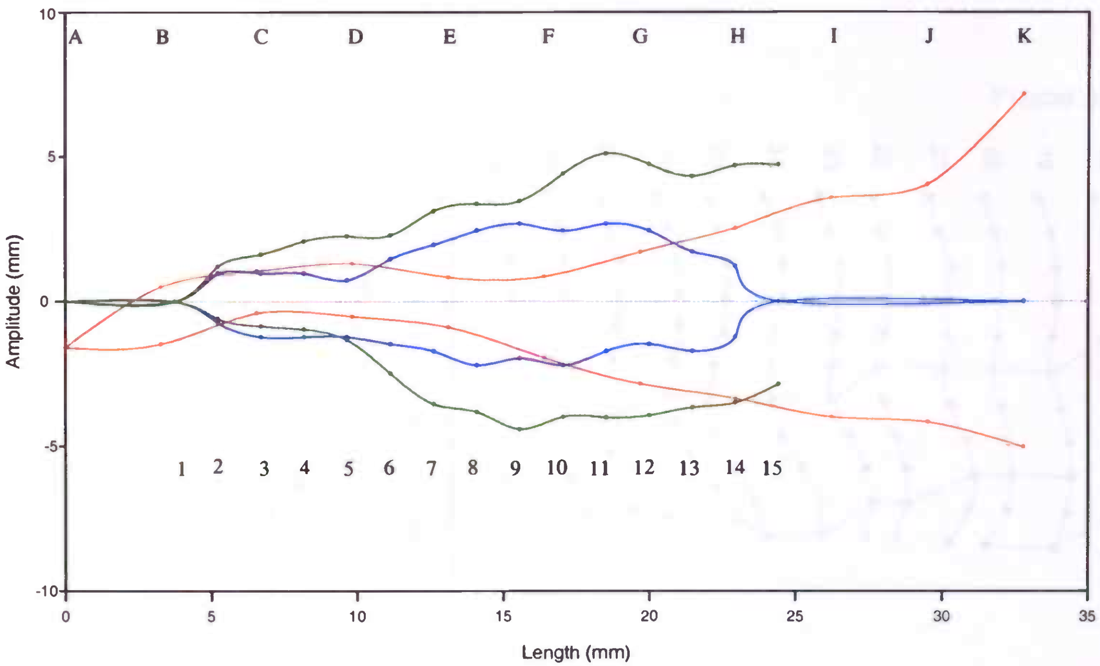


Figure 33. Amplitude envelopes of flounder 3, showing the most upward and downward amplitude maxima of the points on the body (red line), the fin (blue line) and the fin tip (green line). The nose of the flounder is at the left-hand side and the tail at the right-hand side. Letters at the top indicate the individual points on the body, A at the nose and K at the tail. Numbers indicate points on the fin, 1 at the start and 15 at the end of the fin. The reference axis for the body is a linear regression through body points B to E, and the reference axis for the fin lines is set as the line between the first fin point and the last, both fixed on the body.

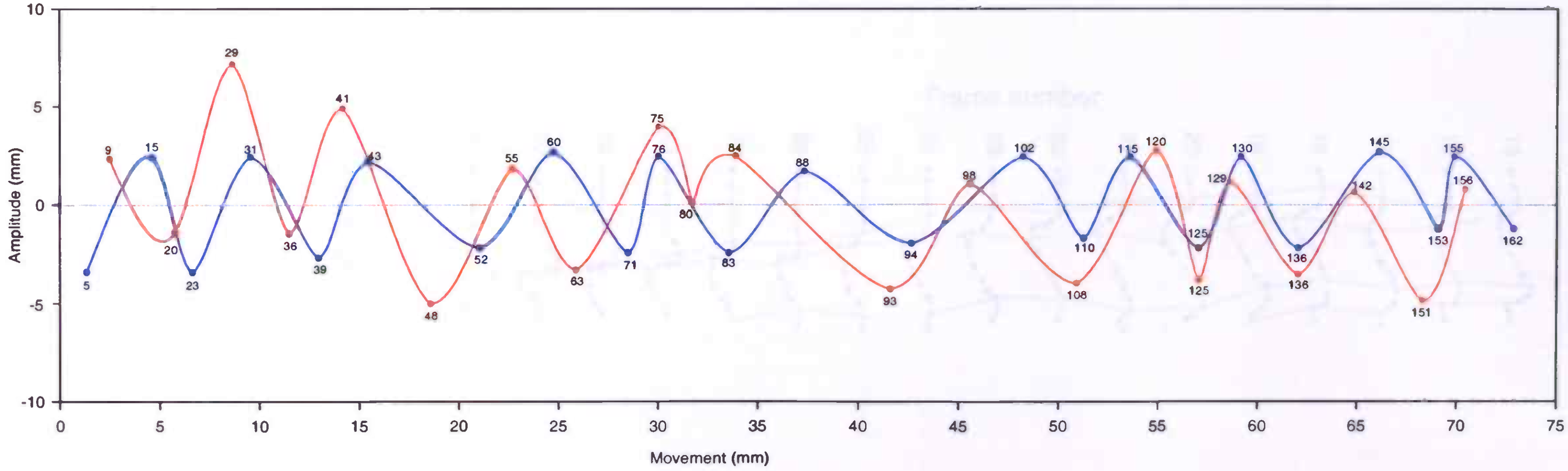
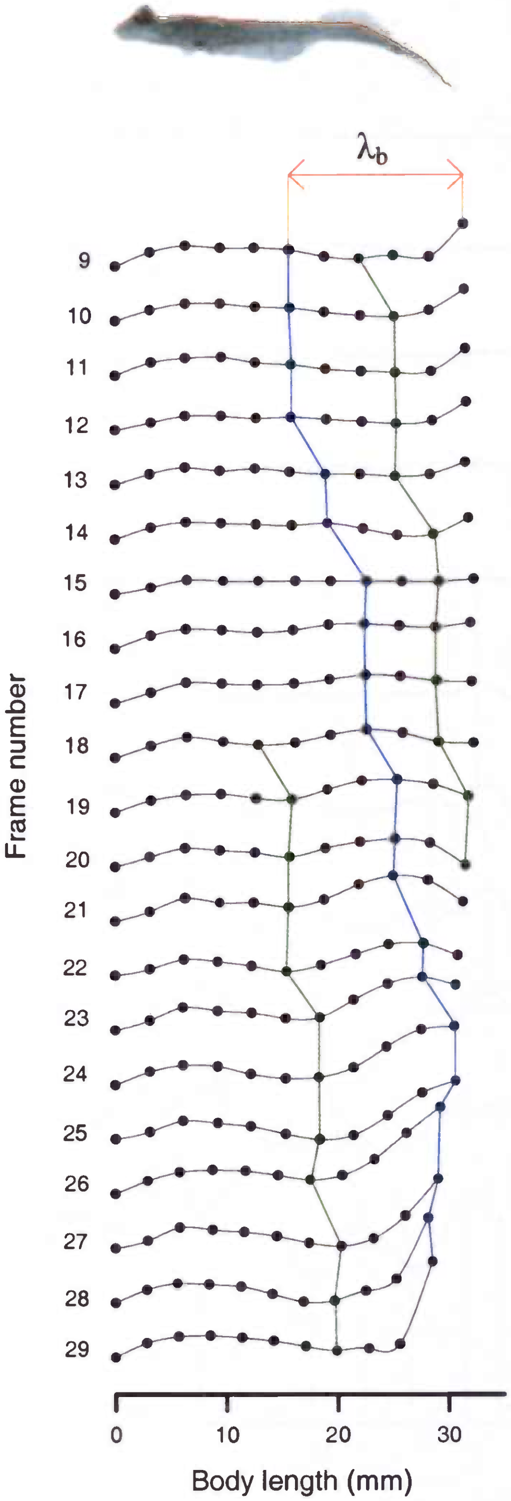


Figure 34. The upward and downward amplitude maxima of flounder 3 of the tail of the body (red line) and of fin point 10 (blue line) set against the movement of the flounder. Numbers close to the amplitude maxima indicate the frame number in which it appears. The reference axis for the body is a linear regression through body points B to E, and the reference axis for the fin lines is set as the line between the first fin point and the last, both fixed on the body. The movement of the flounder was set at zero on frame number 1.



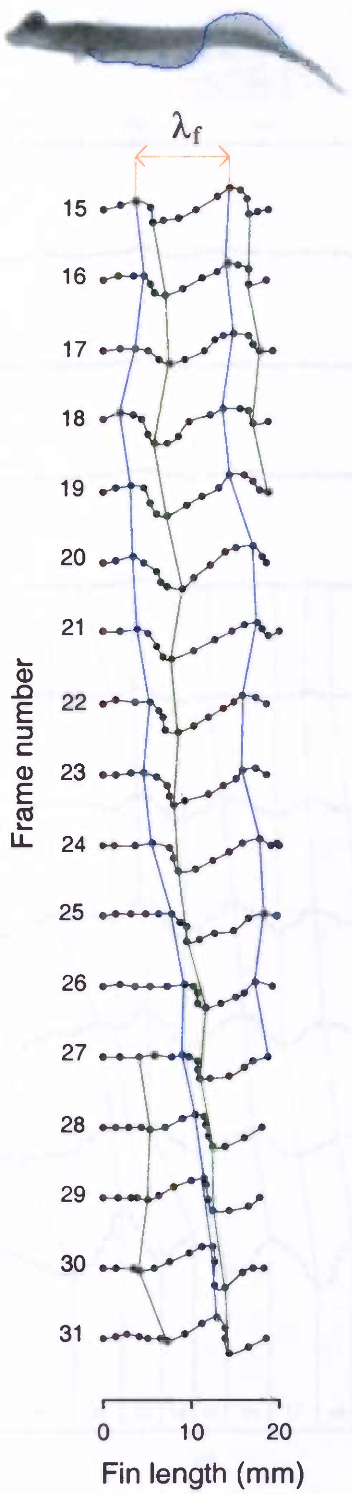


Figure 35. Body lines of flounder 3, taken from successive pictures of a film fragment. The body lines are shifted down over a defined distance to show wave crests running over the body. Head of the flounder is at the left-hand side and the tail at the right-hand side of the graph. The wave crests connecting the downward amplitude maxima are shown as a green line, and the upward amplitude maxima are connected with blue lines. The wave length λ_b of the body line of frame number 9 is shown by red lines but λ_b was calculated from the mean wave lengths of the frames with amplitude maxima.

Figure 36. Fin lines of flounder 3, taken from successive pictures of a film fragment. The fin lines are shifted down over a defined distance to show wave crests running over the fin. Beginning of the fin is at the left-hand side and the end of the fin is at the right-hand side of the graph. The wave crests connecting the downward amplitude maxima are shown as green lines, and the upward ones as blue lines. The wave length λ_f of the fin line of frame 15 is shown by red lines but λ_f was calculated from the mean wave lengths of the frames with amplitude maxima.

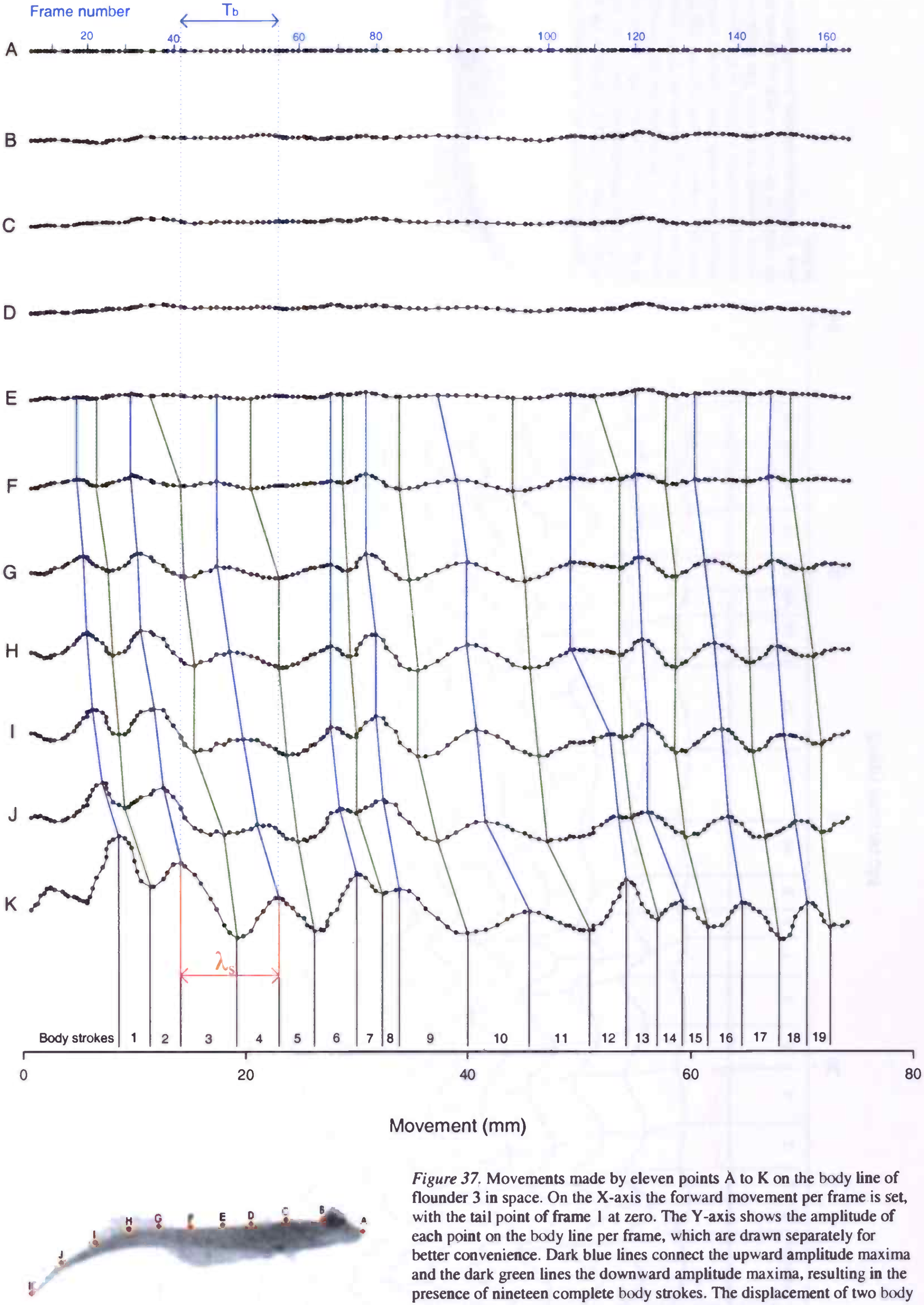
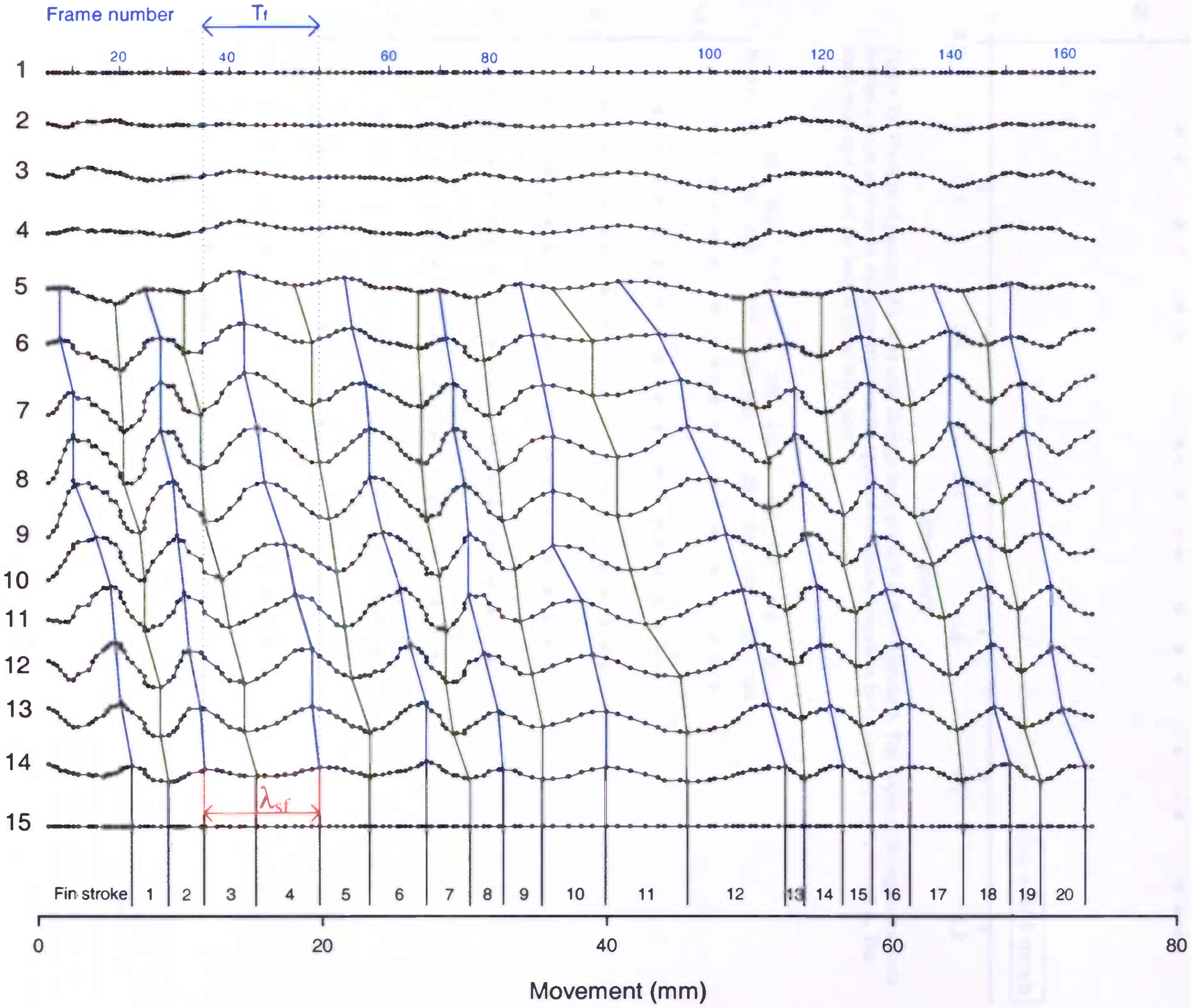


Figure 37. Movements made by eleven points A to K on the body line of flounder 3 in space. On the X-axis the forward movement per frame is set, with the tail point of frame 1 at zero. The Y-axis shows the amplitude of each point on the body line per frame, which are drawn separately for better convenience. Dark blue lines connect the upward amplitude maxima and the dark green lines the downward amplitude maxima, resulting in the presence of nineteen complete body strokes. The displacement of two body strokes is the stride length λ_s, shown in red. The time T_b it takes to complete two body strokes is shown in blue.



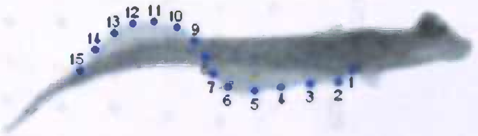


Figure 38. Movements made by fifteen points 1 to 15 on the fin line of flounder 3 in space. On the X-axis the forward movement per frame is set, with the end of the fin of frame 1 at zero. The Y-axis shows the amplitude of each point on the fin line per frame, which are drawn separately for better convenience. Dark blue lines connect the upward amplitude maxima and the dark green lines the downward amplitude maxima, resulting in the presence of twenty complete fin strokes. The displacement of two fin strokes is the stride length λ_{sf}, shown in red. The time T_f it takes to complete two fin strokes is shown in blue.

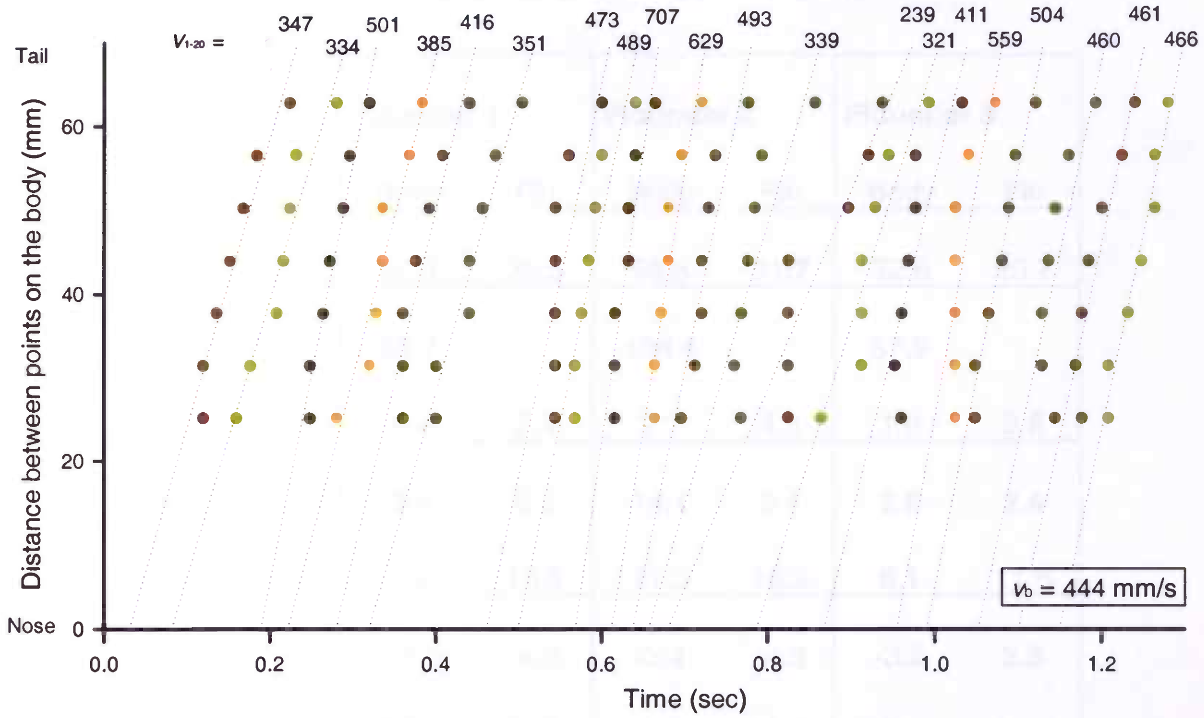


Figure 39. The time of passage of a wave crest through body points E to K of flounder 3. The slopes of the regression lines through a series of points in this graph represent the speed of successive propulsive body waves v_1, v_2, v_3, v_4 and v_5. The mean wave speed v_b of the body is given in the box.

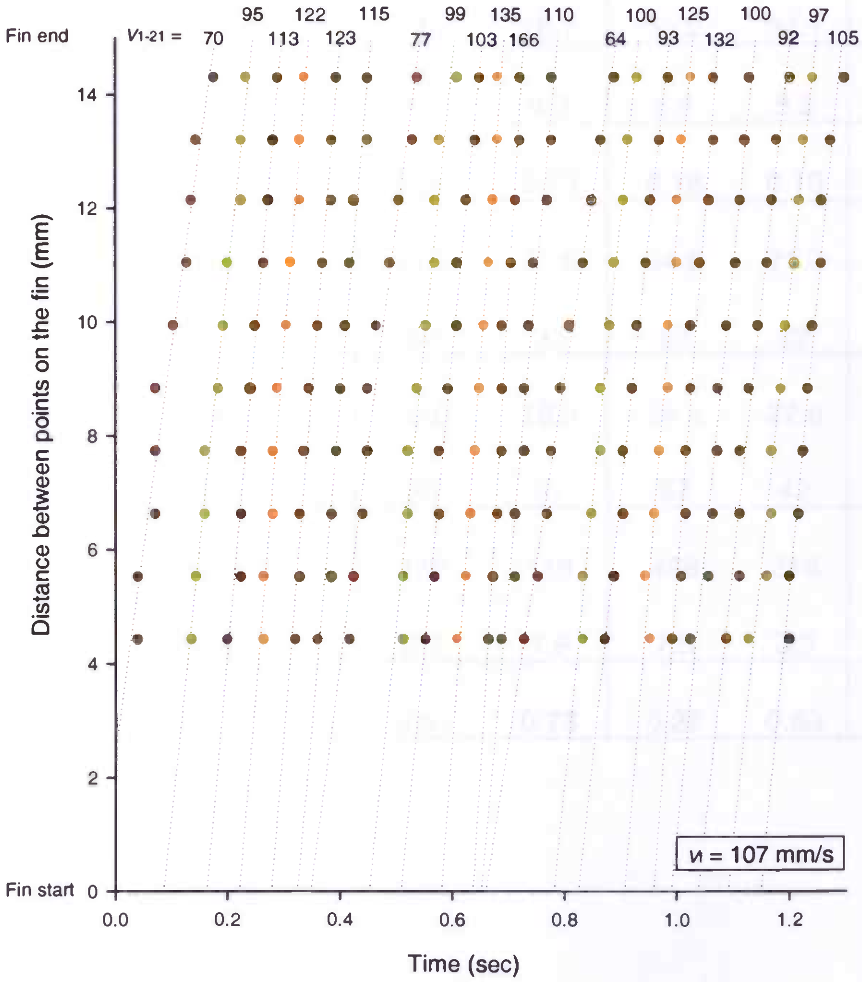


Figure 40. The time of passage of a wave crest through fin points 5 to 14 of flounder 3. The slopes of the regression lines through a series of points in this graph represent the speed of successive propulsive fin waves v_1, v_2, v_3, v_4 and v_5. The mean wave speed v_f of the fin is given in the box.

Table 1
All values of the various parameters describing the kinematics of the three swimming flounders. The parameters are given in mm and as a proportion (%) of body or fin length (L).

Parameter		**Flounder 1**		**Flounder 2**		**Flounder 3**	
		Body	Fin	Body	Fin	Body	Fin
Length	(mm)	62.8	35.5	66.3	31.7	32.8	20.7
U	(mm s^{-1})	86.7		136.4		57.9	
	(L s^{-1})	1.4	2.4	2.1	4.3	1.8	2.8
A_{up}	(mm)	-5.6	5.5	14.1	5.4	2.6	2.4
	(%L)	9.0	15.5	21.3	16.9	8.1	11.6
A_{down}	(mm)	-14.6	-4.0	-3.4	-4.8	-3.2	2.3
	(%L)	23.3	11.2	5.1	15.2	9.6	10.9
A_{max}	(mm)	10.5	10.2	20.7	10.8	9.9	5.9
	(%L)	16.7	28.7	31.2	34.1	30.2	28.5
F	(Hz)	4.5	4.3	5.6	5.2	8.6	8.9
T	(s)	0.22	0.23	0.18	0.19	0.12	0.11
λ_b / λ_f	(mm)	31.6	21.6	34.8	21.0	15.2	11.2
	(%BL)	50	35	53	32	46	34
λ_s / λ_{sf}	(mm)	19.0	19.5	24.4	27.8	6.8	6.7
	(%BL)	30	31	37	42	21	20
v	(mm s^{-1})	170	119	496	218	444	107
	(BL s^{-1})	2.7	1.9	7.5	3.3	13.5	3.2
U/*v*		0.51	0.73	0.27	0.63	0.13	0.54

5 Discussion

The aim of this project was to investigate the kinematics of the free swimming of juvenile flounders and in particular the relation between the two propulsion systems, which are the body and the big fins. As already mentioned free swimming does not occur very often in flounders. However, in routine observations it was already seen that there is high variation within the swimming towards food parts. In the following the three analysed film sequences will be compared and discussed for each of the kinematic parameters separately and possible conclusions will be drawn. Further, a relation between the body and fin will be given, the gained results will be compared to data of other flat fish species and to those of round fishes. The used methods will be discussed and finally an attempt will be made for an interpretation of the way of lift production of the flounders. For better convenience, the performing flounders will be named after the sequence numbers (respectively flounder 1, flounder 2 and flounder 3) when discussed.

5.1 Amplitudes

There is a large difference in the directions of the vertical movements of the body in the three film sequences (*figure 41 A*). In this figure the most upward and most downward amplitudes of the body (at the tail) are put next to each other for comparison. The fin shows far less variation in amplitude ranges (*figure 41 B*). The upper body line was taken as reference axis for the amplitudes of the body in stead of the mid line (see section 5.8). However, even when the reference axis is shifted down distinct variations are seen in the direction of the vertical movements of the tail between the flounders.

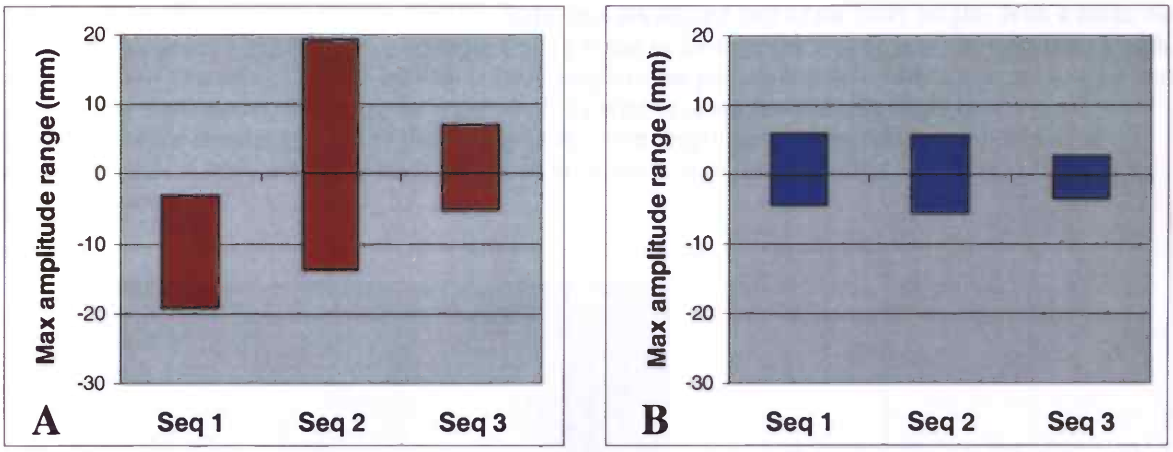


Figure 41. Maximum amplitude ranges of three analysed sequences of free swimming of flounders. *A*: tail beat amplitudes. *B*: amplitudes of fin movements.

Flounder 1 has a dominant downward amplitude course, in which the upward amplitudes do not cross the upper body line. For that whole sequence the upward and downward amplitudes stay at the same level. This stands in contrast to flounder 2 which has large upward amplitudes at the beginning and decreasing amplitude size towards the end of its swimming performance. Flounder 3 shows an almost symmetrical amplitude range with relatively regular deviation in vertical direction. However, all three flounders also swim in strongly differing tracks (*see figure 42 A-C*). Flounder 1 is swimming from obliquely ascending to a more horizontal position, and has accordingly a declining slope. Flounder 2 is the opposite of flounder 1, with a strong inclining slope at the beginning and a straight vertical direction at the end. Flounder 3 instead is swimming in a straight direction. It might be possible that the differences in amplitude size and direction are an effect of steering. However, more data are needed to test this suggestion.

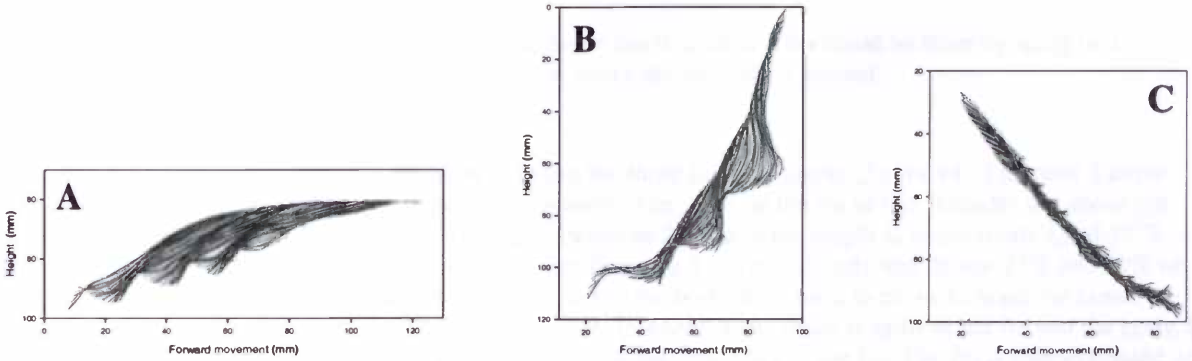


Figure 42. The swimming tracks of the three flounders. *A*: Sequence 1 has a declining slope. *B*: Sequence 2 has an inclining slope. *C*: Sequence 3 with a steady slope.

Because the fin is attached to the body, the body movements should add to the movements of the fin. To test this idea, data of the fin base as well as data of the fin tip were taken as described in section 3.3. The figures 13, 23 and 33 show the amplitude envelopes of all three analysed lines on the fish. In all three sequences the amplitudes of the fin tip are larger than those of the fin line, indicating that the fin tip does describe the body movements. Subtracting the fin base of the fin tip shows that the fin undulates independently from the undulations of the body and that it is not just an extension of the body.

5.2 Wave lengths

In all three flounders the wave lengths λ_b of the body lines are around half of the body length. With a mean wave length λ_b for flounder 1 of 50%, λ_b for flounder 2 of 53% and λ_b for flounder 3 of 46% of the total body length (*see figure 43*). Correlating λ_b to the individual body length of the performing fishes leads towards a weak trend that the larger the flounder, the larger the wave length λ_b relative to the body length might be.
Comparison of the undulating parts of the body with the wave length λ_b indicates that for all performing flounders there is at least one whole wave present at the body at once (respectively 1.2, 1.1 and 1.0 waves for flounder 1,2 and 3).

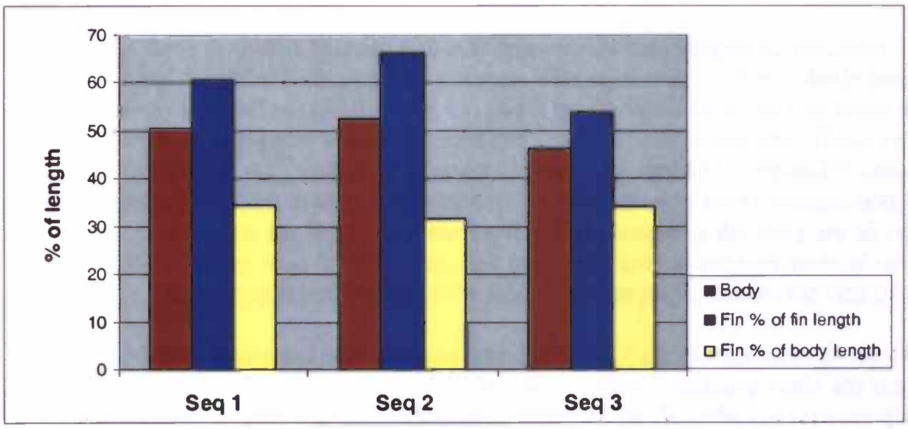


Figure 43. The wave lengths of undulating body λ_b and fin λ_f in swimming performance of flounders relative to the body length (red and yellow bars), respectively the length of the fin (blue bars) of the performing flounder.

The length of the waves λ_f on the fin is more or less the same for all three flounders. For flounder 1 λ_f is 34% of the total body length, for flounder 2 λ_f is 32% and for flounder 3 λ_f is 34% of the total body length (*see figure 43*). These values indicate that a fin wave is about one third of the body length of the flounders. From all three flounders the whole fin is involved in the undulations. With the mean wave length in percentage of the fin length an indication is given about the amount of waves present at the same time on the fin. Flounder 1 has a wave length of 61% of the fin length, flounder 2 66% and flounder 3 54 % of the fin length (*see figure 43).*
Accordingly, all flounders have a whole wave and a large part of the next wave present at one time on the fin; 1.6 waves on the fin for flounder 1, 1.5 waves for flounder 2 and flounder 3 has 1.9 waves on its fin at once. When looking at these data, it is striking, that λ_f of the three flounders are about the same size, but in flounder 3 there are 23% more waves present on the fin than in the other two flounders. A possible explanation for this difference might be the fact that from flounder 3 the dorsal fin is analysed, which is about 35% longer than the anal fin analysed in flounder 1 and 2. Because of this longer fin, more waves can be present at the same time. An interesting idea is if the two fins were undulating in phase, this would mean that the dorsal fin first starts undulation and that the anal fin follows when the wave on the dorsal fin arrives at the same height as the beginning of the anal fin. The movements of both large side fins should be investigated at the same time to learn

more about the coordination of the propelling systems of the flounders. This could be done by using two synchronised cameras or installing a mirror below or above the swimming animal.

5.3 Stride lengths

The stride lengths λ_s respectively λ_{sf} do differ between the three film sequences (*figure 44*). Flounder 1 move forward about 30% of its own body length per body wave. The wave on the fin of this flounder has about the same stride length λ_{sf} with 31 % of the body length. Flounder 2 has a stride length λ_s respectively λ_{sf} of 37 % body length for the body line, and 42% for the fin. For flounder 3 $\lambda_{s(f)}$ of the body and fin are 21% and 20% of the body length respectively. Because the fin is attached to the body, they have to move forward the same distance. However, especially for flounder 2, there are differences in the stride lengths of the fin and the body. It is possible to think that a difference can appear, because of the flexibility of the fin. The fin is able to expand and shrink due to the large amount of fin rays (Gesser, R; pers. comm.). This can be an explanation for the found differences in stride lengths of the body and fin of flounder 1 and 3, but it can not explain the large difference of 5% for flounder 2, even not when the measuring inaccuracies are taken into account. Therefore there must be another possible explanation for this effect which could not be detected in this study.

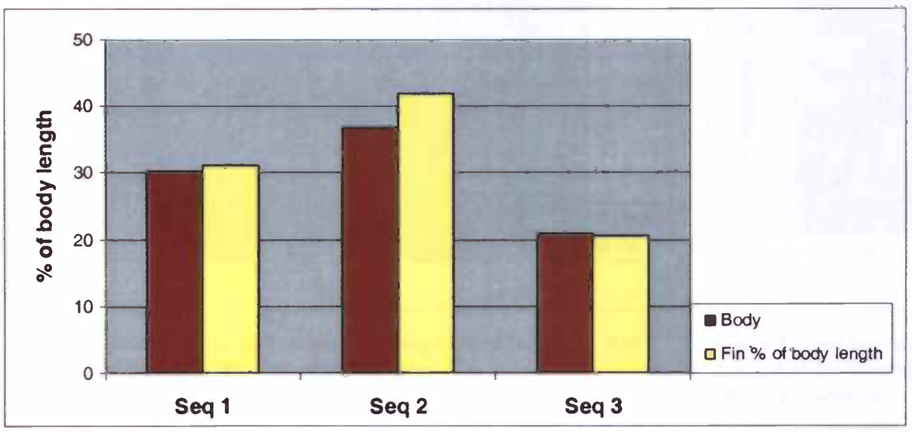


Figure 44. The stride lengths λ_s of body (red bars) and λ_{sf} of fin (yellow bars) in swimming performance of three flounders relative to the body length of the performing individual.

Between the three flounders there is also a difference of stride lengths λ_s. Flounder 2 travels the longest distance per tail beat and flounder 3 the smallest distance. This coincides with their body lengths; flounder 2 is the largest and flounder 3 the smallest (*see figure 45 A*) and it could therefore mean that there might be a relation between the body length of a flounder and the force it can produce with its tail beat. However, for the size of the maximum amplitudes A_{max} and for the forward swimming speed U comparable situations are seen (*see figure 45 B*). It is therefore difficult to conclude which difference between the flounders, body length, size of amplitude or motivation to swim, has the most influence on the stride length or that they are all related. Further research with only one difference between the flounders and more data should explain more about the relations. But even than other factors like the individual health of the flounders can play a role in the size of the stride length λ_s.

When looking at the patterns of the wave crests (*figure 5.7 e.g.*) differences in the characters of the waves are visible. Within one wave cycle variations in the wave speed *v* and amplitude are present. These irregular patterns of the wave crests indicate that the undulatory system of the flounders is very complex.

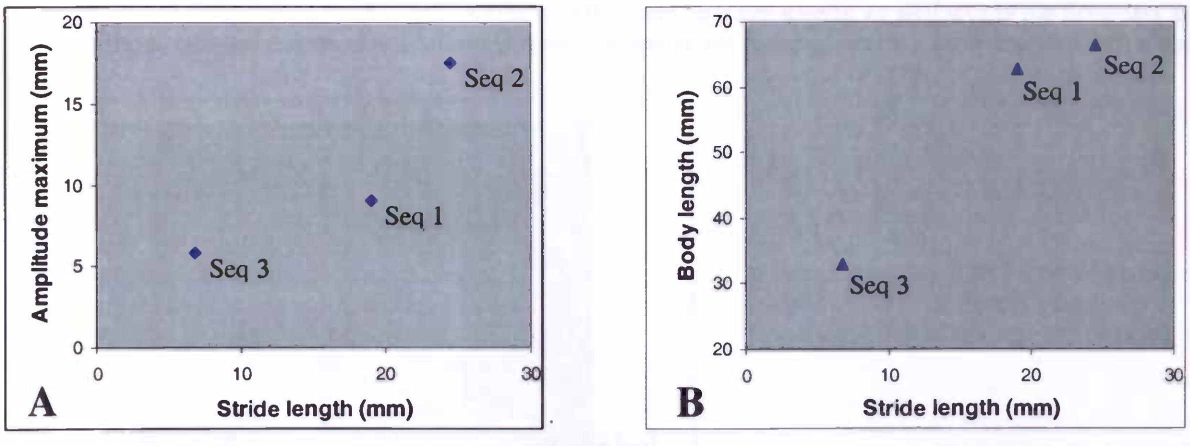


Figure 45. The relation between the stride length λ_s and the (*A*) maximum amplitudes A_{max} respectively (*B*) the body lengths of the swimming of three individual flounders in the three film sequences.

5.4 Frequency

Frequencies F of tail and fin within flounders are close to each other, differing in about 5 % (*see figure 46*). Flounder 1 has a frequency F of 4.5 for the tail and 4.3 for the fin, flounder 2 has respectively 5.6 and 5.2 for tail and fin and flounder 3 has a frequency F of 8.6 for tail and 8.9 for fin. However between the flounders there is a strong difference in frequency F. Flounder 3 has a frequency F which is twice as large as that of flounder 1. When looking at the body size of the flounders and the forward speed U (*see table 1 and figure 47*), no direct correlation appears. For round fishes a straight relation had been shown between the frequency F and the forward speed, in the way that the faster the forward swimming speed U the higher the frequency F (Videler, 1993). It is however possible that such a strong relation does not occur in flat fishes. Webb (2002) found in adult plaice also no indication that the frequency F of the tail beat is related to swimming speed U. Other factors like the different swimming situations or individual preferences of the flounders might influence the frequency F. To investigate this, standardized experiments with one individual in a flow channel might be useful.

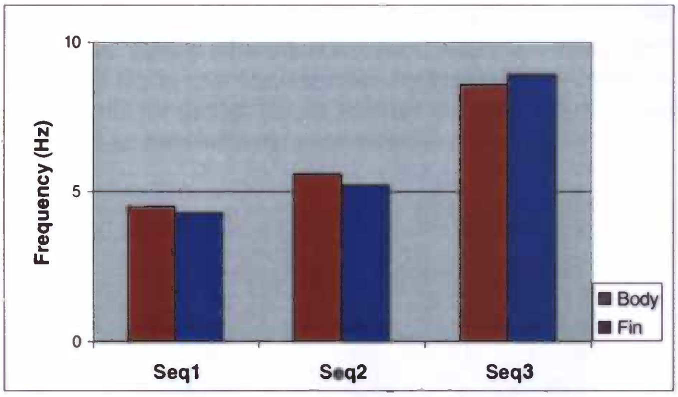


Figure 46. Wave frequencies F in free swimming of three flounders. Red bars: tail beat frequency. Blue bars: fin frequency.

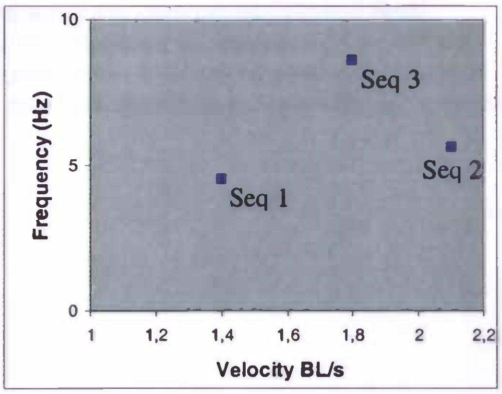


Figure 47. Tail beat frequencies F plotted as a function of the forward speed U (expressed in body lengths per second).

5.5 Wave speeds

Comparison of the wave speeds v of the fin and of the body per flounder shows that the speed of the wave running down the body is higher than that of the wave running down the fin (*see figure 48*). Flounder 1 has a body wave speed v of 170 mm s^{-1} and fin wave speed v of 119 mm s^{-1} and flounder 2 has a speed v of 496 mm s^{-1} for the body wave and a speed v of 218 mm s^{-1} for the fin wave. Flounder 3 has a wave speed v of the body four times the wave speed of the fin, 444mm s^{-1} and 107 mm s^{-1} respectively. The differences in wave speeds between body and fin are probably due to the difference in length of the body and fin. Both have the same number of waves in a time period and because the fin is shorter than the body, the waves on the fin have to travel with less speed in order to follow the waves of the body.

The standard deviations of flounder 2 and 3 notes that within a film sequence wave speeds can change quite strongly. This indicates that the flounders can shift very quickly between speeds during swimming and the forward swimming movements are not steady, but indeed very irregular.

The differences in wave speeds between the three flounders are large as well. Just like the frequency F, flounder 3 has the highest body wave speed, followed by flounder 2 and 1, but for the fin flounder 2 and 3 have the same wave speed and flounder 1 a smaller one. All these differences in wave speeds, as well within the flounders as between them, indicate that there is a lot of variation possible in the speed of which a wave travels down a body or fin.

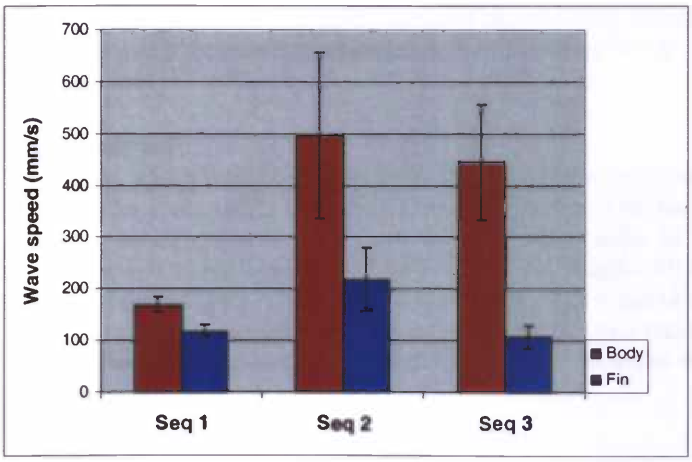


Figure 48. Mean wave speeds v of the body (red bars) and the fin (blue bars) of three free swimming flounders.

5.6 Swimming efficiency

The ratio of the forward swimming speed U of a fish and the wave speed *v* gives an indication for the so called 'slip'. A fish is progressing through the water while slipping when its forward speed U is less than the backward speed of the propulsive wave *v*. In a non-slip situation U/*v* would be 1. It is a theoretical value for the amount of energy which is wasted in the water and is not used for forward swimming. Here, the efficiency is given by the relation between the forward swimming speed U and the wave speeds *v* of the body respectively the fin. It appears that the fin waves are more efficient than the body waves (*see figure 49*). This is due to the wave speed *v* of the fin which is less than that of the body. In the previous paragraph this difference was explained by the fact that on the fin waves have to travel a shorter distance than on the body. Having the same number of waves travelling on both structures, the waves on the body have to travel faster than those of the fin to cover a longer distance at the same time.

In flounder 1 the highest efficiency is found in both the body and the fin, followed by flounder 2 and than flounder 3. No correlation with the body size of the fish or the forward moving speed U alone could be found, but still there might be a connection between these two. To find and prove any correlations between these parameters, more standardized circumstances are needed. Furthermore, evaluating the amount of slip from the relation of U/*v* is a theoretical value designed for the use of round fishes. It is still to prove whether this method is applicable for flatfish too, or whether one should find a relation where all propelling systems a flatfish uses are taken into account with the same theoretical weight.

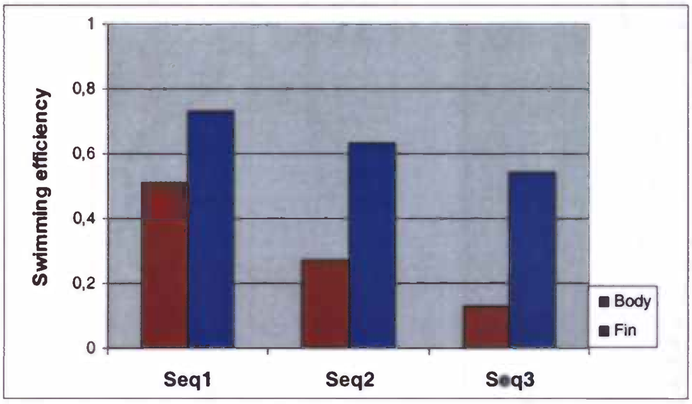


Figure 49. Swimming efficiency U/*v* of the body (red bars) and fin (blue bars) movements of three freely swimming flounders.

5.7 Relation between body and fin line

To make a comparison of the body and the fin, the movements of the two propulsion systems have to be followed from two points which lay close to each other. From the amplitude envelope graphs (*figures 13, 23, 33*) for each flounder a point on the body and a point on the fin were selected. The points had to lie close to each other and had to show waves clearly. These are point H and 12 (flounder 1), point H and 13 (flounder 2) and point G and 12 (flounder 3). The amplitude tracks of the points were selected from the graphs in figures *17, 27, 37* and *18, 28, 38* and the pairs were plotted together each in one graph for every flounder (*see figures 50, 51 and 52*). The resulting graphs contain the movements in time and space of a pair of a body point and a fin point, which lay close to each other. Comparison of the two points shows that the movements of the body point and the fin point are in phase. With the fins moving in phase with the body they might act effectively as an extension of the body surface. Since fins do move independently (see section 5.1), this extending effect might hydro dynamically be even more effective than simply having a wide and flat surface undulating.

However, there are some differences between the two moving systems. Especially in the movements of flounder 2 this is visible in the second upward wave (*figure 51*). The waving pattern of body point H is regular and distinct, while that of the fin shows irregularities that may be sub harmonics or underlying oscillations. These might serve as little steering components or stabilisation factors. Further analysis is needed for certain interpretation.

5.8 Accuracy

The points, which were used to describe the movements of the body and the fin, were marked manually. This was done for every single frame of a filming sequence. Marking the points manually was done very carefully and on widely enlarged frames. Still a mistake of one pixel approximately must be taken into account. One pixel is equivalent to 0.24 millimetres or 0.38% of the body length of flounder 1, 0.36% of flounder 2 and 0.73% of flounder 3 respectively. These inaccuracies could have occurred for the body length of the flounders, which was measured as the maximum body length over all frames in a sequence. However, in most cases, the eventually gained values of the kinematic parameters are mean values, so the marking inaccuracy in single frames has not a strong impact.

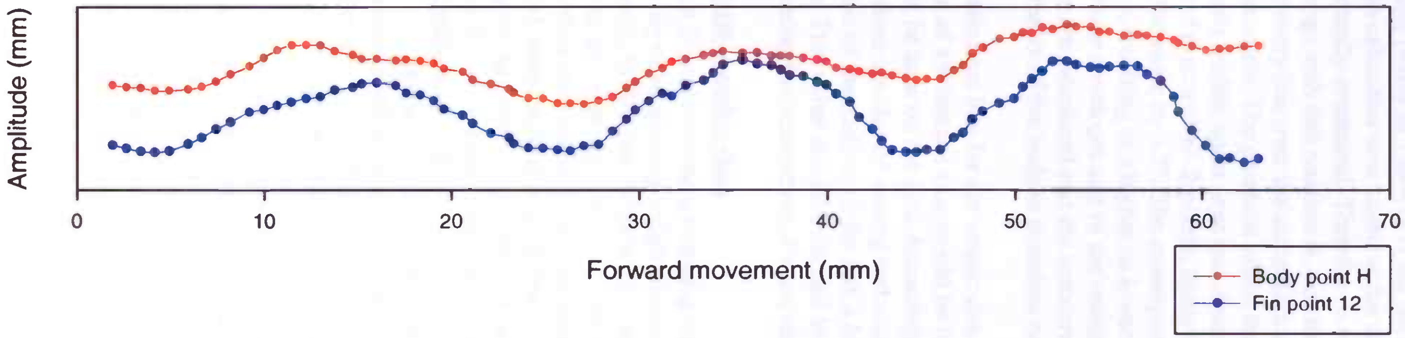


Figure 50. The amplitude tracks in time and space from body point H (red line) and fin point 12 (blue line) of flounder 1. These points indicate how the waves on the body and fin are related.

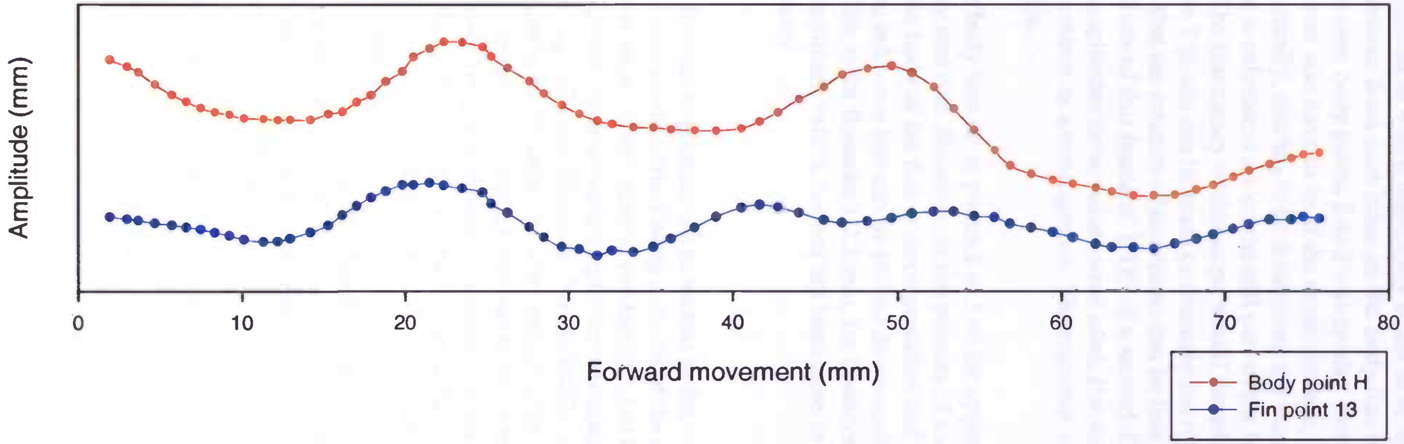


Figure 51. The amplitude tracks in time and space from body point H (red line) and fin point 13 (blue line) of flounder 2. These points indicate how the waves on the body and fin are related.

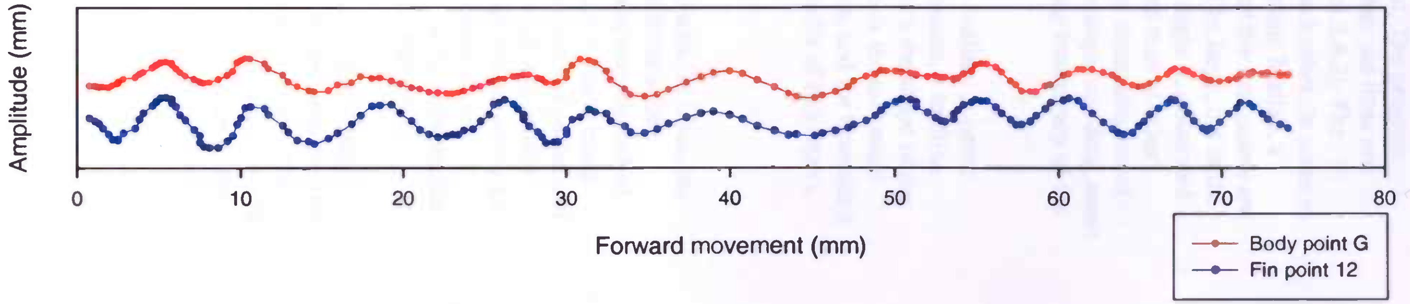


Figure 52. The amplitude tracks in time and space from body point G (red line) and fin point 12 (blue line) of flounder 3. These points indicate how the waves on the body and fin are related.

Further, in some frames the light was too bright to see the thin tail edge. In these cases the point on the tail edge was estimated, which can lead to an inaccuracy of +/- 2 pixels (0.76% of the body length of flounder 1, 0.72% of flounder 2 and 1.46% of flounder 3 respectively). When the maximum body length was found in a frame of an estimated tail, the body length of the flounder can have an overestimation of 3 pixels at the most. For flounder 1 this is a maximum inaccuracy of 1.15% of the body length, for flounder 2 the maximum inaccuracy is 1.09% of the body length and flounder 3 has a maximum inaccuracy of 2.20% of the body length. Because some kinematics are expressed in body lengths, they are also inaccurate with the above mentioned percentages.

In the fins a possible inaccuracy could have appeared mainly in the measurements of the maximum fin amplitudes A_{max}. As described in section 3.3 both the fin tip and fin base were marked and for obtaining a representative of the fin line the fin base was subtracted from the fin tip. Marking the fin base points, which are corresponding to points on the fin tip, happened by eyesight and logical estimates, which was the most accurate way available. Inaccuracy is estimated of a range of +/- 1 pixel, equivalent to a maximum inaccuracy of 2.3 % of the maximum fin amplitude A_{max} of flounder 1, 2.2% for flounder 2 and 4.0% for flounder 3 respectively.

Marking points in TimWin is not the only process in which inaccuracy could have appeared. The program Matlab calculates new points at the same distance from each other on the body line only when the lines are horizontally orientated. Therefore a rotation over body points 2 to 5 was needed (see section 3.4.2). The challenge with this rotation is, that these points also have to be at the same distance from each other, in order to rotate every line over the same distance. Ironically, this has to be done using the same program, Matlab, a vicious circle. The points at which the slope is calculated are on the still part of the body and the first points are at clearly visible spots (eye and stomach). The inaccuracy of this slope would therefore not be large, but in the order of maximal +/- 2 pixels, though. These 2 pixels can increase or decrease the rotation angle α, calculated from the slope by 1.5°. The consequence is that the rotation of one frame can be less or more than of other frames, resulting in a higher or lower amplitude of that frame of 1/125 of a second. Only for determination of amplitude envelopes and of the maximum amplitudes these values were used. For the other amplitude data, mean values are calculated and the inaccuracy decreases as a consequence. The maximal appearing inaccuracy of the amplitudes of the body is therefore negligible.

The reference line for the amplitudes of the body was set at points 2 to 5 of the upper body outline. A better choice of a reference axis would be the body mid line. However, in the process of making points, a midline cannot be seen on the fish. Assuming that the body of the fish is incompressible and therefore the shape of the body does not change during undulation, the reference line can be shifted downwards towards the estimated position of the midline of the fish's body. This is for flounder 1 2.5 mm, for flounder 2 3 mm and for flounder 3 2 mm. This value should be added by the amplitude values, but has not been done in the results of this report, preventing the occurrence of more inaccuracies.

5.9 Lift production

Since a flounder has no swimming bladder it needs to produce lift to ascend in the water column. In birds, the necessity of supporting weight is associated with asymmetrical wing motions of the up and down stroke (Norberg, 1990). For flatfishes this might also be an opportunity to produce lift, but it had not been described often so far. Verspuy (2001) has shown for plaice the downward amplitude maximum A_{down} (-4.8mm) being larger than the upward amplitude maximum A_{up} (2.2mm). However, Webb (2002), who also studied plaice, did not find asymmetrical amplitudes. In this experiment flounder 1 shows indeed larger downward amplitudes (-14.6mm) than the upward ones (-5.6mm). Flounder 2, in contrast, showed upward amplitudes which were a lot larger (A_{up} of 14.1mm) than the downward ones (A_{down} of -3.4mm). Flounder, on the other hand, shows comparable amplitudes (A_{up} of 2.6mm and A_{down} of –3.2mm). Overall, large differences are found between the maximum upward and downward amplitudes of the ascending flatfish. This indicates that the theory of asymmetrical lift production is very weak for flatfish.

Another way for the flounders to produce lift is to swim with their heads tilt up, as observed in other fishes without swimming bladder, like mackerel (He and Wardle, 1986), plaice (Webb, 2002) and winter flounder (He, 2002). In this study it is hard to say if the flounders swim with their heads tilt up. They do swim under a 'tilt' angle, but that is probably because they swim towards a food piece, which is higher in the water column than the fish itself. Though there is an indication of flounder 1 using this technique. At the end of film sequence 1, the flounder tends to swim in the horizontal direction, while the end of its body is a little bit pointing in downward direction. This could be an indication for swimming with its head up to produce lift, but for more confidence films in which flounders swim in horizontal direction should be analysed. However it is very hard to get these films, because flounders in an aquarium do not voluntary swim horizontally. When they swim, it is from the bottom towards a food piece in the water column. A possible solution for this problem is to let the fish swim in a flow channel. Webb (2002) used this technique with plaice and to refuse the flatfish to lie down the bottom he

had a grid installed, which prevented the fish from lying on the bottom. If this technique also works with flounders, the body attack angle might be observed, which is comparable with the tilt angle. This 'body attack angle' might be usable as an indicator for lift production in flatfish. To prove this suggestion however, flow visualisation might be a suitable technique.
Also, there is suggested, that when flatfish swim at high speeds, their asymmetrical body generates enough lift to encounter the negative buoyancy of their bodies (He, 2002). The winter flounder which had a maximum speed of 0.95 BL s^{-1} in the study of He (2002) needed to lift up its head, so this speed is not fast enough to prove this theory. However, the flounders in the present study had a swimming speed of 1.4 to 2.1 L s^{-1}, which might be enough to compensate for their negative buoyancy.

5.10 Comparison of flounders to other flatfish

There is one known study to the relation between the body and fin line and the kinematics of juvenile flatfishes, which is an (unpublished) study of Verspuy (2001). Verspuy used the same methods as described here, but he used a different flatfish species, namely the plaice (*Pleuronectes platessa*). One film sequence of a plaice, freely swimming in still water, was analysed. The fish had a body length of 43.6mm and anal fin length of 27.0mm. This is comparable with the sizes of the three flounders used for the experiments described in this report and is therefore good reference material. The values of the kinematic parameters of the plaice are depicted in table 2.

- With a forward swimming speed U of 2.7 BL s^{-1} Verspuy's plaice swam 48% faster than flounder 1, 22% faster than flounder 2 and 33% faster than flounder 3. Although there are differences, it is not possible to say with this data, that the differences in swimming speed are due to the fish species.
- The maximum downward amplitude A_{down} of the body of the plaice was -4.8mm, twice as large as the upward amplitude A_{up} (2.2mm) and is measured based on the upper body outline. Flounder 3 shows comparable amplitude values (A_{up} of 2.6 and A_{down} of -3.2), but the other two flounders have different amplitude courses. Both have a larger range in which their tail moves up and down.
- The frequency F of the tail (8.3) and fin (8.3) beats of the plaice, are also comparable with flounder 3 (F of 8.6 for body and 8.3 for tail); both make more than 8 beats per second, while flounder 1 (F of 4.5 for body and 4.3 for fin) and flounder 2 (F of 5.6 for body and 5.2 for fin) make less beats in a second. It is possible that these results, of frequency F and amplitudes can be related. Flounder 3 and the plaice have a smaller amplitude range and therefore it is likely that they produce more beats per second than the other two flounders.
- The wave lengths, as percentage of the body lengths, of the body λ_b and of the fin λ_f of the plaice are both larger (62% and 43% respectively) than those of the flounders. It might be possible that this difference is due to the different species, but more data should proof this.
- The stride lengths, as percentage of the body lengths, λ_s for the body and λ_{sf} for the fin of the plaice (33% and 35% respectively), on the other hand, are comparable with flounder 1, which also moves forward about a third of the body length per tail or fin beat.
- Comparison of the wave speeds *v* gave a difference between the plaice and the flounders. For the plaice the waves of the body (239 mm s^{-1}) and of the fin (200 mm s^{-1}) have about the same speed, but for the flounders these speeds differ.
- Accordingly this is also visible in the comparison of the swimming efficiency of the body and the fin, which lay closer to each other in the plaice (0.48 for the body and 0.58 for the fin) than of the flounders. The swimming efficiency of both body and fin of the plaice lay between the values of the flounder, so no big difference is seen here.

Overall can be said that the kinematics of the flounders and of the plaice are comparable, but this is also due too the large variation in the kinematics of the flounders.

The relation between the body and fin line of the plaice were determined by Verspuy based on the maxima amplitudes. The maxima amplitudes of the body occurred at the tail and the maxima of the fin at 2/3 of the fin length. At the same time the maxima of the tail were positive, those of the fin had been negative. Verspuy interpreted this as the waves were in counter phase. However the movements of the tail and the movements of the fin point at 2/3 of the fin length at a particular time are not the result of the same wave. Therefore these movements could not be compared. Points on the body and fin which lay close to each other should be followed in space, in order to see if there is a relation between the body and fin movements. For the flounders this was also done and showed that the body and fin waves were in phase, while their maximum amplitudes were in counter phase sometimes. This difference in analysis of the flounder data shows that for the plaice there also might be found that the waves of the body and the fin are moving in phase, when analysed correctly.

Recently other studies of experiments with flatfishes had been published. One of them is a study on the swimming behaviour of winter flounder (*Pleuronectes americanus*), with special respect to the relation of the water temperature (He, 2002). During observation of adult winter flounder on natural fishing grounds, the fish stayed very close to the seabed, never rising more than 0.6m off the bottom. This is understandable for flatfishes which adapted a benthic life style. Their average swimming speed U was 0.52 BL s^{-1} at a water temperature of -1.2 °C and 0.95 BL s^{-1} at 4.4°C. These speeds are lower than the speeds of the flounders of this research, but in line with the research of He this can be due to the higher water temperature of which the flounders in the present study stayed. However, the winter flounders should be used to these low temperatures and probably their metabolism has been adapted to it.

A second research considers the body kinematics of adult plaice (*Pleuronectes platessa*) at different heights above the bottom (Webb, 2002).Webb found the tail beat amplitude being independent of the swimming speed U, but dependent on swimming height, averaging 15mm (6.8% of body length) direct above the bottom and 25mm (11.3%BL) at >1cm height. The flounders, which swam >1cm height, have a tail beat amplitude which is higher in percentage of body length, respectively 9.0mm (14.3%BL), 17.5mm (26.4%BL) and 5.8mm (17.7%BL) for flounders 1, 2 and 3. The juvenile plaice in Verspuy's study has a tail beat amplitude of 7mm (16.1%BL). The difference between the flatfishes can be the difference in adulthood; it might be possible that the juvenile flatfish are more flexible and more active. It can though also have other explaining factors like the difference of the water current which was present by the adult plaice, but absent by the juvenile fish. And because of the large differences between the juvenile flounders, it can also be of the large variation in swimming performance. However, these suggestions are based on the comparison of one adult with four juvenile flatfishes and differing species, so more data are needed to make any conclusions.

The tail beat frequency F of the adult plaice in Webb's paper swimming at 1, 5 and 10cm above the bottom, averaged 4.6, 6.0 and 5.8Hz respectively. These values are comparable with the larger juvenile flounders of this study, but flounder 3 and Verspuy's juvenile plaice swim at a higher frequency. Webb found that the tail beat frequency F was independent of swimming speed U, so differences in swimming speed U is probably not an explanation for the differences in frequencies. The adult plaice has a wave length λ_b on its body of 0.74 body lengths. This is a larger wave than the juvenile fish, although the juvenile plaice did already outreach the juvenile flounders with their wave length λ_b. This indicates a difference of wave length λ_b in age and between the two species, however more data are needed to test this suggestion.

5.11 Comparison to batoid fish

Flatfish use their body as well as their fins at the same time for propulsion, which is rather special in fish. Most of the kinematic descriptions of swimming fish mention the use of either the body undulations (Videler, 1993) or the use of the fins for propulsion (Blake, 1979; Rosenberger, 2001). One group of fish, which is specialized in the use of their pectoral fins to create propulsion are batoid fish (Rosenberger, 2001). Most batoid fish have a benthic lifestyle and according to Rosenberger they mainly use a movement Webb (1994) calls the 'undulatory type'. This type of movement is defined as having more than one wave present on the fin at a time (Webb, 1994) and allows the fish high manoeuvrability of quick turning and swimming at fairly slow velocities. The flounders in this study also have more than one wave present at the fin at one time, and swim therefore with the undulatory swimming type.

5.12 Comparison to round fish

For round fish it is known that the frequency F is related to the forward swimming speed U, in the way that the faster the forward swimming speed U the higher the frequency F (Videler, 1993). However this was not found for the flounders in the present study as well as the adult plaice which Webb (2002) studied. For flatfish this relation is therefore not likely.

General kinematics of round fish (Videler, 1993) indicate that round fish have a higher wave length λ_b (92%BL) and stride length λ_s (72%BL) than the flatfish (*see table 2*). It indicates that flatfish are rather bad forward swimmers. The swimming efficiency is also smaller for flatfish. However, the determination of the swimming efficiency is based on round fishes and not on flatfishes which move their body and fin both for forward propulsion. This is therefore the largest difference with general round fishes (e.g. Cod), which only move their body for forward movements. Other round fishes like the angelfish (Blake, 1979, 1980) and the bird wrasse (Walker and Westneat, 1997), only move their fins, but comparison of kinematic parameters are very difficult, because of the different use of the fins, swimming styles and appearances of these fishes.

For better comparison of the swimming efficiency between flatfish and round fish the rather simple relation between U and v of the tail beat cycle should be thought over and adapted.

5.13 Conclusions

The flounders in the three sequences all showed that the body and fin are moving in phase, which might be an advantage hydro dynamically, because it enlarges the moving surface and therefore also the effect of the forward propulsion. The three sequences do not demonstrate that flounders always move their body and fin in phase, but it proves that this is a possibility of propulsion which is used by those fish.

Furthermore, a high variation in kinematic parameters between and within the three flounders was seen. This indicates that the juvenile flounders are able to swim with a lot of possible combinations of various parameters and can change their style during swimming. An example is flounder 3, which changed its wave speed of body and fin a lot during swimming.

The three analysed film sequences do not provide enough data to make general conclusions about the swimming kinematics of juvenile flounders. All three sequences showed upward swimming, but under different angles. This can be the cause that so many differences in the kinematic data between the three flounders were found. However, also the length, the forward speed and the swimming motivation of the individual flounder can have its influence on the data. For future studies it is advisable to create more standardized conditions, in which the flounders have to swim with the same speed and with the same angle of swimming direction. Using a flow channel can create these circumstances, but it is unsure if the flatfish would cooperate by swimming voluntary and not lie and hide at the bottom. To decrease the influence of the body length on the kinematic parameters, flounders of the same length should be chosen, or better, one single flounder should be filmed in a row of swimming performances.

Table 2
Comparison between the kinematic data of flounders, plaice, cod and general trends of round fish.
The parameters are given in mm and as a proportion (%) of body or fin length (L).

								Verspuy (2001)		Webb (2002)		Videler (1993)
Parameter		**Flounder 1**		**Flounder 2**		**Flounder 3**		**Plaice**		**Plaice**	**Cod**	**Round fish** general trends
		Body	Fin	Body	Fin	Body	Fin	Body	Fin	Body	Body	
Length	(mm)	62.8	35.5	66.3	31.7	32.8	20.7	43.6	27.0	221	250	
U	(mm s^{-1})	86.7		136.4		57.9		115.9		200	100	
	(L s^{-1})	1.4	2.4	2.1	4.3	1.8	2.8	2.7	4.3	1,1	2.5	
A_{up}	(mm)	-5.6	5.5	14.1	5.4	2.6	2.4	2.2	2.0			
	(%L)	9.0	15.5	21.3	16.9	8.1	11.6	5	7			9
A_{down}	(mm)	-14.6	-4.0	-3.4	-4.8	-3.2	2.3	-4.8	-4.6			
	(%L)	23.3	11.2	5.1	15.2	9.6	10.9	11	17			
A_{max}	(mm)	10.5	10.2	20.7	10.8	9.9	5.9			15	29	
	(%BL)	16.7	28.7	31.2	34.1	30.2	28.5			6.8	11.6	
F	(Hz)	4.5	4.3	5.6	5.2	8.6	8.9	8.3	8.3	6,0	1,8	
T	(s)	0.22	0.23	0.18	0.19	0.12	0.11	0.12	0.12	0,17	0,56	
λ_b / λ_f	(mm)	31.6	21.6	34.8	21.0	15.2	11.2	27.0	18.7	164,0	233,0	
	(%BL)	50	35	53	32	46	34	62	43	74	93	92
λ_s / λ_{sf}	(mm)	19.0	19.5	24.4	27.8	6.8	6.7	14.6	15.1			
	(%BL)	30	31	37	42	21	20	33	35			72
v	(mm s^{-1})	170	119	496	218	444	107	239	200			
	(BL s^{-1})	2.7	1.9	7.5	3.3	13.5	3.2	5.5	4.6			
U/v		0.51	0.73	0.27	0.63	0.13	0.54	0.48	0.58			

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8 Appendix

A TimWin

Program for TimWin version 1.38.0.
The following text is the program written for TimWin to mark points manually on the fish. It is set to mark 10 points on the body, 15 points on the fin tip and 15 points on the fin base.

```
; ### FINpoint ### comand file adapted from - see below- by Regine + Martine van Oostveen 9/2002 ###
; ### NPOINTSR ### ejs may21/98 ### adapted for RUG use by Regine + Eize ### 11/2000 ###
; ### adapted from NpointsN ### active image = m (512 x 512) ###
; ### for marking points on outline of body AND along tip of fin AND along base of fin of a swimming juvenile
flatfish ###
;
Variables:
;
 char CImPath [60]
 char CImName [60]
 char FName [40]
 char RFName [60]
 char FileName [40]
 char RFileName [40]
 char RName [40]
 char ImFileName [40]
 char ResFileName [40]
 char TotImFileName [60]
 char TotResFileName [60]
 char TotalFileName [40]
 file TotFileName
 file TotalImFileName
 file TotalResFileName

 int Data [2] [70]
 int Spacer [20]
 int SpacerPos
 int FirstImNr
 int LastImNr
 int Counter
 int PntCntr
 int SerCntr
 int Split
 int Button
 int ImNr
 int PNr
 int DatNr
 int NOS
 int Xc
 int Yc

 string ResName
 string ImPath
 string ImName
 string ImExt = ".tif"
 string ResPath = "D:\\Martine\\Seq1\\"
 string ResExt = ".txt"
 string OrFName          ;filename without extensions
;-----------------------------------------------------------------------------------------------------------
```

```
MainProgram:
 cls
 dest m
 show m
 show m 20 500 4
 dis m
 edit m
 era
 call FillIbuf
 call Introduction
 call Initialisation
 for ImNr = FirstImNr to LastImNr
    call COMPOSEIMFILENAME
     cursx 0
     cursy 0
     tcopy TotalImFileName m
     cls
     beep
    call GetPoints
    call WriteData
 next ImNr
 call ProgEnd
stop
;------------------------------------------------------------------------------------
FillIbuf:
 ibuf 0  0
 ibuf 1  0
 ibuf 2  4
 ibuf 3  4
 ibuf 4  4
 ibuf 5  4
 ibuf 6  0
 ibuf 7  0
 ibuf 8  6
 ibuf 9  6
 ibuf 10 2
 ibuf 11 2
 ibuf 12 2
 ibuf 13 2
 ibuf 14 6
 ibuf 15 6
 ibuf 16 255

return
;--------------------------------------------------------------------------------------
Introduction:
 cls
 print ""
 print " ", @i "################### Finpoint ################### ejs98/ejs+rg2000/rgmmvo2002
#######" @n
 print
 print " This program writes the coordinates of a number of user defined points"
 print " per image to a file. The points have to be indicated manually in a user"
 print " defined but strict sequence to avoid mixing up in during post-processing."
 print " The data are stored as X- and Y- data in a .txt file"
 print
 print
 pause " Press a key ......"
 wait 0.5
 cls
```

```
return
;------------------------------------------------------------------------------------------
Initialisation:
 cls
 print
 beep
 print " Give the path and name of the TIF image file series"
 readkb CImPath
 ImPath = CImPath
  beep
  print " Give the image series file name (max 2 characters, no nrs, no ext.!)..."
  readkb CImName
  ImName = CImName
  fprint FName 0 "%s%s", ImPath, ImName
  FileName = FName
  beep
  FirstImNr = " Frame number FIRST image ?  >"
  beep
  LastImNr = " Frame Number LAST image ?  >"
  beep
  print " Give a name for the file with the resulting data"
  readkb RName
  ResName = RName
  fprint RFName 0 "%s%s%s",ResPath,ResName,ResExt
  beep
 PNr = 40
 Split = 1
 if Split == 1
   NOS = 3
   if NOS > 1
     for Counter = 1 to ( NOS - 1 )
        SpacerPos = 11
        Spacer [Counter] = SpacerPos
     next Counter
     for Counter = 2 to NOS
        SpacerPos = 26
        Spacer [Counter] = SpacerPos
     next Counter
     DatNr = PNr + Counter - 1
   endif
  else
   NOS = 1
   DatNr = PNr
 endif
return
;------------------------------------------------------------------------------------------
COMPOSEIMFILENAME:                              ; compose imagefilename
 switch ImNr
    case < 10
              fprint ImFileName 0 "%s%s",FileName,"00000"
    case < 100
              fprint ImFileName 0 "%s%s",FileName,"0000"
    case < 1000
              fprint ImFileName 0 "%s%s",FileName,"000"
    case < 10000
              fprint ImFileName 0 "%s%s",FileName,"00"
    case < 100000
              fprint ImFileName 0 "%s%s",FileName,"0"
    endsw
 fprint TotImFileName 0 "%s%d%s",ImFileName,ImNr,ImExt
```

```
 TotalImFileName = TotImFileName
 TotalResFileName = RFName
 print TotalImFileName
 return
;---------------------------------------------------------------------------------
GetPoints:                                ; reads the marked points as X-Y- coordinates;
 curs ch 1
 SerCntr = 1
 for Counter = 1 to DatNr
   PntCntr = Counter - SerCntr + 1
   if PntCntr == Spacer [SerCntr]
     Data [0] [Counter] = 0
     Data [1] [Counter] = 0
     SerCntr = SerCntr + 1
    else
     SamePoint:
     print
     print " Indicate and click point nr. ",PntCntr
     Button = mouse
     if Button == 1
       Xc = cursx
       Yc = cursy
       drpat
      else
       curs cr 0
       beep
       goto SamePoint
     endif
     if Button < 2
       print "   X=",Xc," en Y=",Yc
       Data [0] [Counter] = Xc
       Data [1] [Counter] = Yc
     endif
   endif
 next Counter
return
;-------------------------------------------------------------------------------------
WriteData:                                ; writes the data to a file;
 for Counter = 1 to DatNr
   fprint TotalResFileName "%4.0d",Data [0] [Counter]
   fprint TotalResFileName ""
   fprint TotalResFileName "%4.0d",Data [1] [Counter]
   fprint TotalResFileName "\n"
 next Counter
 fprint TotalResFileName "\n"
return
;---------------------------------------------------------------------------------------
ProgEnd:
 curs cr 0
 show z 0
 cls
 beep
 beep
 print
 print " ####### END ##############################"
 print " ---------------- of -------------------"
 print " ######################## Finpoint #######"
return
```

B Matlab

Program for Matlab version 6.5
The following text is the program written for Matlab to calculate eleven fixed coordinates by means of a spline interpolation.

```
n=188
global X
global Y
dlmwrite('Body1',Res1Body,' ')
data=dlmread('Body1',' ');
a=(1:2:n);
b=(2:2:n);
X=data(:,[a]);
Y=data(:,[b]);
Xmax=data(1,[a]);
Xmin=data(10,[a]);
Stap=abs((Xmin-Xmax)/10);
for i=(1:n/2)
   xx=(Xmin(1,i):Stap(1,i):Xmax(1,i));
          yy=spline(X(:,i),Y(:,i),xx);
          XX(:,i)=xx';
          YY(:,i)=yy';
          plot(X,Y,'o',XX,YY)
end
dlmwrite('BodySeq1X.txt',XX,' ')
dlmwrite('BodySeq1Y.txt',YY,' ')
```

C Kinematic data

In the results of this paper only mean or maxima values of the kinematic data are given. In the following pages kinematic data of every wave of the three flounders are given, subdivided in the body and the fin waves.

Body 1

Length	(mm)	SD
Gem	61.4	0.8
Max	62.8	
Min	59.4	

Distance of forward swimming (mm)	64.5
Total time of sequence (sec)	0.744

94 frames of 125 frames per second

Amplitude tail

max/min	frame	Deviation (mm)	
max	7	-3.8	
min	20	-14.2	10.4
max	34	-7.1	7.1
min	51	-16.0	8.9
max	66	-8.4	7.6
min	78	-13.6	5.3
max	92	-3.1	10.5

	mm	SD	L(%)
A up (gem)	-5.6	2.5	9.0
A down (gem)	-14.6	1.2	23.3

A max 10.5

Wave period (Tb)

Frames	sec
27	0.216
31	0.248
32	0.256
27	0.216
26	0.208
gem	SD
0.229	0.022

Frequence (Hz) 4.4

Bodywave (λb)

frame	mm		
7	31.1		
20	32.5		
34	32.0		
51	31.5		
66	31.8		
78	31.3		
92	31.3		
	gem	SD	L(%)
	31.6	0.5	50.4

Stride Length (λs)

frame	moveme	1/2-λs		λs		
7	4.9	mm		mm		
20	15.2	10.3				
34	25.6	10.4		20.7		
51	37.5	11.9		22.3		
66	46.7	9.2		21.1		
78	54.0	7.3		16.5		
92	63.0	9.0		16.3		
		gem	SD	gem	SD	L(%)
		9.7	1.6	19.4	2.8	30.8

smoothed data

Wave period (Tb)

frame	frames	sec
7		
20		
35	28	0.224
50	30	0.240
66	31	0.248
75	25	0.200
92	26	0.208
	gem	SD
	0.224	0.020

Frequence (Hz) 4.5

smoothed data

Stride Length (λs)

frame	moveme	1/2-λs		λs		
7	4.9					
20	15.2	10.3				
35	26.3	11.1		21.4		
50	37.0	10.7		21.8		
66	46.7	9.7		20.4		
75	51.9	5.2		14.9		
92	63.0	11.0		16.3		
		gem	SD	gem	SD	L(%)
		9.7	2.2	19.0	3.1	30.2

Body 1

Speed Bodywave (v) Point E-K Mean forward speed (U) Propellor efficiency (U/v)

wave	mm/sec
3	188.0
4	144.3
5	155.4
6	168.9
7	160.4

mm/sec gem	SD	L/sec L(%)	mm/sec gem	L/sec L(%)	
163.4	16.4	2.6	86.7	1.4	0.53

smoothed data

Speed Bodywave (v) Point F-K

wave	sec
3	169.9
4	191.4
5	163.3
6	169.8
7	156.1

mm/sec gem	L/sec SD	L/sec L(%)	
170.1	13.2	2.7	0.51

Body 2

Length	(mm)	SD
Gem	59.1	3.7
Max	66.3	
Min	50.8	

Distance of forward swimming (mm)	77.5
Total time of sequence (sec)	0.568

72 frames of 125 frames per second

Amplitude tail max/min	frame	Deviation (mm)		Wave period (Tb) frames	sec
max	8	19.4			
min	21	5.9	13.5		
max	32	15.9	10.0	24	0.192
min	43	-2.5	18.4	22	0.176
max	56	7.1	9.6	24	0.192
min	72	-13.6	20.7	29	0.232

	mm	SD	L(%)
A up (gem)	14.1	6.3	21.3
A down (gem)	-3.4	9.8	5.1
A max	20.7		

Wave period gem	SD	Frequence (Hz)
0.198	0.024	5.1
without frame 72		
0.187	0.009	5.4

Bodywave (λb) frame	mm
8	31.1
21	35.9
32	33.8
43	37.6
56	35.4
72	37.0

gem	SD	L(%)
35.1	2.4	53.0
34.8	2.5	52.5

Stride Length (λs) frame	moveme	1/2-λ-s mm	λ-s mm
8	6.6		
21	18.8	12.2	
32	29.5	10.7	23.0
43	42.7	13.1	23.9
56	59.4	16.8	29.9
72	77.5	18.0	34.8

gem	SD	gem	SD	L(%)
14.2	3.1	27.9	5.5	42.1
13.2	2.6	25.6	3.8	38.6

smoothed data

frame	Wave period (Tb) frames	sec
7		
22		
32	25	0.200
44	22	0.176
52	20	0.160

gem	SD	Frequence (Hz)
0.179	0.020	5.6

smoothed data

Stride Length (λs) frame	moveme	1/2-λ-s mm	λ-s mm
7	5.7		
22	19.8	14.1	
32	29.5	9.7	23.8
44	44.0	14.5	24.2
52	54.6	10.6	25.1

gem	SD	gem	SD	L(%)
12.2	2.4	24.4	0.6	36.8

Body 2

Speed Bodywave (*v*) Point E-K

Mean forward speed (U)

Propellor efficiency (U/*v*)

wave	mm/sec
2	310.6
3	497.0
4	233.8
5	731.1
	225.2

mm/sec gem	SD	L/sec L(%)	mm/sec gem	L/sec L(%)	
399.6	215.2	6.0	136.4	2.1	0.34

smoothed data

Snelheid Bodywave (v) Point G-K

wave	mm/sec
2	310.6
3	423.6
4	671.7
5	579.9

mm/sec gem	SD	L/sec L(%)	mm/sec gem	L/sec L(%)	
496.4	160.7	7.5	136.4	2.1	0.27

Body 3

Length	(mm)	SD
Gem	30.7	1.1
Max	32.8	
Min	27.9	

Distance of forward swimming (mm)	76.4
Total time of sequence (sec)	1.320

166 frames of 125 frames per second

Amplitude tail max/min	frame	Deviation (mm)		Wave period (Tb) frames	sec	Frequence (Hz)	frame	Bodywave (λb) mm
max	9	2.3					9	15.6
min	20	-1.4	3.7				20	15.7
max	29	7.2	8.6	20	0.160		29	14.2
min	36	-1.5	8.6	16	0.128		36	15.7
max	41	4.9	6.4	12	0.096		41	14.5
min	48	-5.0	9.9	12	0.096		48	15.5
max	55	1.9	6.9	14	0.112		55	15.6
min	63	-3.3	5.2	15	0.120		63	15.8
max	75	4.0	7.3	20	0.160		75	15.2
min	80	0.1	3.9	17	0.136		80	15.7
max	84	2.5	2.4	9	0.072		84	15.0
min	93	-4.3	6.8	13	0.104		93	15.1
max	98	1.1	5.3	14	0.112		98	15.7
min	108	-4.0	5.0	15	0.120		108	16.0
max	120	2.8	6.8	22	0.176		120	15.4
min	125	-3.8	6.6	17	0.136		125	15.2
max	129	1.2	5.0	9	0.072		129	14.8
min	136	-3.5	4.7	11	0.088		136	14.7
max	142	0.6	4.2	13	0.104		142	14.7
min	151	-4.9	5.5	15	0.120		151	14.4
max	156	0.8	5.6	14	0.112		156	14.5

	mm	SD	L(%)	gem	SD		gem	SD	L(%)
A up (gem)	2.6	2.0	8.1	0.117	0.028	8.5	15.2	0.5	46.4
A down (gem)	-3.2	1.7	9.6						

A max 9.9

Wave period (Tb) frame	frames	sec	Frequence (Hz)
10			
19			
29	19	0.152	
36	17	0.136	
41	12	0.096	
49	13	0.104	
56	15	0.120	
64	15	0.120	
76	20	0.160	
81	17	0.136	
84	8	0.064	
91	10	0.080	
98	14	0.112	
108	17	0.136	
118	20	0.160	
125	17	0.136	
130	12	0.096	
135	10	0.080	
141	11	0.088	
150	15	0.120	
156	15	0.120	

gem	SD	
0.117	0.028	8.6

Body 3

Stride Length (λs)

frame	moveme	1/2-λs	λs
9	2.5		
20	5.8	3.3	
29	8.6	2.9	6.1
36	11.5	2.8	5.7
41	14.2	2.7	5.5
48	18.6	4.4	7.1
55	22.7	4.1	8.5
63	25.9	3.2	7.3
75	30.0	4.1	7.3
80	31.7	1.7	5.9
84	33.9	2.2	3.9
93	41.6	7.7	9.9
98	45.6	4.0	11.7
108	50.9	5.3	9.3
120	54.9	4.0	9.3
125	57.0	2.1	6.1
129	58.6	1.6	3.7
136	62.1	3.4	5.0
142	64.9	2.8	6.3
151	68.3	3.4	6.2
156	70.4	2.1	5.5

gem	SD	gem	SD	L(%)
3.4	1.4	6.9	2.1	20.9

smoothed data

Speed Bodywave (v)

wave	mm/sec
3	347
4	334
5	501
6	385
7	416
8	351
9	473
10	489
11	707
12	629
13	493
14	339
15	239
16	321
17	411
18	559
19	504
20	460
21	461
22	466

mm/sec		L/sec
gem	SD	L(%)
444.3	110.8	13.5

Mean forward speed (U)

mm/sec	L/sec
gem	L(%)
57.9	1.8

Propellor efficiency (U/v)

0.13

smoothed data

Stride Length (λs)

frame	moveme	1/2-λs	λs
10	2.5		
19	5.8	3.3	
29	8.6	2.9	6.1
36	11.5	2.8	5.7
41	14.2	2.7	5.5
49	19.3	5.1	7.8
56	23.0	3.8	8.8
64	26.2	3.2	7.0
76	30.0	3.8	7.0
81	32.4	2.4	6.2
84	33.9	1.5	3.9
91	40.0	6.1	7.6
98	45.6	5.6	11.7
108	50.9	5.3	11.0
118	54.2	3.2	8.6
125	57.0	2.9	6.1
130	59.2	2.1	5.0
135	61.5	2.4	4.5
141	64.5	3.0	5.4
150	67.9	3.4	6.4
156	70.4	2.5	5.9

gem	SD	gem	SD	L(%)
3.4	1.2	6.8	2.0	20.9

Fin 1

Length	(mm)	SD
Gem	35.5	0.8
Max	37.3	
Min	33.0	

Distance of forward swimming (mm)	64.5
Total time of sequence (sec)	0.744

94 frames of 125 frames per second

Amplitude (Max=punt 10, Min=punt6)

max/min	frames	point 6	point 10	deviation (mm)
max	17	1.0	5.4	
min	21	-4.1	-2.4	9.5
max	47	0.5	5.1	9.3
min	50	-3.4	-2.2	8.5
max	74	2.2	5.6	9.0
min	79	-4.4	-3.2	10.0
max	93	1.0	5.9	10.2

	mm	SD	FL(%)
A up (gem)	5.5	0.3	15.5
A down (gem)	-4.0	0.5	11.2

A max 10.2

Wave period (Tf)

frames	sec
30	0.240
29	0.232
27	0.216
29	0.232
19	0.152

gem	SD
0.214	0.036

Frequence (Hz)

4.7

Finwave (λf)

frame	mm
17	24.4
21	20.1
47	26.9
50	17.5
74	20.1
79	23.1
93	18.8

gem	SD	FL(%)
21.6	3.3	60.8

Speed Bodywave (*v*)

golf	mm/sec
1	133.6
2	107.5
3	119.3
4	112.6
5	120.1

mm/sec gem	SD	FL/sec FL(%)
118.6	9.9	3.3

Mean forward speed (U)

mm/sec gem	FL/sec FL(%)
86.7	2.4

Propellor efficiency (U/*v*)

0.73

Fin 1

Stride Length (λs)

	point5			point6			point7			point8			point9			point10			point11			point12		
	frame	Xdata	λs	frame	Xdata	λs	frame	Xdata	λs	frame	Xdata	λs	frame	Xdata	λs	frame	Xdata	λs	frame	Xdata	λs	frame	Xdata	λs
max	3	25.6		5	24.7		10	26.4		12	25.8		12	23.4		15	23.3		15	20.9		21	23.1	
min	17	36.7		19	36.1		21	35.0		24	34.9		28	35.3		30	34.9		32	33.6		35	33.4	
max	31	47.0	21.5	34	47.0	22.2	35	45.3	18.9	37	44.4	18.6	43	46.0	22.5	44	44.3	21.0	45	42.9	22.0	48	42.6	19.5
min	44	56.2	19.5	47	55.8	19.7	50	56.0	21.0	52	54.6	19.7	56	54.6	19.3	58	53.5	18.6	61	52.9	19.3	63	51.8	18.4
max	61	67.1	20.1	65	67.3	20.3	65	64.9	19.6	67	63.8	19.4	70	63.3	17.4	73	62.7	18.4	75	61.4	18.5	76	59.8	17.2
min	77	76.9	20.7	78	75.3	19.5	82	75.5	19.5	84	74.3	19.7	85	72.7	18.0	87	71.3	17.8	89	70.4	17.5	91	69.3	17.5
	gem	SD	L(%)	gem	SD	L(%)	gem	SD	L(%)	gem	SD	L(%)	gem	SD	L(%)	gem	SD	L(%)	gem	SD	L(%)	gem	SD	L(%)
	20.4	0.9	57.6	20.4	1.2	57.7	19.8	0.9	55.7	19.3	0.5	54.6	19.3	2.3	54.5	18.9	1.4	53.4	19.3	1.9	54.5	18.1	1.0	51.2

Stride Length (λs)

point 5-12

gem	SD	FL(%)
19.5	1.4	54.9

Wave period Freq (Hz)

point5			point6			point7			point8			point9			point10			point11			point12		
frames	sec	Hz	frame	sec	Hz	frame	sec	Hz	frame	sec	Hz	frame	sec	Hz	frame	sec	Hz	frame	sec	Hz	frame	sec	Hz
28	0.224		29	0.232		25	0.200		25	0.200		31	0.248		29	0.232		30	0.240		27	0.216	
27	0.216		28	0.224		29	0.232		28	0.224		28	0.224		28	0.224		29	0.232		28	0.224	
30	0.240		31	0.248		30	0.240		30	0.240		27	0.216		29	0.232		30	0.240		28	0.224	
33	0.264		31	0.248		32	0.256		32	0.256		29	0.232		29	0.232		28	0.224		28	0.224	
gem	SD		gem	SD		gem	SD		gem	SD		gem	SD		gem	SD		gem	SD		gem	SD	
0.236	0.021	4.2	0.238	0.012	4.2	0.232	0.024	4.3	0.230	0.024	4.3	0.230	0.014	4.3	0.230	0.004	4.3	0.234	0.008	4.3	0.222	0.004	4.5

Wave period Frequency (Hz)

point 5-12

gem	SD	
0.232	0.01464	4.31965

Fin 2

Length	(mm)	SD
Gem	31.7	2.5
Max	36.1	
Min	26.8	

Distance of forward swimming (mm)	77.5
Total time of sequence (sec)	0.568

72 frames of 125 frames per second

Amplitude (Max=point 10, Min=point6)					Wave period (Tf)	
max/min	frames	point6	point10	Deviation (mm)	frames	sec
max	18	-0.9	5.6			
min	21	-4.2	3.3	9.7		
max	40	2.0	5.2	9.4	22	0.176
min	47	-5.5	3.1	10.7	26	0.208
max	68	-1.7	5.3	10.8	28	0.224

	mm	SD	FL(%)
A up (gem)	5.4	0.2	16.9
A down (gem)	-4.8	1.0	15.2

A max 10.8

Wave period (Tf) gem	SD
0.203	0.024

Frequentie (Hz) 4.9

Finwave (λf) frame	mm
15	22.4
16	21.0
17	24.8
27	16.5
28	17.6
29	18.5
30	18.9
39	23.7
40	24.4
41	23.8
42	22.9
43	21.8
44	20.9
45	22.3
46	16.8
49	23.1
50	20.4
51	20.1
52	21.1
53	16.7
54	14.1
62	21.6
63	22.8
64	25.2
65	27.0
66	26.7
67	22.6
68	22.7
69	20.3
70	18.4
71	16.9
72	17.1

gem	SD	FL(%)
21.0	3.2	66.3

Speed Bodywave (*v*) wave	mm/sec
1	206.14
2	169.21
3	307.46
4	188.06

mm/sec gem	SD	FL/sec FL(%)
217.7	61.7	6.9

Mean forward speed (U) mm/sec gem	FL/sec FL(%)
136.4	4.3

Propellor efficiency (U/*v*) 0.63

Fin 2

Stride Length (λs)

	p2	X	λs	p3	X	λs	p4	X	λs	p5	X	λs	p6	X	λs	p7	X	λs	p8	X	λs	p9	X	λs	p10	X	λs	p11	X	λs	p12	X	λs	p13	X	λs
max	10	37.8		9	34.64		10	33.25		11	31.87		12	30.48		13	29.43		15	28.82		16	27.77		18	27.47		20	25.2		22	26.58		24	26	
min	19	46.5		18	43.34		19	41.95		20	40.56		22	40.18		22	37.92		24	37.35		29	39.84		31	39.77		32	38.6		33	37.42		34	36.2	
max	35	62.1	24.3	36	61.1	26.5	36	58.83	25.6	36	56.57	24.7	36	54.3	23.8	37	53.25	23.8	38	52.08	23.3	39	51.23	23.5	43	54.01	26.5	43	51.7	26.5	43	49.47	22.9	42	46.1	20.1
min	45	74.9	28.4	45	72.67	29.3	45	70.4	28.4	46	69.23	28.7	48	69.99	29.8	48	67.72	29.8	52	70.47	33.1	53	69.43	29.6	53	67.16	27.4	56	68.5	29.9	58	68.87	31.5	61	70.1	33.9
max	55	87.6	25.5	55	85.31	24.2	57	85.58	26.7	59	85.74	29.2	60	84.79	30.5	61	83.74	30.5	63	84.1	32.0	64	82.84	31.6	69	86.06	32.1	69	83.8	32.1						
	gem	SD	L(%)	gem	SD	L(%)	gem	SD	L(%)	gem	SD	L(%)	gem	SD	L(%)	gem	SD	L(%)	gem	SD	L(%)	gem	SD	L(%)	gem	SD	L(%)	gem	SD	L(%)	gem	SD	L(%)	gem	SD	L(%)
	26.1	2.146	82.2	26.7	2.564	84.0	26.9	1.443	84.9	27.5	2.448	86.7	28.0	3.666	88.4	28.0	3.666	88.4	29.5	5.405	92.9	28.2	4.239	88.9	28.7	2.971	90.3	29.5	2.78	93.0	27.2	6.055	85.6	27.0	9.76	85.1

Stride Length (λs)
point 2-13

gem	SD	FL(%)
27.8	3.4	87.7

Wave period Freq (Hz)

point2			point2			point2			point2			point2			point2			point2			point2			point2			point2			point2			point2		
frames	sec	Hz	frames	sec	Hz	frames	sec	Hz	frames	sec	Hz	frames	sec	Hz	frames	sec	Hz	frames	sec	Hz	frames	sec	Hz	frames	sec	Hz	frames	sec	Hz	frames	sec	Hz	frames	sec	Hz
25	0.20		27	0.22		26	0.21		25	0.20		24	0.19		24	0.19		23	0.18		23	0.18		25	0.20		23	0.18		21	0.17		18	0.14	
26	0.21		27	0.22		26	0.21		26	0.21		26	0.21		26	0.21		28	0.22		24	0.19		22	0.18		24	0.19		25	0.20		27	0.22	
20	0.16		19	0.15		21	0.17		23	0.18		24	0.19		24	0.19		25	0.20		25	0.20		26	0.21		26	0.21							
gem	SD		gem	SD		gem	SD		gem	SD		gem	SD		gem	SD		gem	SD		gem	SD		gem	SD		gem	SD		gem	SD		gem	SD	
0.19	0.03	5.28	0.19	0.04	5.14	0.19	0.02	5.14	0.20	0.01	5.07	0.20	0.01	5.07	0.20	0.01	5.07	0.20	0.02	4.93	0.19	0.01	5.21	0.19	0.02	5.14	0.19	0.01	5.14	0.18	0.02	5.43	0.18	0.05	5.56

Wave period		Frequence (Hz)
point 2-13		
gem	SD	
0.19	0.02	5.16

Fin 3

Length	(mm)	SD
Gem	20.7	1.1
Max	23.7	
Min	18.4	

Distance of forward swimming (mm) 76.4
Total time of sequence (sec) 1.3

166 frames of 125 frames per second

Amplitude (min/max = point 10)				Wave period (Tf)		Frequence (Hz)	Finwave (λf)		Speed Bodywave (*v*)		Mean forward speed (U)
max/min	frames	Deviation (mm)		frames	sec		frame	mm	wave	mm/sec	
min	5	-3.4					5	9.9	1	70.3	
max	15	2.4	5.9				15	11.0	2	94.8	
min	23	-3.4	5.9	18	0.144		23	14.0	3	113.3	
max	31	2.4	5.9	16	0.128		31	11.3	4	121.8	
min	39	-2.7	5.1	16	0.128		39	14.0	5	122.9	Propellor efficiency (U/*v*)
max	43	2.2	4.9	12	0.096		43	17.7	6	114.8	
min	52	-2.2	4.4	13	0.104		52	13.7	7	77.1	
max	60	2.7	4.9	17	0.136		60	8.9	8	99.0	
min	71	-2.4	5.1	19	0.152		71	7.5	9	103.3	
max	76	2.4	4.9	16	0.128		76	9.2	10	134.8	
min	83	-2.4	4.9	12	0.096		83	10.9	11	166.3	
max	88	1.7	4.1	12	0.096		88	9.9	12	110.1	
min	94	-2.0	3.7	11	0.088		94	9.5	13	64.1	
max	102	2.4	4.4	14	0.112		102	11.7	14	99.7	
min	110	-1.7	4.1	16	0.128		110	10.9	15	92.5	
max	115	2.4	4.1	13	0.104		115	10.4	16	125.0	
min	125	-2.2	4.6	15	0.120		125	10.2	17	131.6	
max	130	2.4	4.6	15	0.120		130	10.9	18	100.4	
min	136	-2.2	4.6	11	0.088		136	14.1	19	92.2	
max	145	2.7	4.9	15	0.120		145	8.7	20	96.5	
min	153	-1.2	3.9	17	0.136		153	8.5	21	104.8	
max	155	2.4	3.7	10	0.080		155	11.1			
min	162	-1.2	3.7	9	0.072		162	12.4			

										mm/sec		FL/sec	mm/sec	FL/sec	
	mm	SD	FL(%)	gem	SD		gem	SD	FL(%)	gem	SD	FL(%)	gem	FL(%)	
A up (gem)	2.4	0.3	11.6	0.113	0.022	8.8	11.2	2.3	53.9	106.5	23.2	5.1	57.9	2.8	0.54
A down (gem)	-2.3	0.7	10.9												

A max 5.9

Fin 3

Stride Length (λs)

	p5	X	λs	p6	X	λs	p7	X	λs	p8	X	λs	p9	X	λs	p10	X	λs	p11	X	λs	p12	X	λs	p13	X	λs	p14	X	λs
max	6	12.6		6	11.5		10	11.3		10	10.2		10	12.1		14	9.6		17	9.5		18	8.8		19	8.0		23	7.7	
min	18	16.5		19	15.7		21	14.9		21	13.8		24	13.8		25	13.0		26	11.9		29	12.0		29	10.9		30	10.3	
max	26	18.5	5.9	29	18.6	7.1	29	17.5	6.1	29	16.4	6.1	31	16.2	4.1	32	15.3	5.7	34	14.7	5.2	35	13.9	5.2	36	13.7	5.7	37	12.8	5.1
min	34	21.3	4.8	34	20.2	4.5	36	20.3	5.5	36	19.2	5.5	37	18.4	4.6	39	18.5	5.4	40	17.9	6.0	42	17.8	5.9	42	16.7	5.9	43	16.5	6.2
max	41	25.2	6.7	42	24.5	5.9	42	23.4	5.9	43	23.1	6.8	44	22.6	6.4	46	22.9	7.6	47	22.5	7.8	49	22.6	8.6	49	21.5	7.8	50	20.9	8.1
min	47	29.1	7.8	49	29.2	9.0	49	28.1	7.8	50	27.5	8.3	51	27.1	8.8	52	26.6	8.1	53	26.0	8.1	54	25.4	7.6	57	25.6	8.8	57	24.5	7.9
max	53	32.6	7.4	54	32.1	7.6	56	31.8	8.5	57	31.1	7.9	57	30.0	7.4	59	29.8	6.9	62	29.9	7.5	64	29.5	7.0	67	29.6	8.1	68	28.5	7.6
min	65	37.8	8.7	65	36.7	7.5	66	35.8	7.8	66	34.7	7.2	68	34.0	6.9	70	33.8	7.2	72	33.1	7.2	72	32.0	6.6	73	31.4	5.9	77	31.5	7.0
max	70	39.3	6.7	72	38.7	6.6	73	38.0	6.2	73	36.9	5.9	75	36.6	6.6	77	35.9	6.1	77	34.8	4.8	79	34.7	5.2	81	34.6	5.1	82	33.8	5.3
min	77	41.4	3.6	79	41.3	4.6	80	40.6	4.7	81	40.1	5.4	82	39.3	5.3	83	39.1	5.3	84	38.3	5.2	85	38.1	6.0	86	37.7	6.3	86	36.6	5.2
max	84	44.9	5.6	85	44.7	6.0	86	44.4	6.3	87	44.0	7.0	87	42.9	6.2	87	41.7	5.9	89	42.6	7.8	90	42.3	7.6	91	42.2	7.6	91	41.1	7.3
min	87	47.3	5.9	90	48.9	7.6	90	47.8	7.2	92	48.5	8.3	92	47.4	8.1	93	47.1	8.1	94	47.1	8.8	97	48.4	10.4	98	47.8	10.1	98	46.7	10.1
max	92	51.8	6.9	95	53.5	8.8	97	53.9	9.6	98	53.3	9.4	100	53.8	10.9	102	53.8	12.0	105	53.9	11.3	107	53.7	11.4	109	53.5	11.3	112	53.6	12.5
min	105	60.5	13.3	105	59.4	10.5	107	59.2	11.4	109	59.0	10.5	109	57.9	10.5	111	57.5	10.3	112	56.9	9.8	114	56.4	7.9	115	55.8	8.0	117	54.9	8.2
max	110	62.3	10.5	112	62.4	8.9	114	61.9	7.9	114	60.8	7.4	116	60.2	6.4	117	59.4	5.6	119	59.1	5.2	120	58.2	4.5	122	57.8	4.3	124	57.6	4.0
min	120	66.0	5.4	119	64.6	5.2	121	64.1	4.9	122	63.3	4.3	124	63.1	5.2	124	62.0	4.5	126	61.8	4.9	126	60.7	4.3	127	59.9	4.1	129	59.7	4.8
max	125	68.1	5.8	127	67.7	5.3	128	67.1	5.2	128	66.0	5.2	129	65.2	5.0	129	64.1	4.8	131	63.9	4.8	133	63.9	5.7	134	63.4	5.6	134	62.3	4.7
min	129	69.7	3.7	133	70.6	6.0	134	70.0	5.9	135	69.2	5.9	135	68.1	5.0	137	68.3	6.3	139	68.1	6.3	140	67.3	6.6	141	66.7	6.8	142	66.0	6.3
max	137	73.8	5.7	140	73.9	6.3	140	72.8	5.7	140	71.7	5.7	142	71.5	6.3	144	71.1	6.9	146	71.1	7.1	147	70.2	6.3	148	69.4	6.0	151	69.4	7.1
min	142	75.9	6.3	146	76.6	6.0	147	75.7	5.7	147	74.6	5.4	149	74.3	6.2	150	73.5	5.2	152	73.2	5.2	153	72.4	5.1	154	71.5	4.8	156	71.5	5.5
max	151	79.3	5.5	151	78.2	4.3	153	77.9	5.1	153	77.0	5.3	155	76.5	5.0	156	75.9	4.8	158	75.6	4.5	158	74.4	4.2	160	74.1	4.8	163	74.7	5.3
	gem	SD		gem	SD		gem	SD		gem	SD		gem	SD		gem	SD		gem	SD		gem	SD		gem	SD		gem	SD	
	6.6	2.3		6.7	1.7		6.7	1.8		6.7	1.6		6.6	1.9		6.7	1.9		6.7	1.9		6.6	2.0		6.7	2.0		6.7	2.1	

Mean λs of points 5-14

gem	SD	FL(%)
6.7	1.8703	32.3

Fin 3

Wave period

point 5		Freq (	point 6			point 7			point 8			point 9			point 10			point 11			point 12			point 13			point 14		
frames	sec	Hz	frames	sec	Hz	frames	sec	Hz	frames	sec	Hz	frames	sec	Hz	frames	sec	Hz	frames	sec	Hz	frames	sec	Hz	frames	sec	Hz	frames	sec	Hz
20	0.160		23	0.184		19	0.152		19	0.152		21	0.168		18	0.144		17	0.136		17	0.136		17	0.136		14	0.112	
16	0.128		15	0.120		15	0.120		15	0.120		13	0.104		14	0.112		14	0.112		13	0.104		13	0.104		13	0.104	
15	0.120		13	0.104		13	0.104		14	0.112		13	0.104		14	0.112		13	0.104		14	0.112		13	0.104		13	0.104	
13	0.104		15	0.120		13	0.104		14	0.112		14	0.112		13	0.104		13	0.104		12	0.096		15	0.120		14	0.112	
12	0.096		12	0.096		14	0.112		14	0.112		13	0.104		13	0.104		15	0.120		15	0.120		18	0.144		18	0.144	
18	0.144		16	0.128		17	0.136		16	0.128		17	0.136		18	0.144		19	0.152		18	0.144		16	0.128		20	0.160	
17	0.136		18	0.144		17	0.136		16	0.128		18	0.144		18	0.144		15	0.120		15	0.120		14	0.112		14	0.112	
12	0.096		14	0.112		14	0.112		15	0.120		14	0.112		13	0.104		12	0.096		13	0.104		13	0.104		9	0.072	
14	0.112		13	0.104		13	0.104		14	0.112		12	0.096		10	0.080		12	0.096		11	0.088		10	0.080		9	0.072	
10	0.080		11	0.088		10	0.080		11	0.088		10	0.080		10	0.080		10	0.080		12	0.096		12	0.096		12	0.096	
8	0.064		10	0.080		11	0.088		11	0.088		13	0.104		15	0.120		16	0.128		17	0.136		18	0.144		21	0.168	
18	0.144		15	0.120		17	0.136		17	0.136		17	0.136		18	0.144		18	0.144		17	0.136		17	0.136		19	0.152	
18	0.144		17	0.136		17	0.136		16	0.128		16	0.128		15	0.120		14	0.112		13	0.104		13	0.104		12	0.096	
15	0.120		14	0.112		14	0.112		13	0.104		15	0.120		13	0.104		14	0.112		12	0.096		12	0.096		12	0.096	
15	0.120		15	0.120		14	0.112		14	0.112		13	0.104		12	0.096		12	0.096		13	0.104		12	0.096		10	0.080	
9	0.072		14	0.112		13	0.104		13	0.104		11	0.088		13	0.104		13	0.104		14	0.112		14	0.112		13	0.104	
12	0.096		13	0.104		12	0.096		12	0.096		13	0.104		15	0.120		15	0.120		14	0.112		14	0.112		17	0.136	
13	0.104		13	0.104		13	0.104		12	0.096		14	0.112		13	0.104		13	0.104		13	0.104		13	0.104		14	0.112	
14	0.112		11	0.088		13	0.104		13	0.104		13	0.104		12	0.096		12	0.096		11	0.088		12	0.096		12	0.096	
gem	SD		gem	SD		gem	SD		gem	SD		gem	SD		gem	SD		gem	SD		gem	SD		gem	SD		gem	SD	
0.113	0.026	8.83	0.115	0.023	8.73	0.113	0.019	8.83	0.113	0.016	8.83	0.114	0.021	8.80	0.112	0.020	8.90	0.112	0.018	8.90	0.111	0.017	9.00	0.112	0.018	8.93	0.112	0.028	8.93

Wave period		Frequence (Hz)
point 5-14		
gem	SD	
0.113	0.021	8.87