KILLER WHALES (*ORCINUS ORCA*) FEEDING ON SCHOOLING HERRING (*CLUPEA HARENGUS*) USING UNDERWATER TAIL-SLAPS: KINEMATIC ANALYSES OF FIELD OBSERVATIONS

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Summary

Killer whales (*Orcinus orca*) feeding on herring (*Clupea harengus*) in a fjord in northern Norway were observed using underwater video. The whales cooperatively herded herring into tight schools close to the surface. During herding and feeding, killer whales swam around and under a school of herring, periodically lunging at it and stunning the herring by slapping them with the underside of their flukes while completely submerged. The kinematics of tail-slapping were analysed in detail. Tail-slaps were made up of a biphasic behaviour consisting of two phases with opposite angles of attack, a preparatory phase (negative angles of attack) and a slap phase (positive angles of attack). During the slap phase, the mean maximum angle of attack of the flukes was 47 °. The maximum speed of the flukes, measured at the notch, increased with whale length (L_w) and was $2.2 L_w \, s^{-1}$, while the maximum acceleration of the flukes was size-independent and was $48 \, m \, s^{-2}$.

When killer whales slapped the herring successfully, disoriented herring appeared on the video at approximately the time of maximum fluke velocity, in synchrony with a loud noise. This noise was not heard when the tail-slaps 'missed' the target, suggesting that the herring were stunned by physical contact. Killer whales then ate the stunned herring one by one. Of the tail-slaps observed, 61 % were preceded by lunges into the school. We suggest that lunging was aimed at directing the school rather than at capturing the herring, since it occurred at a relatively low speed and there were no observations of the killer whales attempting to capture the herring during lunging behaviour. Given the high performance of the tail-slaps in terms of speed and acceleration, we suggest that tail-slapping by killer whales is a more efficient strategy of prey capture than whole-body attacks, since acceleration and manoeuvrability are likely to be poor in such large vertebrates.

Key words: killer whale, *Orcinus orca*, herring, *Clupea harengus*, tail-slap, kinematics, feeding behaviour.

Introduction

Cooperative hunting by killer whales (*Orcinus orca*) has been reported by various authors (Smith et al., 1981; Guinet, 1992; Similä and Ugarte, 1993; Florez-Gonzales et al., 1994; Dahleheim and Towell, 1994; Goley and Straley, 1994; Similä, 1997). These studies provide a descriptive analysis of the predatory behaviour of killer whales. However, no previous study has provided a quantitative analysis of killer whales' attacks on fish. It has been suggested that the unsteady swimming performance (i.e. acceleration and manoeuvrability) of aquatic vertebrates should decrease with increasing animal size (Webb and de Buffrenil, 1990). This is expected because thrust (proportional to an area) is used to 'manoeuvre a resistance' (i.e. the inertia of the body and entrained water, which is proportional to body volume, resists acceleration) (Webb and de Buffrenil, 1990). As a result, it has been proposed that large aquatic vertebrates may have developed a variety of means of prey capture to avoid accelerating the whole body (Norris and Møhl, 1983; Webb and de Buffrenil, 1990). When feeding on small, elusive prey such as schooling fish, many marine mammals, including killer whales, feed cooperatively and use a variety of feeding methods that do not involve chases. For instance, killer whales (Similä and Ugarte, 1993) and bottlenose dolphins (*Tursiops truncatus*) (Hult, 1982; Smolker and Richards, 1987) have been observed to stun fish by slapping them with their tails. Humpback whales (*Megaptera novaeangliae*) use a variety of foraging techniques such as bubble curtains (Jurasz and Jurasz, 1979; Hain et al., 1982) and surface lobtailing (Weinrich et al., 1992), possibly as means of 'trapping' and/or gathering the schooling fish on which they feed.

The cooperative feeding technique utilized by killer whales in northern Norwegian fjords is a complex behaviour that can be

thought of as consisting of two main phases, school-herding and feeding (Similä and Ugarte, 1993). During school-herding, the killer whales swim around and under a school of herring in a highly coordinated fashion and use vocalization sounds, gathering the school into a 'ball' close to the surface (Similä and Ugarte, 1993). During the feeding phase, the whales still swim closely around and under the school and they perform lunging and underwater tail-slaps. The whales stun the herring using these powerful tail-slaps and eat the stunned fish one by one. Similä and Ugarte (1993) reported that killer whale sounds recorded during this phase included echolocation clicks, whistles, calls and banging sounds associated with the tail-slaps.

The objective of this study was to conduct a kinematic analysis of the tail-slaps of killer whales with the aim of understanding the mechanisms underlying this particular feeding behaviour within the context of predator–prey encounters between killer whales and schooling herring.

Materials and methods

Field work was carried out during November 1992 in Tysfjord, northern Norway, within the main wintering area for adults and part of the adolescent stock of Norwegian spring-spawning herring (*Clupea harengus*). Video recordings were made in the upper 15 m of water, where the water temperature was 6–8 °C. The fish were dominated by the 1983 year class, whose average total length was 35 cm (Anon., 1993). Some herring, which were floating on the surface as a result of the killer whales' (*Orcinus orca*) slaps, were collected during the recording sessions and measured. Their total length was 34.7±0.15 cm (mean ± S.E.M., range 34–36 cm; *N*=20). The video material analysed in this study consists of 5 h of recordings of killer whales, of which 167 min (seven recording sessions) are of feeding behaviour, i.e. of tail-slaps and lunges at herring schools. All recordings were made between 10:00 h and 15:00 h on four consecutive days (14–17 November 1992). Killer whales from three different pods were recorded, pod NC (on 14, 15 and 16 November, in five recording sessions totalling 109.8 min), pod NG (on 16 November, in one recording session totalling 17.7 min) and pod NÅ (on 17 November, in one session totalling 39.15 min). The number of killer whales participating in the feeding behaviour varied throughout each recording session. In each of the recording sessions, a minimum of 10 and a maximum of 20 killer whales participated in the feeding behaviour on herring. Underwater video recordings were taken using a monochrome video camera (50 frames s⁻¹) with a 6 mm wide-angle lens viewing the whales and herring from a lateral perspective. The camera was mounted on a rig on an inflatable raft equipped with an electric outboard motor. The camera was remote-controlled by a joystick *via* teleflex cables and connected to a monitor and a video-8 recorder on board a 3.8 m Zodiac. Calm weather and sea conditions and the absence of wind allowed the camera to be kept steady.

Video analysis

The camera was calibrated under water by filming objects of known sizes at fixed distances. The equation of the calibration line is $y=2.32x$, where y represents the ratio between the real size of the object and its apparent size (in meters) and x represents the distance from the camera (in meters) (Graves, 1977). In addition, image distortion at the periphery of the field of view was evaluated by filming tiles (11.5 cm×11.5 cm) on the interior walls of a swimming pool with the camera at three distances (1, 4 and 8 m) from the wall. The edge length of tiles near the periphery of the camera's field of view was measured and compared with the edge length of a reference tile in the centre of the field of view. The underestimation (relative to the reference tile) of the edge length was 3.68±0.53 % (mean ± S.E.M., *N*=32) with a maximum of 7.5 %. Video analysis of killer whales near the periphery of the field of view was nevertheless avoided.

For reference points, we used a minimum of three inanimate objects (mainly fish scales, of which many were visible at any one time) in different regions of the field of view. We assumed that their apparent movements, which were minimal and the same for the three objects, were due to the movement of the camera. Analysis was performed in three dimensions, following Graves (1977). Dimensions in the plane perpendicular to the camera lens were estimated by assuming that the herring were 35 cm long (see above). To estimate the third dimension (i.e. the distance from the camera), the apparent size (on the video screen, JVC, 41 cm×34 cm) of herring swimming perpendicular to the camera was used (Graves, 1977). The distance between any fish and the camera was determined by calculating the ratio of the herring standard length (35 cm) to its apparent length and then substituting this value into the calibration equation of the underwater video camera. The x and y values were corrected for parallax errors in three dimensions. Only those sequences in which the killer whales appeared to be perpendicular to the camera (judging by the alignment of the whale's fins) and in which the length of the whale varied by less than 5 % between the first and last frames of the event (tail-slap or lunge) recorded were used. Estimates of distances in the plane perpendicular to the camera and of the whale's length were based on the apparent length of fish affected by the tail-slap or the lunge and, therefore, close to the same vertical plane as the whale. Analysis of tail-slaps that did not affect any herring was based on the dimensions of the whales (L_w, whale length) (i.e. velocity and acceleration were expressed as $L_w s^{-1}$ and $L_w s^{-2}$, respectively).

A killer whale lunge was defined as rapid swimming towards and into the school. Not all the lunges were within the field of view for their entire duration. Therefore, we only analysed lunges in which the distance travelled recorded was at least L_w. The lunging speeds were estimated by digitising successive positions of the tip of the head or, in cases in which the tip of the head was hidden by herring, other fixed points on the whale's head such as the eye or the white spot behind the eye. Average and maximum lunging speeds were calculated over a period of approximately 1 s during the final phase of the lunge.

The kinematics of tail-slaps was estimated by digitising the position of the notch of the tail of the killer whale during the
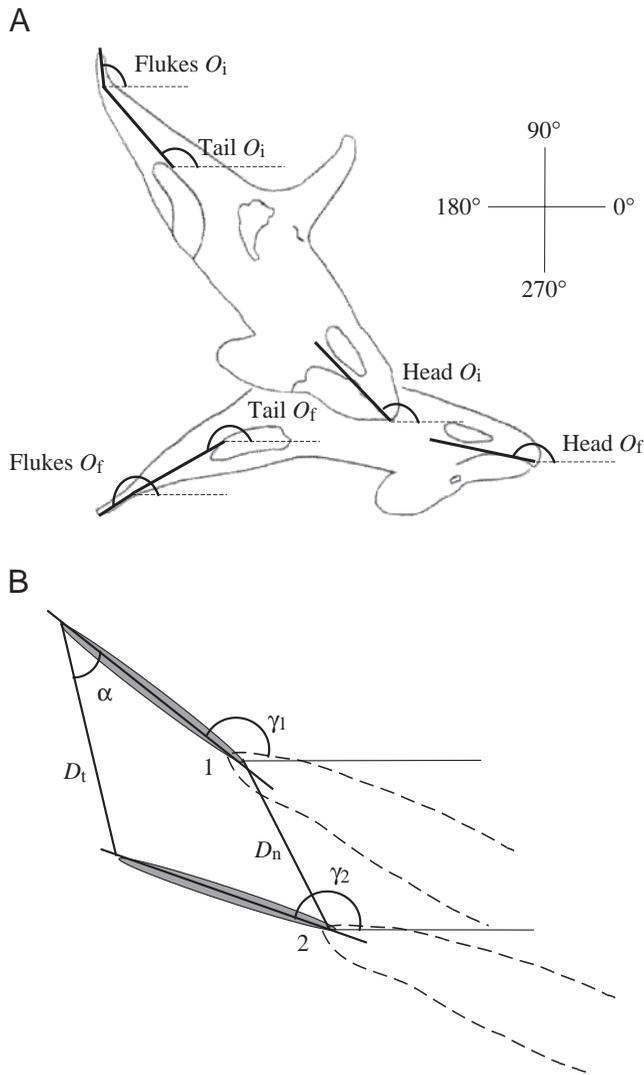
Fig. 1. (A) The orientation of the flukes, tail and head at the beginning (O_i) and the end (O_f) of the tail-slap phase. Solid lines show the segments indicating fluke, tail and head orientation relative to the horizontal (broken line). The angles were measured as shown in the inset in the upper right of the figure. The slaps were analysed as if the whale had been filmed from its right, even if the slaps were recorded from its left side. (B) Angle of attack (α) of a tail-slap in lateral view. Two successive frames are shown. The flukes of the killer whale (grey area) and part of the body (discontinuous lines) are shown. α is the angle between the flukes (in lateral view) at a given position and the line passing through two successive positions of the tips of the flukes. 1 and 2 indicate two successive positions of the tail notch, and their corresponding orientations (γ_1 and γ_2) are used to derive the angular velocity of the tail-slap. D_t and D_n correspond to the distance travelled between two successive frames by the flukes' tip and the tail notch, respectively.

tail-slap. Tail-slap velocity and acceleration were calculated by using successive positions of the tail notch.

For sequences in which the entire fluke (both the tail notch and tail tip in horizontal view) was visible, the following additional variables were measured in the lateral view.

(1) The orientations of three body segments: the flukes, the tail (estimated as the midline of the whale at the posterior quarter of body length excluding the flukes) and the head (estimated as the midline of the whale at the anterior quarter of body length excluding the flukes). The orientations of each of these segments at the beginning and the end of the slap phase were defined as O_i and O_f, respectively (Fig. 1A). The tail-slaps were analysed as if the whale had been filmed from its right, even if the slaps were recorded from its left side.

(2) The angular velocity of the flukes, the tail and the head, calculated as the difference between two successive orientations in horizontal view, per unit time (Fig. 1B). Positive angular velocity indicates a downward change in the orientation (i.e. movement in a dorso-ventral direction relative to the killer whale).

(3) The fluke's angle of attack (α), defined as the angle between the orientation of the flukes at a given frame and the line passing through two successive fluke tip positions (Fig. 1B) (see Videler and Kamermans, 1985). Positive angles of attack are in the dorso-ventral direction relative to the killer whale.

(4) The duration and amplitude of the preparatory phase and the slap phase. Here, we define the preparatory phase as the first phase of the tail-slap, during which the angle of attack is negative, and the slap phase as the subsequent phase during which the angle of attack is positive. The amplitudes were measured in body lengths (L_w), and corresponded to the distance between the tail tips at the beginning and the end of each phase.

(5) The volume of water per unit time ($m^3\,s^{-1}$) crossed by the whales' flukes (V_i) was estimated in consecutive frames using the following equation:

$$V_i = F D_m S \sin\omega, \qquad (1)$$

where F is the filming frequency (50 Hz), S is the planar surface of the tail of each whale (the surface of the flukes on one side of the flukes; Fish, 1998a), estimated by using the relationship between body length (L_w) and the flukes' planar surface (S) determined from 11 Icelandic whales from Sea World Orlando: $S = 0.004727 L_w^{2.7}$ ($P < 0.001$; $r^2 = 0.79$, $N = 11$).

$$D_m = (D_t + D_n)/2, \qquad (2)$$

where D_m is the mean of D_t (the distance travelled by the flukes' tip) and D_n (the distance travelled by the tail notch between two successive frames) (Fig. 1B).

$$\omega = (\alpha + \beta)/2, \qquad (3)$$

where ω is the mean of α and β, the angle of attack of the flukes in the first and second frames of a consecutive pair, respectively.

(6) V_{tot}, the estimated total volume of water crossed by the flukes during the slap phase, i.e. from the first pair (f) to the last pair (l) of frames of the tail-slap, and was calculated as:

$$V_{tot} = \sum_{f}^{l} D_m S \sin\omega. \qquad (4)$$

Values for these variables were smoothed using a five-point weighted mean (Savitzky and Golay, 1964) and Prism software. When digitising tail-slaps, the view of the tail was occasionally hidden by stunned fish. This resulted in a missing point in the velocity curve and may have resulted in an underestimation of the maximum speeds.

Acoustic analysis

An Offshore Acoustics omnidirectional hydrophone with a flat response (± 3 dB) from 6 Hz to 14 kHz was used to detect sound, which was recorded directly on the videotape audio track. Oscillograms (amplitude *versus* time) were obtained by sampling at 44.2 kHz using AVID MCXpres for Windows NT, which allowed us to synchronise the oscillogram with the video images. This technique allowed the temporal relationship between the tail movement, the loud sound and the appearance of disoriented fish to be interpreted. A single oscillogram from a slap that was successful (a 'hit') is compared with the oscillogram of an apparent 'miss'.

Event recording

All tail-slaps and lunges recorded (but not necessarily analysed) were counted during the feeding behaviour of each pod, as were lunges followed by tail-slaps. This allowed us to measure the proportion of tail-slaps that occurred after a lunge relative to the total number of tail-slaps, the proportion of lunges followed by a tail-slap relative to the total number of lunges, and the frequency of occurrence of tail-slaps and lunges. The whales were not within the field of view at all times, so the number of tail-slaps and lunges we recorded is an underestimation of the actual number of events.

Results

Lunging

While encircling the herring, killer whales periodically lunged into the school. The lunges we recorded were all approximately in the horizontal plane (i.e. between $-30°$ and $+30°$ relative to the horizontal plane). Lunging was often followed by tail-slaps and was never observed to be followed
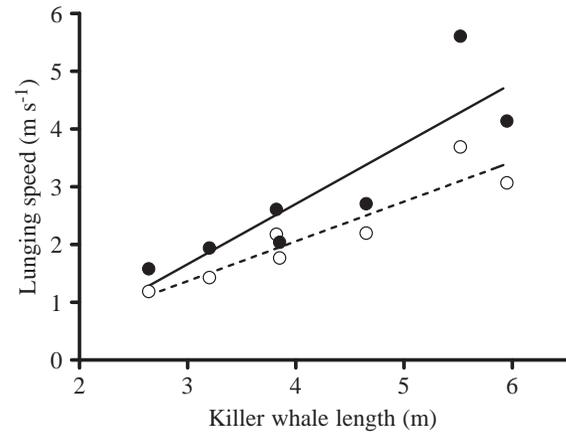

Fig. 2. The relationship between mean (open circles, V_{mean}) and maximum (filled symbols, V_{max}) lunging speeds and killer whale total length. The corresponding linear regressions (V_{mean}, $y=0.69x-0.77$, $r^2=0.86$, $P<0.01$, $N=7$; V_{max}, $y=1.02x-1.47$, $r^2=0.77$, $P<0.05$, $N=7$) are shown as discontinuous and continuous lines, respectively.

by fish capture. Lunging speed (in m s^{-1}) was calculated for seven sequences (three for pod NC, one for pod NG and three for pod NÅ) and was related to whale length (Fig. 2: mean speed V_{mean}, $y=0.69x-0.77$, $r^2=0.86$, $P<0.01$; maximum speed, V_{max}, $y=1.02x-1.47$, $r^2=0.77$, $P<0.05$). For all the lunges analysed, average lunging speed was 0.51 ± 0.03 L_w s^{-1} and maximum lunging speed was 0.67 ± 0.06 L_w s^{-1}. The highest individual lunging speeds recorded were 5.6 m s^{-1} (maximum speed) and 3.7 m s^{-1} (average speed) by a whale estimated to be 5.5 m long, equivalent to 1.02 L_w s^{-1} and 0.67 L_w s^{-1}, respectively. Although the sample sizes were too small to compare data among pods, there was no qualitative difference between the lunging speeds of killer whales from the three different pods observed.

Tail-slapping

Killer whales were observed to slap the herring school with the underside of their flukes while completely submerged. These tail-slaps were either preceded by a lunge or occurred

Table 1. *Kinematic variables of the tail-slaps*

| | Whale length (m) | Maximum tail-slap speed | | | Maximum tail-slap acceleration | | T_{Vmax} (s) | α | | V_i (m^3 s^{-1}) | V_{tot} (m^3) |
		(m s^{-1})	(L_w s^{-1})	(L_h s^{-1})	(m s^{-2})	(L_w s^{-2})		Maximum (degrees)	Mean (degrees)		
Mean	4.7	10.5	2.2	30	47.7	9.7	0.29	47	29	3.3	1.3
S.E.M.	0.4	0.8	0.1	2.4	4.0	1.0	0.07	5	2	1.1	0.5
Range	3.7–6.0	7.9–13.6	1.6–2.7	23–39	32–59	6–15	0.16–0.48	35–60	26–32	1.2–4.9	0.4–1.9
N	6	6	9	6	6	9	4	4	4	3	3
Type	6h	6h	6h+3m	6h	6h	6h+3m	3h+1m	3h+1m	3h+1m	3h	3h

Values include means of hits only (h) or of hits and misses pooled (h+m).

L_w is killer whale length, L_h is herring length (35 cm), T_{Vmax} is the time to maximum tail velocity, α is fluke angle of attack, V_i is the volume of water per unit time crossed by the whales' flukes, V_{tot} is the estimated total volume of water crossed by the flukes during the slap phase.

as the whales were swimming along the perimeter of the school. The velocity and acceleration of tail-slaps were analysed in nine sequences (four for pod NC, two for pod NG and three for pod NÅ). In six of these sequences, herring were observed within the region of the slap, and the tail-slap was accompanied by a loud sound that corresponded to the appearance of disoriented fish in the video image (these sequences were considered 'hits'), while in three sequences no such noise was detected and no herring were observed within the region of the slap (these sequences were considered 'misses'). Four of these tail-slap sequences (one 'miss' and three 'hits') were suitable for further kinematic analyses (i.e. both tail notch and tail tip were visible in the horizontal view) which included digitisation of both the flukes' tips and the tail notch. Statistical comparison between misses and hits was performed only for velocity and acceleration, since a sufficient sample size was attained for these variables (three misses and six hits), and not for those variables (i.e. T_{Vmax}, angle of attack α, V_i and V_{tot} in Table 1; all variables in Tables 2 and 3) for which sample sizes were too low to permit statistical comparison (one miss and three hits). Nevertheless, for all these variables, the value for the miss was within the range for the hits or at least no more than 10 % higher or lower than the extremes of the range of values found in the hits. Since there were no large qualitative differences, mean values for these variables are for the pooled data (one miss and three hits). Similarly, the scaling relationship with killer whale length was investigated only for velocity and acceleration of hits (*N*=6),

since only hits permitted the estimation of the killer whales' total length by relating the apparent length of the whales to that of the herring affected by the hit.

An example of a tail-slap is shown in Fig. 3, in which the estimated midline of a killer whale is shown in lateral view. Fig. 4 shows the tracing of the tail in lateral view for a hit (Fig. 4A) and a miss (Fig. 4B). Their relative kinematic variables plotted against time and the relative oscillogram are shown in Fig. 5. The two events appear qualitatively similar kinematically, but only the hit produced a loud noise in conjunction with the appearance of disoriented fish on the screen (Fig. 5F). We suggest that the killer whales hit the herring (i.e. there was physical contact between the killer whales' flukes and the herring), producing the loud noise. This is in accordance with the physical conditions of some of the herring recovered floating at the surface (e.g. with broken backs and large scratches). Both oscillograms in Fig. 5F show a relatively high noise level, possibly due to the various events occurring while the whales were circling the herring, which may include vocalization, sonar click trains and water surface splashes produced by the killer whales (Similä and Ugarte, 1993). The oscillogram for the miss (Fig. 5Fii) shows a lower relative noise level than that for the hit (Fig. 5Fi), as well as what could be a train of sonar clicks, corresponding to almost
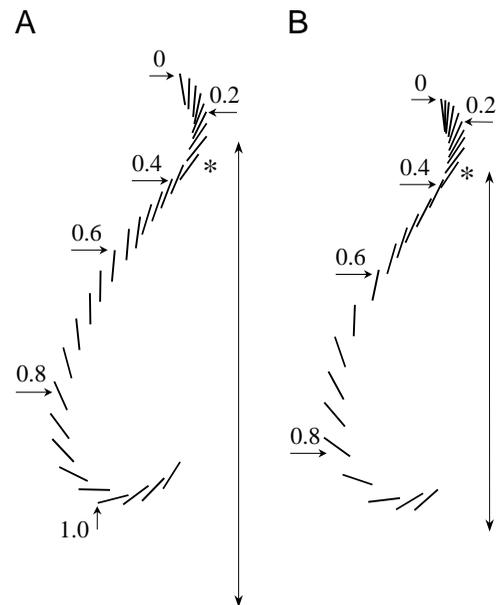
Fig. 4. Tracing of the flukes during a hit (A) and a miss (B) in lateral view. The flukes are completely submerged throughout the tail-slap. The orientations of the tracings are similar for the purpose of comparison and do not reflect their relative orientations in the water column. Numbers indicate time (s) and are associated with a given frame by arrows. Only the tracings from every second image are shown (i.e. 25 Hz). The killer whale is oriented as in Fig. 3, i.e. with the tail on the left side of the figure and the head looking to the right of the figure. Asterisks indicate the end of the preparatory phase, corresponding to the beginning of the slap phase. Double-pointed arrows next to the tracings show the total killer whale length for each tail-slap. The whale length in A was estimated to be 6 m.
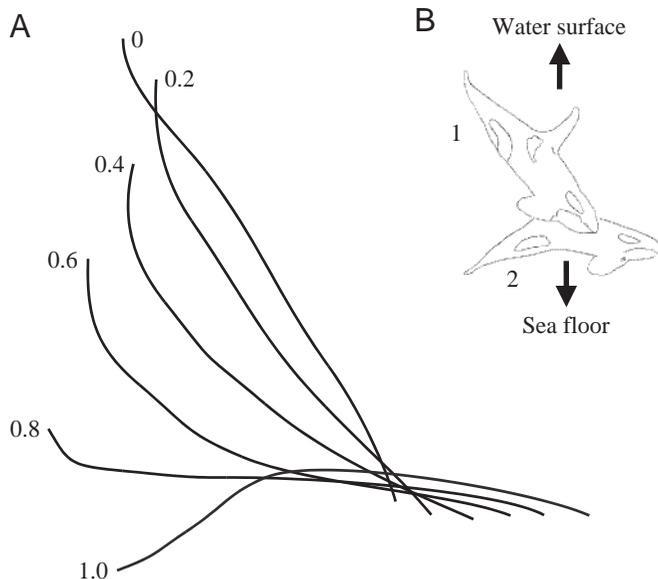

Fig. 3. (A) Tracing of the estimated midline of a killer whale during a tail-slap in lateral view. The killer whale is completely submerged throughout the tail-slap, with the water surface and sea floor oriented at the top and bottom of the figure, respectively. The estimated killer whale length is 6 m. Numbers indicate time (s) and are positioned by the tail end of the animal. (B) Small-scale drawings of the killer whale outlines at the beginning (1) and at the end (2) of the tail-slap traced in A.
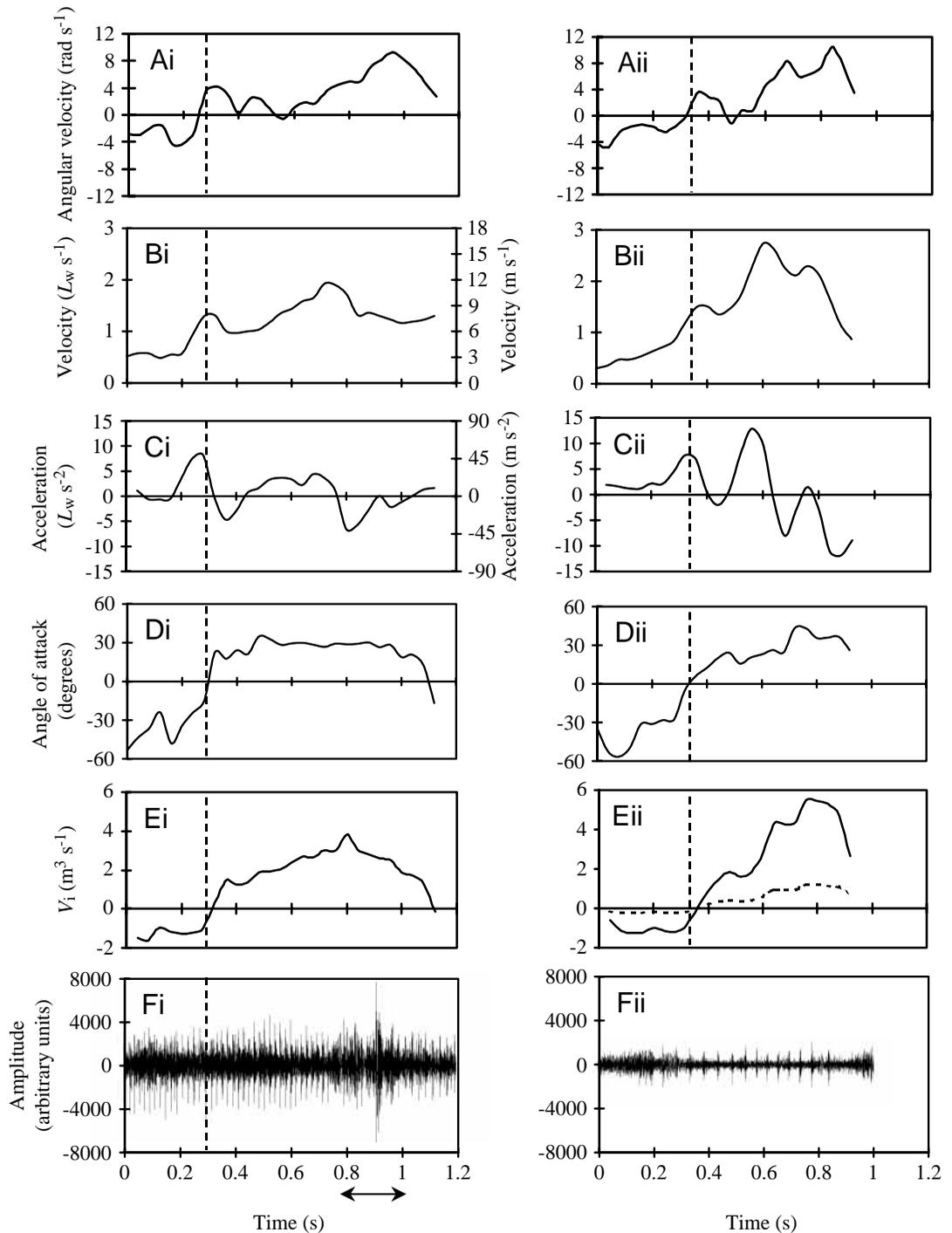
Fig. 5. Kinematic variables (A–E) and oscillograms (F) during a hit (i) and a miss (ii) corresponding to the tracings of Fig. 4. V_i (the volume of water crossed by the whale's flukes in unit time) in Eii is estimated for a killer whale of 6 m (continuous line) and 4 m (broken line). The double-pointed arrow below the graphs indicates the period over which disoriented herring appear on the video recording. Vertical dashed lines indicate the transition from the preparatory phase to the slap phase. L_w, whale length. Velocity in m s^{-1} and acceleration in m s^{-2} are indicated only for the hit (right-hand y-axis in Bi and Ci, respectively), for which whale length was estimated.

evenly spaced high-frequency spikes between approximately 0.2 and 0.8 s in the oscillogram. These high-frequency spikes are similar to those observed by Barrett-Lennard et al. (1996) during feeding of killer whales preying on fish.

Fluke kinematics

The kinematics of tail-slaps showed a biphasic pattern on the basis of the velocity, acceleration, angle of attack and angular velocity profiles. Here, we define the preparatory phase (PP) as the phase during which the angle of attack is negative,

and the slap phase (SP) as the phase during which the angle of attack is positive. Therefore, the preparatory phase and the slap phase (Fig. 4) do not correspond precisely to an upstroke and downstroke in swimming (which are defined relative to the direction of motion). At the beginning of the preparatory phase (Fig. 3), the killer whale body is relatively straight. The killer whale (including the flukes) is completely submerged during the entire tail-slap, and there is therefore no contact with the water surface. During the preparatory phase, the tail was swept in a ventro-dorsal direction, with a small amplitude. At the

Table 2. *Amplitude and duration of the preparatory phase (PP) and slap phase (SP)*

	PP amplitude (L_w)	SP amplitude (L_w)	PP duration (s)	SP duration (s)	Amplitude ratio, SP/PP	Duration ratio, SP/PP
Mean	0.2	0.88	0.3	0.68	4.5	2.3
S.E.M.	0.01	0.07	0.02	0.05	0.25	0.2
Range	0.17–0.24	0.73–1.02	0.24–0.34	0.60–0.80	4.0–5.2	1.8–2.5
N	4	4	4	4	4	4
Type	3 h+1 m	3 h+1 m	3 h+1 m	3 h+1 m	3 h+1 m	3 h+1 m

Values include means of hits and misses pooled (h+m).
L_w is killer whale length.

beginning of the slap phase, the body of the whale is bent into a 'C', with the concave side dorsally. During the slap phase, the body contracts into an opposite 'C' (i.e. with the concave side ventrally) while the tail makes a large-amplitude movement (Fig. 3). The durations and amplitudes of these two phases are given in Table 2. The amplitude and duration of the slap phase are larger and longer, respectively, than those of the preparatory phase (Mann–Whitney test; $P<0.05$ in both cases). The ratios (SP/PP) are 4.5±0.25 and 2.3±0.2 for amplitude and durations, respectively (Table 2).

In both the hit and the miss, the angular velocity of the flukes is mostly negative during the preparatory phase and positive throughout the slap phase (Fig. 5A) (maximum values were 9.2±0.6 rad s^{-1}; $N=4$, Table 3), although it approaches zero in the middle of the slap phase (i.e. the orientation of the flukes is kept constant). The flukes' maximum angular velocity for misses and hits could not be compared statistically because of the small sample size (three hits and one miss). However, the maximum angular velocity of the only miss measured (10.4 rad s^{-1}) is only 9 % higher than the highest angular velocity measured in hits (range 7.5–9.6 rad s^{-1}), and the pooled data are shown in Table 3.

Tail-slap velocity shows a biphasic increase (Fig. 5B). Local maxima in acceleration occur during the transition from the preparatory phase to the slap phase and in the middle of the slap phase, when angular velocity is minimal (Fig. 5A,C). Maximum tail-slap velocity (in m s^{-1}) could be measured only for hits, since the dimension of the whales were estimated on the basis of the apparent dimension of the herring affected by
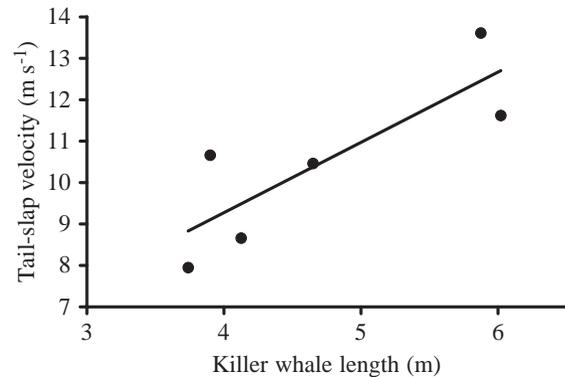

Fig. 6. The relationship between maximum tail-slap velocity (y), measured at the tail notch, and killer whale length (x). A linear regression line has been fitted to the data: $y=1.7x+2.5$; $r^2=0.69$; $P<0.05$, $N=6$.

the slap. Maximum tail-slap velocity was linearly related to whale length (L_w) (Fig. 6: $y=1.7x+2.5$; $r^2=0.69$; $P<0.05$) and on average was 10.5±0.8 m s^{-1} (mean ± S.E.M., $N=6$). The highest tail-slap velocity recorded was 13.6 m s^{-1} for a whale estimated to be 5.9 m long. Maximum relative tail-slap velocity (i.e. in L_w s^{-1}) was measured in both hits (mean 2.2±0.1 L_w s^{-1}, $N=6$) and misses (mean 2.2±0.3 L_w s^{-1}, $N=3$) and no difference was found between them (t-test; $P>0.5$). The time from the beginning of the tail-slap phase to maximum tail velocity (T_{Vmax}) was calculated for tail-slaps in which the tail tip and notch were clearly visible. T_{Vmax} was 0.29±0.07 s [$N=4$; three hits (range 0.16–0.48 s) and one miss (0.32 s) pooled; Table 1].

Table 3. *Angular variables of the tail-slaps*

	Maximum angular velocity (rad s^{-1})			O_i (degrees)			O_f (degrees)			O_f–O_i (degrees)		
	Flukes	Tail	Head	Flukes	Tail	Head	Flukes	Tail	Head	Flukes	Tail	Head
Mean	9.2	6.0	3.4	61	111	167	220	244	173	158	132	6
S.E.M.	0.6	0.3	0.4	21	16	13	19	14	12	11	4	11
Range	7.5–10.4	5.3–6.6	2.5–4.2	5–100	65–135	141–201	164–245	205–272	142–198	132–186	121–140	−17–26
N	4	4	4	4	4	4	4	4	4	4	4	4
Type	3 h+1 m	3 h+1 m	3 h+1 m	3 h+1 m	3 h+1 m	3 h+1 m	3 h+1 m	3 h+1 m	3 h+1 m	3 h+1 m	3 h+1 m	3 h+1 m

Values include means of hits and misses pooled (h+m).
O_i and O_f are the initial and final positions, respectively, of the body segments (head, tail and flukes).

Maximum acceleration during a tail-slap was $47.7\pm4.0\,\mathrm{m\,s^{-2}}$ (hits only; $N=6$; range $32.2-59.2\,\mathrm{m\,s^{-2}}$; Table 1) and was not related to whale length ($P>0.5$). Maximum relative tail-slap acceleration (i.e. in $L_\mathrm{w}\,\mathrm{s^{-2}}$) was calculated for both hits ($10.4\pm1.1\,L_\mathrm{w}\,\mathrm{s^{-2}}$; $N=6$) and misses ($8.3\pm2.3\,L_\mathrm{w}\,\mathrm{s^{-2}}$; $N=3$). No difference was found between these values (t-test; $P>0.25$). The mean acceleration during T_Vmax was calculated for hits and was $27.6\pm12.4\,\mathrm{m\,s^{-2}}$ ($N=3$).

The angle of attack *versus* time curve does not vary greatly during the slap phase (Fig. 5D), and its maximum value is $47\pm5\,^\circ$ for all tail-slaps pooled (three hits and one miss). As for angular velocity, the maximum angle of attack of misses and hits could not be statistically compared because of small sample sizes. However, the maximum angle of attack of the only miss measured ($43\,^\circ$) is within the range of the maximum angles of attack observed for hits ($35-60\,^\circ$). The mean angle of attack during the slap phase was $29\pm2\,^\circ$ (range $26-32\,^\circ$; Table 1).

V_i reaches a maximum around the time of maximum tail-slap velocity (Fig. 5E). Maximum values for hits are $3.3\pm1.1\,\mathrm{m^3\,s^{-1}}$ (range $1.2-4.9\,\mathrm{m^3\,s^{-1}}$; Table 1). V_i was measured for only one miss and was $1.2-5.5\,\mathrm{m^3\,s^{-1}}$, assuming a lower and upper limit of killer whale lengths of 4 or 6 m, respectively. This range is similar to that observed in hits.

Angular variables along the killer whale body

An example of the time course of the angular variables (orientation and angular velocity) for various body segments (i.e. flukes, tail and head) is shown in Fig. 7. Mean values are shown in Table 3. The curve for the tail orientation is similar to that of the flukes, although it is greater by approximately $30\,^\circ$ (i.e. the flukes are 'bent' backwards by approximately $30\,^\circ$) throughout most of the tail-slap except towards the end of the slap, when the orientation of the flukes and tail is similar. This is reflected in similar curves for angular velocity for the tail and the flukes, albeit with a larger amplitude for the flukes. The head shows orientation and angular velocity curves of smaller amplitude than those of the flukes and the tail, and in an almost opposite direction during the slap phase. Mean values of O_i were $61\pm21\,^\circ$, $111\pm16\,^\circ$ and $167\pm13\,^\circ$ for the flukes, the tail and the head, respectively. Mean values of O_f were $220\pm19\,^\circ$, $244\pm14\,^\circ$ and $173\pm12\,^\circ$ for the flukes, the tail and the head, respectively. The angular differences between O_f and O_i are $158\pm11\,^\circ$, $132\pm4\,^\circ$ and $6\pm11\,^\circ$ for the flukes, the tail and the head, respectively (Table 3).

Considerations on sample sizes for the kinematics of tail-slaps

While sample sizes were too small to make statistical comparisons among pods, there was no qualitative difference between the kinematics of tail-slaps of killer whales from the three pods. The sample size (N) considered here for both tail-slaps and lunges corresponds to the number of events recorded. Sample size may appear low compared with laboratory studies of kinematics or with ecological field studies. However, measuring kinematic variables in the field is a challenging task, and observations of this kind are extremely rare and difficult to obtain.

Estimate of the maximum number of herring hit by the whale

The total volume of water crossed by the flukes during the slap phase (V_tot) was $1.3\pm0.5\,\mathrm{m^3}$ (Table 1). Using the observed herring density ($24.6\,\mathrm{fish\,m^{-3}}$; P. Domenici, R. S. Batty and T. Similä, in preparation), the theoretical maximum number of herring physically touched by the flukes is 33 ± 12 (range $10-47$). This is possibly an overestimation, since herring did not appear to be hit throughout the whole slap phase, as suggested by the video images (the tail-slap was within the region occupied by the school for no more than $50\,\%$ of the slap phase, around the time of maximum velocity).

Event recording

Table 4 gives details of all the lunges, the tail-slaps and the lunges followed by tail-slaps recorded (of which only seven were suitable for kinematic analyses) for each pod. More than half the lunges were followed by tail-slaps, and more than half the tail-slaps were preceded by a lunge. The frequency of lunges and tail-slaps is approximately $1.5\,\mathrm{min^{-1}}$, although our observations are likely to underestimate the actual number of events.
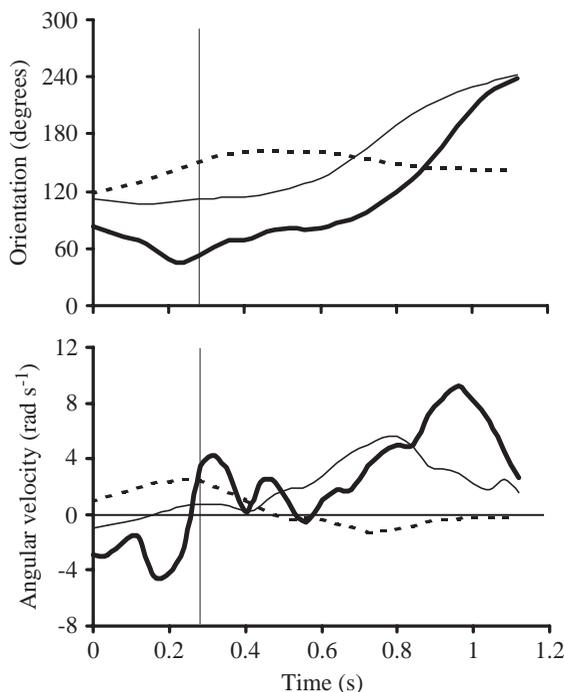

Fig. 7. Orientations and angular velocities of the flukes (thick line), the tail (thin line) and the head (broken line) during a tail-slap. The end of the preparatory phase, corresponding to the beginning of the slap phase, is indicated by the vertical lines in the graphs.

Discussion
The significance of lunging behaviour and tail-slaps

While encircling the herring, killer whales periodically

Table 4. *Total number of tail-slaps, lunges and lunges followed by tail-slaps for each pod*

Pod	Total Tail-slaps	Total lunges	Lunges followed by tail-slaps	% Tail-slaps after lunges	% Lunges followed by tail-slaps	Frequency of tail-slaps (min^{-1})	Frequency of lunges (min^{-1})
NC	79	132	52	66	39	0.72	1.2
NG	34	31	21	62	68	1.92	1.75
NÅ	69	68	39	56	57	1.76	1.74
Mean				61	55	1.47	1.56
S.E.M.				3	8	0.38	0.18

The frequency of tail-slaps and lunges is also given.

lunged into the school. However, lunging behaviour was never followed by fish capture but was often followed by tail-slaps. We hypothesize that lunging was not a chasing behaviour aimed at capturing the swimming herring directly with the mouth, but rather a manoeuvre aimed at directing the school before stunning the herring with a tail-slap. This is confirmed by the relatively low swimming speeds employed by the whales during lunging compared with values in the literature. Fish (1998a) found that cruising speeds of killer whales range between 2 and 5 m s^{-1} and reported burst speeds from the literature ranging between 12.5 and 15.4 m s^{-1}. Therefore, killer whales are capable of much higher speeds than those observed during lunging behaviour in the present study (the maximum lunging velocity recorded was 5.6 m s^{-1}).

To make hypotheses about the significance of lunging behaviour, velocity should also be considered in terms of herring swimming performance. Killer whale lunging speeds ranged between 4.5 and 16 L_h s^{-1} (where L_h is herring length) for peak values, and between 3.4 and 10.5 L_h s^{-1} for mean values. Previous work suggests that a 35 cm escaping herring should be capable of reaching a maximum burst swimming speed of 7 L_h s^{-1} at 7 °C with a stride length of 0.8L_h (based on Wardle, 1975; Batty and Blaxter, 1992). Therefore, lunging speed would not always have been sufficient to capture escaping herring since it did not always exceed the maximum swimming speed achievable by herring. Lunging speed could have been a means of approaching the herring to then capture them with a further acceleration. Other predators use submaximal speeds to approach prey (Webb, 1984). However, in the context that we have observed, lunging was never followed by prey capture.

Tail-slapping was effective in stunning the herring, and the stunned herring were easily picked up and eaten one by one by the whales. Tail-slap velocity far exceeds the maximum velocity of herring, since tail-slap velocity ranged between 23 and 39 L_h s^{-1} (Table 1). We suggest that the use of tail-slaps is a more efficient technique for capturing herring than whole-body attacks for two main reasons.

First, tail-slap velocity can be as high as 13.6 m s^{-1} and can be reached by the killer whale flukes in less than 0.5 s (Table 1). Although previous observations show that similar speeds could be reached by a swimming killer whale (Johannessen and Harder, 1960), they would be achieved only

after a number of tail beats. In addition, the maximum speed of 15.4 m s^{-1} reported by Johannessen and Harder (1960) has been questioned by Kooyman (1989), because the whales were swimming quite close to the boat. Tail-slap acceleration is quite high, averaging 47.7 m s^{-2}. This value is similar to the accelerations of various fish species (Domenici and Blake, 1997) and is unlikely to be achieved by a swimming killer whale, given the low acceleration associated with large size in aquatic vertebrates (Webb and de Buffrenil, 1990).

Second, the strategy of stunning a number of herring with a single tail-slap may imply a more efficient foraging strategy than capturing herring with the mouth using chases, during which whales may be subject to the confusion effect typical of predators that try to capture aggregative prey (Pitcher and Parrish, 1993).

It has been suggested that the unsteady swimming performance (i.e. acceleration and manoeuvrability) of marine vertebrates should decrease with increasing animal size (Webb and de Buffrenil, 1990). No data are available on killer whale acceleration performance, but some data exist on the acceleration performance of other delphinid species. Lang and Pryor (1966) measured a peak velocity for *Stenella attenuata* of 11.03 m s^{-1} during a burst of 2 s, corresponding to an acceleration of 5.52 m s^{-2}. Lang and Daybell (1963) recorded a single run by *Lagenorhynchus obliquidens* with a top speed of 7.76 m s^{-1} within 1 s (i.e. an acceleration of 7.76 m s^{-2}). On the basis of power output, F. E. Fish (personal communication) estimated that the acceleration of a 1600 kg killer whale over a 10 s burst should be approximately 2.8 m s^{-2}. Although all these values are calculated over a burst of a few seconds, and are therefore averages, they can be compared with average accelerations in fish, which are higher, ranging between approximately 10 and 50 m s^{-2} (Domenici and Blake, 1991). Similarly, the mean acceleration attained by the killer whale tail (during the time up to maximum velocity, T_{Vmax}) reaches 27.6 m s^{-2}, which is much higher than that of burst-swimming dolphins. Further studies on cetacean acceleration using similar filming rates and time intervals would be useful to compare data with those for fish.

Cetacean manoeuvrability has been investigated recently by Fish (1996). The relative turning radius (measured in the horizontal plane) of cetaceans is similar to that of fish in terms of percentage of the body length (11–17 % body length in seven

species of cetaceans, Fish, 1996; 5–22 % in six species of fish and 47 % in yellow-fin tuna; Domenici and Blake, 1997), and their absolute turning radii are therefore larger than those of most fish. Maximum turning rate gives an indication of the time required for a fast turn such as that utilized for escaping a predator or catching prey. Maximum turning rate in cetaceans was found to be $455\,°\,s^{-1}$ (Fish, 1996; $287\,°\,s^{-1}$ in killer whales; F. E. Fish, personal communication). These values are lower than those found in teleosts, which range from $2500\,°\,s^{-1}$ in herring (Domenici and Batty, 1997) to $8000\,°\,s^{-1}$ in angelfish (Domenici and Blake, 1997).

Webb and de Buffrenil (1990) suggest that, given their relatively low unsteady swimming performance, many large aquatic vertebrates are plankton-feeders, which implies a feeding mechanism that does not require high manoeuvrability. It is apparent that cetaceans such as killer whales and humpback whales, which feed on elusive schooling prey, have developed particular behavioural (e.g. carousel feeding in killer whales, bubble nets in humpback whales; Hain et al., 1982; Jurasz and Jurasz, 1979) and/or morphological (the large flippers of humpback whales used in manoeuvering; Fish and Battle, 1995) adaptations that allow them cooperatively to hunt schools of fish. Within these behavioural strategies, poor unsteady swimming performance (i.e. poor acceleration and manoeuvrability) is compensated for by the use of 'weapons' such as bubble curtains (Sharpe and Dill, 1997) and tail-slaps, effectively replacing the direct attack/capture technique utilized by many piscivorous fish (Domenici and Blake, 1997). Such feeding strategies are particularly efficient when preying upon relatively small fish, since they can be elusive to single attacks (given their high manoeuvrability relative to that of whales) but become vulnerable when encircled by the whale and stunned by their tail-slaps. We hypothesize that tail-slapping has evolved as a more efficient feeding strategy than chases for capturing schooling herring. This does not imply that tail-slaps are necessary for capturing fish. The relative efficiency of chases and tail-slapping may vary with different prey items. While fish schools may be more efficiently preyed upon using tail-slaps than chases, single prey, and particularly cetaceans whose manoeuvrability is lower than that of fish, may be captured by chases, as observed by Constantine et al. (1998) and George and Suydam (1998). In addition, complex feeding behaviours such as tail-slapping may spread by cultural transmission (Weinrich et al., 1982), and their presence/absence may vary in different killer whale populations.

Kinematics of the tail-slap

Although our sample size is too small to judge the stereotypy of tail-slaps, from the traces we have analysed, tail-slapping appears to be relatively invariable in different trials. Analyses of the movement of the flukes, tail and head (Fig. 7; Table 3) show that there is a relatively large contribution of the tail to the angular excursion of the slap phase. This suggests that the slap phase is the result of a powerful muscular contraction in a dorso-ventral direction, rather than a full body rotation. The

kinematics of tail-slaps is comparable with that of a normal swimming tail-beat during which the up- and downstrokes show angles of attack of opposite sign during most of their duration (Videler and Kamermans, 1985). The main difference from a swimming tail-beat is in the relative amplitude (and duration) of these two phases. While upstrokes and downstrokes are relatively similar in duration and amplitude during routine swimming (in dolphins; Videler and Kamermans, 1985), the slap phase is longer in duration and shows a larger amplitude than the preparatory phase (Fig. 4; Table 2). Tail-slap velocity increases in two steps. The first increase occurs at the beginning of the slap phase, when angular velocity crosses the zero line and the angle of attack is zero (implying minimal drag on the tail, which could be associated with a peak in acceleration). The second velocity increase occurs in the middle of the slap phase (Fig. 5). Since the angle of attack is relatively constant throughout the slap phase, peak acceleration is not related to a local minimum in drag on the tail. Therefore, the peak observed in acceleration may simply be a reflection of the maximum force applied by the tail, which is likely to be in the middle of the slap phase.

The angle of attack showed mean values of $29\,°$ and maximum values of $47\,°$. These values appear to be much higher than those reported for swimming cetaceans (Videler and Kamermans, 1985). For swimming fish and cetaceans, the magnitude of the angle of attack of the tail, which acts as a hydrofoil, will affect the propulsive efficiency of locomotion (Vogel, 1994). As the angle of attack is increased, the lift generated will increase faster than the drag, up to a critical level. Any further increase in the angle of attack would cause an increase in drag and a dramatic reduction in lift, a condition known as stall, in which there is flow separation from the foil surface and, therefore, high turbulence (Vogel, 1994; Fish, 1998b).

Maximum angles of attack for swimming cetaceans range from 12 to $21\,°$ for *Tursiops truncatus* (Fish, 1993) and from 22.5 to $24\,°$ for *Lagenorhynchus obliquidens* (Lang and Daybell, 1963) and are therefore below the $30\,°$ threshold at which stalling occurs in a flapping foil (Triantafyllou and Triantafyllou, 1995). During tail-slaps, maximum angles of attack always exceeded this threshold, ranging between 35 and $60\,°$. Therefore, at least part of the tail-slap may have occurred under stalling conditions. Tail-slaps are aimed at a target consisting of the herring school; therefore, a tail movement that does not imply a forward thrust of the whale (as in stalling conditions) may be desirable. Indeed, tail-slapping killer whales show little forward displacement.

In theory, the angle of attack of a tail-slap to hit a maximum number of herring may be a compromise between the maximization the volume of water affected by the slap (i.e. using a $90\,°$ angle of attack) and the minimization of the drag on the tail (i.e. using a $0\,°$ angle of attack). However, killer whales may not have full control over the angle of attack (at the observed tail-slap velocity, some bending of the flukes related to the body axis may be a passive result of water resistance). If we assume that killer whale tail-slapping behaviour is optimized (i.e. in terms of number of herring

hit), our values for mean and maximum angle of attack (29 ° and 47 °, respectively) suggest that the optimal angle of attack may be in the region of 30–45 °. The volume of water affected by the flukes is proportional to the sine of the angle of attack; therefore, the relationship between V_i and the angle of attack is non-linear. As a consequence, an angle of attack of 45 ° (half of the maximum angle), results in a V_i that is 71 % of the maximum V_i that can be affected by the slap (i.e. with an angle of attack of 90 °).

Effectiveness of the tail-slap

Tail-slapping allows killer whales to stun a theoretical maximum of 33 herring, assuming that herring may be hit throughout the slap phase. This did not occur in our observations, since killer whale tail-slaps were within the volume occupied by the school for no more than 50 % of the slap phase. Therefore, a more reasonable estimate of the maximum number of fish hit by the tail may be approximately 16. To this number, we may have to add fish that may be debilitated through sensory overload, as suggested by Similä and Ugarte (1993). Unfortunately, the number of herring hit during a tail-slap could not be measured. Our observations and theoretical considerations suggest that it can vary from zero, as in misses, to approximately 16, as suggested above. This variation is probably related to a combination of herring and killer whale behaviour. Tail-slap success is likely to be inversely related to the herring's awareness and readiness to escape. The time between the beginning of the slap phase and its maximum velocity ranges from 160 to 480 ms (Table 1). If the herring respond to the beginning of the tail-slap, they may be able to avoid it, as the sum of the escape response latency of herring (varying from approximately 50 to 150 ms; Domenici and Batty, 1994, 1997) and the time needed for a displacement of approximately 1 body length (150–200 ms in a 35 cm herring; P. Domenici and R. S. Batty, unpublished data) ranges from approximately 200 to 400 ms. However, herring may not be startled until later during the slap phase or may not manage to escape outside the volume of water affected by the slap in time to avoid being hit.

Variability in tail-slap success is also likely to be related to various characteristics of the individual killer whale, e.g. to their size (and therefore to their fluke size), their experience in feeding, the timing of their tail-slap, their position relative to the school, etc. Although the whales directed the school before the tail-slap, they may receive no more feedback on the position of the school once they start the tail-slap. This would explain why misses are kinematically similar to hits and do not appear as aborted hits. However, misses occurred rarely, supporting the idea of tail-slapping as an efficient feeding strategy.

The physical contact hypothesis

The tail-slaps of killer whales seemed to stun the herring by physical contact, which could have caused the loud sounds recorded during tail-slaps. A similar hypothesis was presented as the most likely explanation for the loud sounds recorded for bottlenosed dolphins feeding on fish (Smolker and Richards 1987). This hypothesis is supported by the absence of a loud noise during those tail-slaps that missed the school of herring. If the slap itself produced a loud hydromechanical sound regardless of the presence of herring (suggested as a possibility by Similä and Ugarte, 1993), both misses and hits should provoke such sounds, given that they show similar kinematic profiles (Fig. 5). In addition, this hypothesis is in accordance with the physical conditions of some of the herring recovered floating at the surface (e.g. with broken backs and large scratches). However, the fact that some herring were hit by the tail would not exclude the possibility that additional herring may also be stunned by the pressure wave, as suggested by Similä and Ugarte (1993).

It has been suggested that odontocetes may capture prey (particularly fish) by debilitating them with loud sounds (Norris and Møhl, 1983; Marten et al., 1988). These authors suggest various possible mechanisms for producing loud sounds. Although these cannot be ruled out, it is possible that some of the loud noises such as those recorded during predator–prey encounters in the past may include sounds produced by physical contact between the whale's flukes and the prey, as we suggest in our study.

Our results supporting the physical-contact hypothesis, however, are based on a small number of observations of the sound linked to the presence/absence of disoriented herring. A full demonstration may be difficult and could require controlled experiments in a large pool in which a school of herring is hit by artificial flukes that have similar mechanical and kinematic characteristics to those of killer whales' tail-slaps. Further studies will include a test of the correlation between the characteristics of the sound (i.e. its duration and intensity) and the estimated number of herring hit.

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