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Up-beat motion in swinging limbs: new insights into assessing movement in free-living aquatic vertebrates

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Abstract A new system is presented for assessing the movement of animal limbs including, after suitable calibration, quantification of limb stroke frequency and amplitude, which may be used to derive limb angular velocity and acceleration. The system is based on use of an archival unit logging data from a Hall sensor, itself set to sense magnetic-field strength at frequencies of up to 30 Hz. Typically, the Hall sensor is placed on the animal body adjacent to the limb being monitored, while a small magnet is glued to the limb. Changes in limb position result in variation of the magnetic-field strength perceived by the sensor. Captive trials were successfully performed on a harbour seal (*Phoca vitulina*), an Australian sea lion (*Neophoca cinerea*) and a hawksbill turtle (*Eretmochelys imbricata*), as well as on 18 free-living Magellanic penguins (*Spheniscus magellanicus*). The unit performed well in almost all cases, illustrating that stroke frequency was relatively invariant in any species tending, however, to be higher in smaller animals and showing that the primary variance was manifest in stroke amplitude. As an example of the utility of the system, the importance of buoyancy was demonstrated in the penguins, which had longer glide phases and lower flipper beat amplitudes at greater depths, because body air was compressed, which reduced upthrust. The small size of the system (ca. 25 g in air) makes it suitable for a wide range of marine vertebrates. Potential problems of system sensitivity, the suitability of particular recording frequencies and the value of appropriate calibration are discussed.

Introduction

Vertebrate locomotion and its associated costs (Schmidt-Nielsen 1972; Hind and Gurney 1997) is a key element in animal autoecology, being relevant in, for example, migration strategies (Liechti et al. 2000), determination of optimal speeds of movement (Liechti et al. 1994; Boyd et al. 1995; Pennycuik 1997) and dive durations of air-breathers (Williams et al. 1991), and critical in prey capture (Thompson et al. 1993) and predator evasion (Yoda et al. 1999). Detailed assessment of the effort and biomechanics involved in movement is usually carried out in captivity using techniques such as video imagery (e.g. Videler et al. 1999), particle image velocimetry (Wolfgang et al. 1999) and gas respirometry (e.g. Beamish 1978). Although such work often enhances our understanding of locomotion considerably, the study animals are constrained and, thus, may not show the full repertoire of movement available to them, nor, indeed, may they be able to operate efficiently even for the movement types displayed (see e.g. Bannasch 1995 and references therein).

Studies recording detail on animal movement without the confines of a cage are much less common and comprise two types: those that observe, generally tame, animals (e.g. Butler and Woakes 1980; Skrovan et al. 1999) and those that use remote-sensing technology in systems attached to the animals (Butler and Woakes 1980). Examples of this are “crittercam” studies, such as those of Williams et al. (2000), where a video camera is mounted so as to be able to film the movement of the limbs, and studies using loggers or transmitters attached to animals (e.g. Kutsch et al. 1993; Yoda et al. 1999).

We present a new, small system for determination of limb movement in marine animals, which can be deployed on free-living vertebrates. The system was tested on three species in captivity and one species in the wild and gives information on the frequency and amplitude of limb movement from which limb angular velocity and acceleration can be derived.

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Materials and methods

Technology used

The technology was essentially based on the use of a small Hall sensor located on the animal's body reacting to the presence of a magnet fixed to the animal's limb. The Hall sensor produced a voltage output, stored by a logger, the value of which was proportional to the strength of the magnetic field, the magnetic field varying with limb position. A system based on this has been recently described by Wilson et al. (2002; see also Cobern et al. 1983) for determination of feeding activity via beak movement in penguins.

The device (hereafter termed the IMASU – integrated movement assessing sensory unit – Driesen and Kern, Bad Bramsted, Germany) was used in two forms. Both consisted of electronics potted in resin and incorporating a turned titanium battery housing, from which a thin (0.8 mm diam.), four-strand cable of varying length emerged, terminating in the Hall sensor (Siemens KSY 10), itself potted in resin so as to create a small flat end plate (approximate dimensions 5×1.5 mm). This end plate was designed to be readily fixed to the animal body. An older version of the system (IMASU I) had dimensions of 133×25×19 mm, excluding the cable to the sensor (mass: 56 g), was powered by a 3.6 V lithium cell and had a memory of 2 Mb. The newer version (IMASU II) was 65×35×15 mm (mass: 25 g), was powered by a 3 V lithium cell and had a memory of 4 Mb. Both recorded with 16 bit resolution and could be programmed, via an interface to a computer, to record at frequencies between 1 and 30 Hz. During deployment, both systems used Vacodym neodymium iron boron rare earth magnets (Vacuumschmelze, Germany) of varying sizes (see following subsection) as a magnetic field source for the Hall sensors.

Work on captive animals

Three captive marine vertebrates were equipped with the system. During deployment all animals were filmed continuously with a digital video camera (JVC, GR-DVL 100) recording at 24 frames s⁻¹, so as to be able to compare activities with the data recorded by the IMASUs.

A 13-year-old male harbour seal (*Phoca vitulina*), 192 cm long and with a body mass of 90 kg, was equipped with an IMASU I on 4 August 2001 in the Seal Centre in Friedrichskoog, Germany. The Hall sensor was attached with cyanoacrilate glue (Sekundenkleber, Uhu, Germany) to the central phalange of the left, hind flipper (Fig. 1) and orientated to face the adjacent, ventral phalange. A small, coin-shaped magnet (5×9 mm diam.) was glued to this ventral phalange, directly opposite the sensor (Fig. 1). The cable was secured at one site along the length of the flipper and at two sites on the body by gluing it in place underneath small neoprene buttons. The logging unit was attached to the animal's lower back using cyanoacrilate glue. The logger was set to record at 25 Hz, and the animal was released in the pool and allowed to swim at will for 8 h before the unit was removed and the data downloaded.

A 13-year-old male Australian sea lion (*Neophoca cinerea*), 182 cm long and with a body mass of 207 kg, was equipped with an IMASU I at Sea World Enterprises, Queensland, Australia on 19 October 2001. Here, the Hall sensor was attached using cyanoacrilate glue to the axilla adjacent to the left, front flipper (Fig. 1), with the logger being placed on the side of the body. The magnet (coin-shaped; 3.5×28 mm diam.) was glued to an adjacent site on the underside of the flipper (Fig. 1). The logger was set to record at 24 Hz, and the animal was allowed to swim in the pool for 15 min before the system was removed.

A 21-year-old male hawksbill turtle (*Eretmochelys imbricata*), with a curved carapace length of 63.5 cm and a mass of 33 kg, was equipped with an IMASU II on 24 January 2002 in the Museum of Marine Science in Stralsund, Germany. The logger was fixed to the dorsal carapace with cyanoacrilate glue, while the Hall sensor was glued to the dorsal surface of a dorsal scute directly above the left,

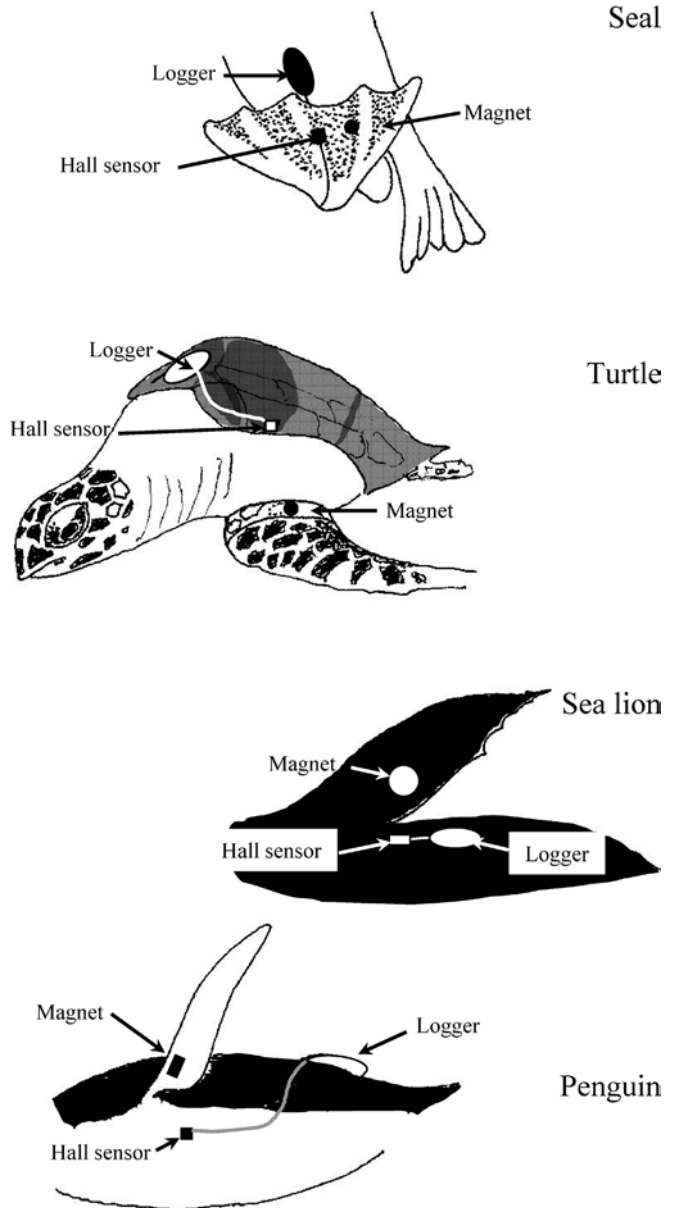


Fig. 1 Schematic diagram showing attachment position of the integrated movement assessing sensory unit (IMASU) to various marine vertebrates: *Phoca vitulina* (seal); *Eretmochelys imbricata* (turtle); *Neophoca cinerea* (sea lion); *Spheniscus magellanicus* (penguin)

front flipper (Fig. 1). The magnet (coin-shaped; 3.5×28 mm diam.) was held in place on the flipper using an elastic latex strap, which was closed using cyanoacrilate glue. The logger was set to record at 24 Hz, and the turtle was allowed to swim around during a feeding session (and for a period following this) for some 50 min before the device was removed.

Work on free-living animals

A total of 18 Magellanic penguins (*Spheniscus magellanicus*) breeding at a colony at Cabo Virgenes (52°24'S; 68°26'W), Santa Cruz, Argentina, was equipped with IMASU II devices during November and December 2001. Birds tending chicks were removed from the nest and restrained with minimum stress by placing them

on the knees with the eyes covered (Wilson 1997). The loggers were fitted using tape (Wilson et al. 1997) to the mid-line of the birds' backs as far back as possible, so as to minimise device-induced drag (Bannasch et al. 1994). The Hall sensor was glued (two-component epoxy – Poxipol Industria, Argentina) in place in the axilla under a flipper (usually the right), and the intervening cable from the logger passed under the feathers so that it was not visible at all. To ensure that this stayed in position, drops of cyanoacrilate glue were used to glue pairs of feathers together around the cable. The magnet (flat, rectangular; 2×7×20 mm) was glued with two-component epoxy to the underside of the flipper directly opposite the Hall sensor (Fig. 1). All devices were set to record at 30 Hz. In addition, birds were also fitted with depth gauges (DKLOG 701; Driesen and Kern) (mass 32 g, dimensions 85×22×31 mm), which recorded hydrostatic pressure with 16 bit resolution at a frequency of 5 Hz. These units were attached immediately anterior to the IMASU devices in the mid-line of the birds' backs. Five of the birds were also equipped with inter-mandibular angle sensors (IMASEN), which recorded the angle between the upper and lower halves of the bill by using another magnet and a Hall sensor-based system similar to that described here (see Wilson et al. 2002 for details).

Birds were allowed to go to sea for only one foraging trip (usually lasting <24 h), after which they were removed from the nest. The use of three devices on birds simultaneously meant that the penguins were likely to be more subject to stress during equipment and possibly more inconvenienced during foraging. We suggest that for future deployments, all parameters be logged in a single unit. This is now possible (see manufacturer's specifications, Driesen and Kern). The recovered IMASU units were calibrated for flipper angle by having the device log while the birds' flippers were held at particular angles to the long axis of the body using a marked plastic card, cut so that it fitted snugly round the bird's body. Flipper angles recorded ranged from +90° (maximum downstroke) through 0° (where the flippers extended perpendicular from the body) to -90° (maximum upstroke) and were executed in 10° steps. Subsequently, devices were removed and the birds allowed to continue brooding their chicks.

Recovered data were analysed using one of two programs according to whether the data originated from the IMASU or the IMASEN (MT-FLIP and MT-BEAK, respectively; Jensen Software Systems, Laboe, Germany). Both programs allow the data to be displayed graphically, together with the corresponding depth data. Special functions within the program allow correction for differential drift between separate systems used on the same bird. MT-FLIP was used to determine flipper beat frequency and amplitude as a function of depth and vertical velocity, whereas MT-BEAK was used to calculate when prey were caught and the prevailing conditions (e.g. depth).

Results

It is not the intention of this work to present an exhaustive compilation of all trends and patterns observed in the swimming behaviour of all the equipped animals. This will be done in later papers. Rather, specific patterns will be illustrated to demonstrate the potential behind the IMASU system for the study of free-living vertebrate movement.

Captive animals

Equipping of the captive animals did not cause any apparent stress to them, over and above the procedure of restraint, which was only applied to the hawksbill turtle (*Eretmochelys imbricata*). Both pinnipeds were trained and so did not need to be restrained during

attachment of their devices. During the short time of carrying the device, no animal attempted to remove the IMASU (although a female hawksbill turtle in the same aquarium as our study animal attempted to eat the attached device on more than one occasion) and no aberrant behaviour or hindrance during swimming was observed.

The five species of animals equipped with IMASUs showed quite different Hall sensor outputs during swimming, reflecting differences in locomotory type and the manner in which the sensor-magnet system was attached. Values given below for limb beat frequency are only approximate, since the confines of the various pools in which the animals swam did not allow for extensive periods of straight swimming.

The harbour seal (*Phoca vitulina*) swam in the characteristic manner of phocids, using pelvic oscillations (Berta and Sumich 1999), whereby the hind limbs were the major force generating propulsion in the water. During swimming, phocids exhibit a lateral, sinusoidal movement, with the rear flippers being used alternately (Fish et al. 1988). Correspondingly, our seal, which had the system effectively measuring inter-phalange distance, showed an almost square-wave pattern (Fig. 2), with the top of the square wave corresponding to the period when the equipped rear flipper was fully extended and pushing the water back during normal stroking. Amplitude was highly variable, but stroke frequency fairly constant at around 0.8 Hz (Fig. 2).

Attachment of the unit to the sea lion (*Neophoca cinerea*) proved less than ideal, since the sensor was too far from the magnet to be able to produce an output from the Hall sensor for all flipper movements. Nonetheless, substantial strokes, which were made with both front flippers simultaneously, as is typical in the pectoral oscillatory movement of otariids (English 1976; Feldkamp 1987), produced marked peaks lasting some 2–3 s (Fig. 2). These major strokes were interspersed with strokes of lesser amplitude, which were recorded as minor peaks. Interim periods consisted of extended gliding phases of up to 5 s, at which time the front flippers were generally held at some distance from the body and signals were not generated by the Hall sensor (Fig. 2). Overall stroke frequencies at normal swimming speeds were of the order of 0.5 Hz.

Although the hawksbill turtle equipped with the IMASU was relatively confined within its aquarium, the classic powerstroking via sweeping of the foreflippers up and down as a pair (Wyneken 1997) could be easily observed and was recorded by the IMASU as a regular double peak, with markedly different peak heights (Fig. 2). The distribution involving the higher peak corresponded to the upstroke bringing the flipper to the front along the shell, while the distribution with the lower peak occurred during the backward downstroke generating the propulsion. As with the other animals, the amplitude was highly variable (not illustrated in Fig. 2), but beat frequency remarkably constant, being of the order of 0.5 Hz.

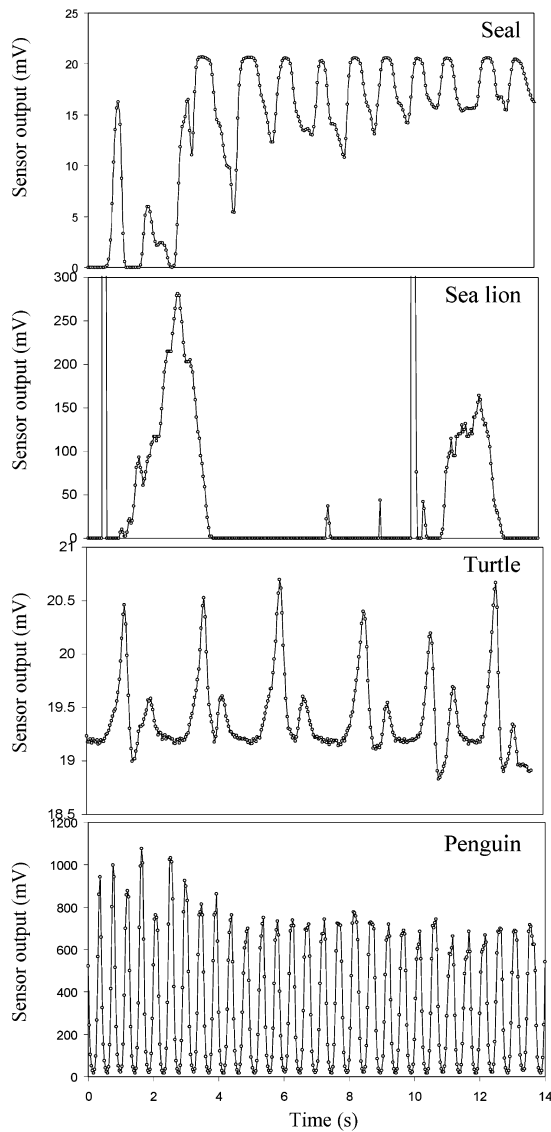


Fig. 2 Hall sensor output from an IMASU recording during swimming in four different marine vertebrates showing substantial differences in stroke frequency and type [*Phoca vitulina* (seal); *Neophoca cinerea* (sea lion); *Eretmochelys imbricata* (turtle); *Spheniscus magellanicus* (penguin)]

Free-living penguins

All birds equipped with devices returned to the nest after a single foraging trip in good condition and had fed, as evidenced by their protruding bellies and by the increased weights of their chicks, which had been fed by regurgitation. Mean foraging trip duration was within the norm for Magellanic penguins (*Spheniscus magellanicus*) at Cabo Virgenes (authors' unpublished data), and there were no signs that birds had attempted to remove attached IMASU systems, or indeed that they impaired performance. One of the IMASU devices deployed did not record for the full duration due to leakage of water into the battery housing. The data from this device were, however, not lost up until this point due to

the flash RA memory. All depth gauges used recorded successfully for all foraging periods. Three of the five IMASEN systems came back having had the cable linking the Hall sensor to the logger either broken, after being caught in vegetation, or bitten through. The vegetation at the study site is a problem, consisting of dense shrubs that easily catch cable loops. The problem would presumably be reduced if stronger cable were used. It is hard to know the extent to which the birds were irritated by the cable. The system that we used was clearly too weak to withstand any sort of biting from these birds with their powerful beaks. More study is needed to examine the extent to which the units might modify bird behaviour. IMASEN units had all recorded good data on beak angles until such time as the cable was severed.

The data gained from deployment of IMASUs on free-living penguins showed a fairly consistent pattern. The synchronous dorso-ventral beating of penguin flippers during locomotion (Nachtigall and Bilo 1980; Oehme and Bannasch 1989; Bannasch 1995) was recorded by the IMASU as a highly regular pattern of approximately bi-laterally symmetrical peaks and troughs (Fig. 2). Beat frequency for birds swimming near the surface during the descent was considerably higher than that of any of the other animals studied, ranging between 2.7 and 3.2 Hz. However, this was highly dependent on depth and swim angle (see below). Individual beats for birds diving near the surface were recorded by the IMASU as having a distinct acutely angled peak, at the moment of the termination of the downstroke, and a parabolic-type trough near the termination of the up-beat (Figs. 2, 3). This feature was not due to a similar pattern in the timing of the wing beats, but was rather a consequence of the non-linear response of the Hall sensor to magnet position (Fig. 4). Correction of the data according to calibrations made on site showed that during descent near the surface, penguin flipper motion was roughly sinusoidal, with peaks and troughs having similar shapes (Fig. 5).

Penguin flipper motion changed dramatically as a function of depth and was dependent on whether the bird swam down, horizontally, or up. Trends in these patterns were most obvious in highly regular dives, in which no prey were captured (Figs. 3, 5). During downward swimming near the surface, immediately after the dive had been initiated, the flippers were beat steadily (Fig. 3) and flipper angular velocity oscillated between 0 and about $1700^{\circ} \text{ s}^{-1}$ (Fig. 5). Higher values were transient, typically being measured only once per beat and were associated with substantial angular acceleration (Fig. 5), whereas values near zero, where the flipper direction was reversed at the end of the down- or up-stroke, were represented by two or three points. This was particularly obvious where upstrokes terminated and downstrokes began (see the left-hand side of the rising peaks in the flipper angular velocity during descent; Fig. 5, A). Periods of stable, lower flipper angular velocity are also very notable when angular acceleration is considered (Fig. 5), appearing as stable

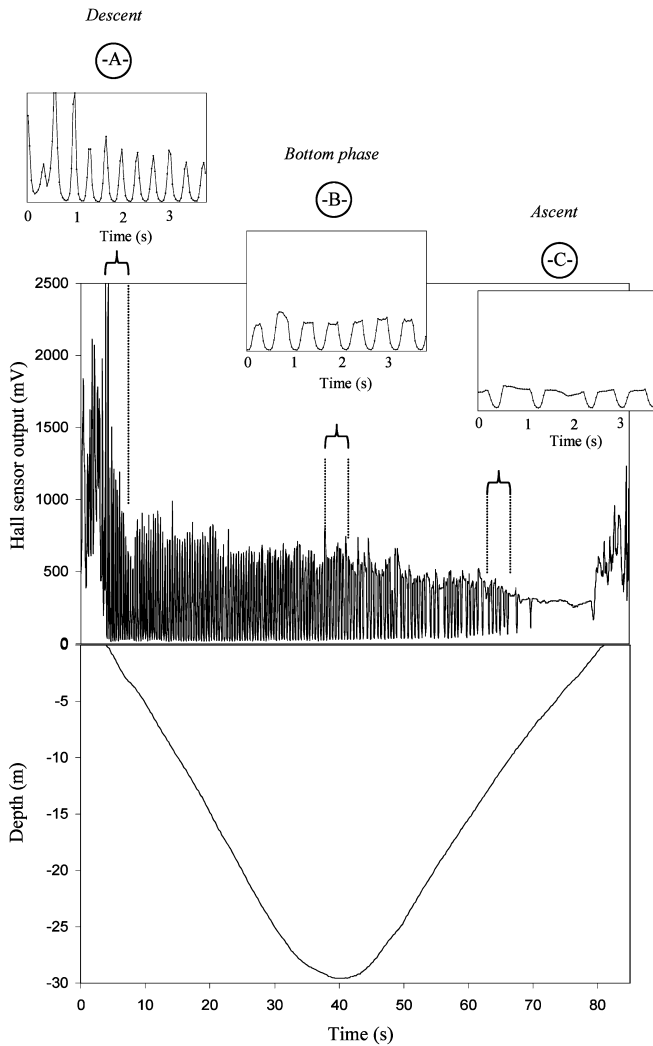


Fig. 3 *Spheniscus magellanicus*. Example of a flipper beat motion during a Magellanic penguin dive (regular, with no evidence of prey pursuit or capture) as recorded by the IMASU. Depth is shown in the lower graph, while particular sections are expanded in the upper insets: initiation of the dive and descent (A), the point at which the bird was swimming horizontally at the point of maximum depth (B), and a period during the return to the surface (C)

zero values between the peaks and troughs. At the bottom of dives, at the point of maximum depth, when the penguins were swimming horizontally for a short period, the downstrokes terminated at noticeably shallower angles than the upstrokes and were followed by an appreciable pause, amounting to almost a quarter of a second during which the bird apparently glided (Fig. 5, B). During actual beating, which was essentially an upstroke followed by a downstroke before the next pause, flipper motion was similar, though less dramatic, to that displayed by birds descending near the surface: there was a slight reduction in maximum flipper angle of the upstroke and a marginal reduction in frequency. These factors, and the reduced amplitude in the downbeat, lead to a marked reduction in flipper angular velocity and acceleration (Fig. 5, B). Maximum angular velocity values were of the order of $1300^\circ \text{ s}^{-1}$, with the slight

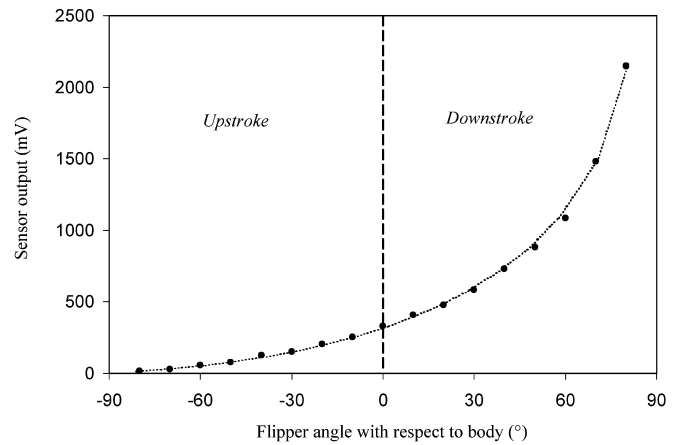
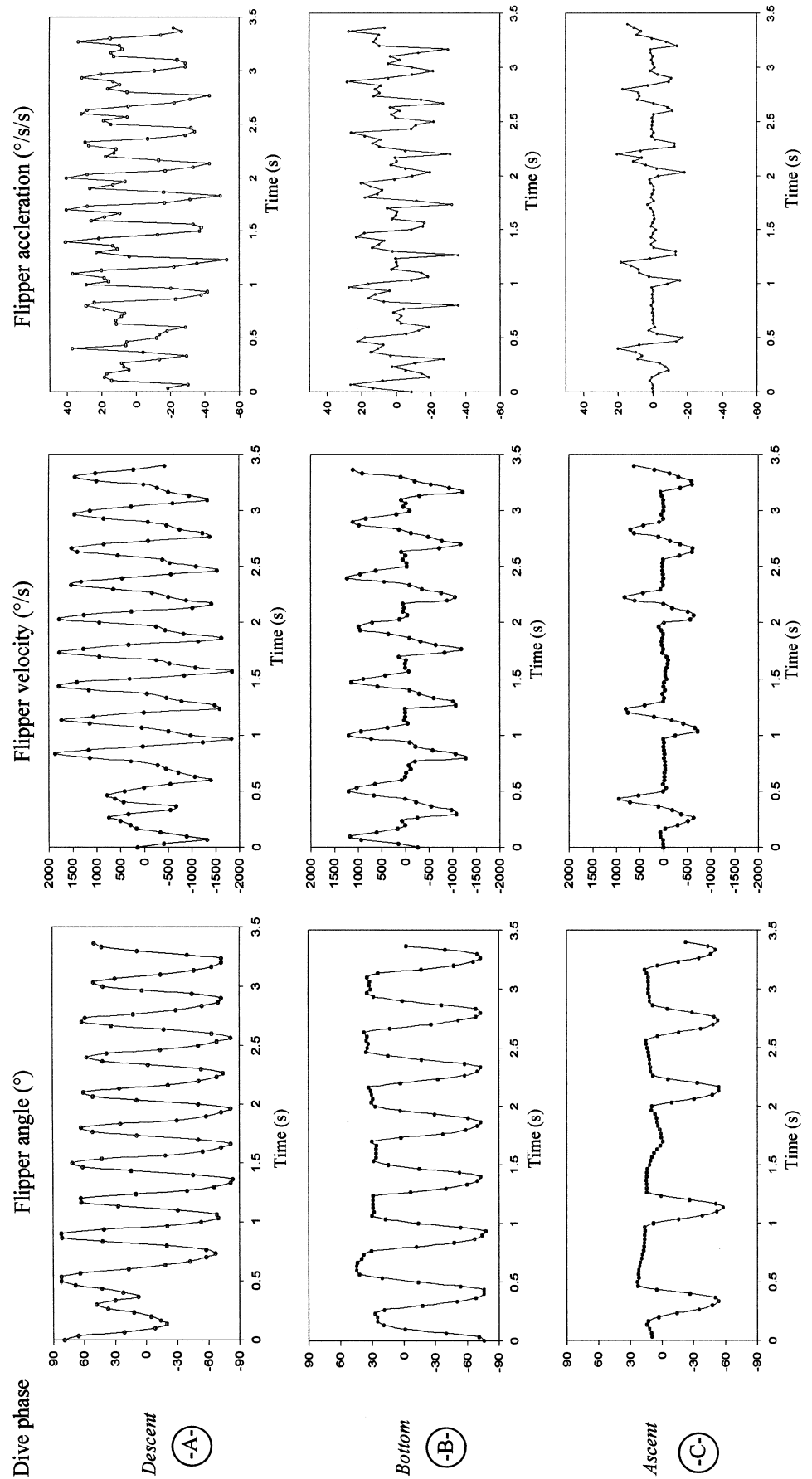


Fig. 4 *Spheniscus magellanicus*. Relationship between flipper angle with respect to the penguin body and Hall sensor output for the data shown in Fig. 2. The line of best fit takes the form: $\text{angle} = -111.97 - (0.07518 \times \text{output}) + [7.634(\sqrt{\text{output}})]$ ($r^2 = 0.999$)

pause in the development of the minus to plus angular velocity associated with the reversal of the upbeat to the downbeat being similar to that found in birds descending near the surface (cf. Fig. 5, A and B). The glide pause at the bottom of the downstroke resulted in an extended shelf on the right hand side of the positive peak in maximum flipper angular velocity and this was also a major feature of the angular acceleration (Fig. 5, B). This trend was further developed during the ascent phase of the dive. Here, the glide phase at the termination of the downbeat became rather more variable and extended over the course of the ascent to terminate in continuous gliding (Fig. 5, C; see below). Flipper-angle maxima were also further reduced, although the reduction was more dramatic at the end of the upstroke, and angular velocities rarely exceeded $1000^\circ \text{ s}^{-1}$. The general picture, therefore, during the course of a simple search dive (see Wilson et al. 1995) was of highly variable angular velocity over the course of single stroke cycles, but a decreasing running mean from the surface down to the point of maximum depth and beyond, although all stroking ceased at some point on the return to the surface (Fig. 6). Plots of the running mean of flipper angular velocity against depth for the descent phase showed a best fit given by a three-order polynomial describing an initial dramatic decrease near the surface followed by a more gentle decrease in flipper angular velocity over much of the rest of the descent phase (Fig. 7). The decrease in flipper angular velocity with decreasing depth as the birds ascended was best described by a simple linear fit (Fig. 7).

The mechanics of swimming in diving penguins is complicated because birds inspire more for deeper dives (Wilson 2002), so that bird buoyancy cannot be taken to be constant at any particular depth, even after correcting for the effects of pressure (cf. Sato et al. 2002). Thus, trends reported here can be taken as indicative of the general situation, but ideally should be considered with respect to maximum depth reached during the dive.

Fig. 5 *Spheniscus magellanicus*. Flipper angle (*left panels*) of the penguin with respect to the body over time for the three periods (*A* descent; *B* bottom; *C* ascent, see Fig. 3), the corresponding angular velocity (*centre panels* – data transformed according to the calibration in Fig. 4) and angular acceleration (*right panels*)



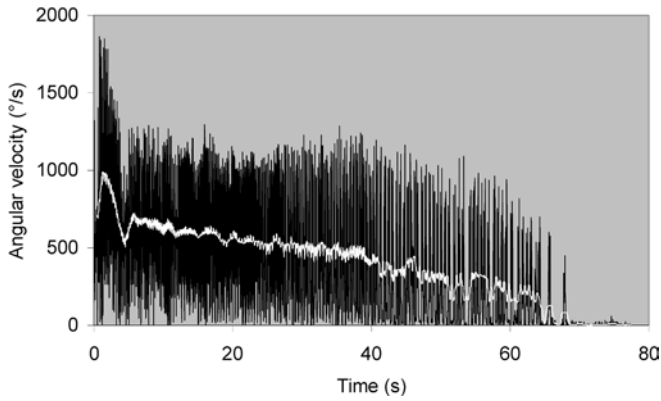


Fig. 6 *Spheniscus magellanicus*. Flipper angular velocity (all values converted to be positive) for the dive depicted in Fig. 3 (black line) and a running mean over 1 s of the angular velocity (white line)

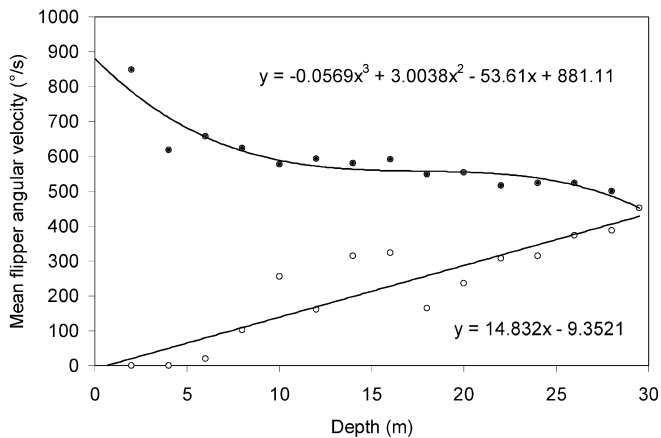


Fig. 7 *Spheniscus magellanicus*. Mean flipper angular velocity (all values converted to be positive and taken from a running mean over 1 s) as a function of depth in a diving Magellanic penguin. The descent phase of the dive is shown by filled symbols; the ascent phase by open symbols. The dive from which these data were taken is shown in Fig. 3, with corresponding flipper angle and flipper angular velocity data shown in Fig. 5

In order to eliminate this factor, we considered a series of dives to a highly specific depth, in order to illustrate trends. Thus, within such dives, vertical velocity (rate of change of depth) varied little from the surface to the point of maximum depth and back, although rates of descent tended to be lower than those of ascent ($t = 2.51$, $P < 0.01$; Fig. 8). Overall flipper beat frequency changed little during the descent, although it decreased slightly and steadily from ca. 3.2 to 2.8 Hz until the point of maximum depth, at which time the frequency dropped dramatically to ca. 1.9 Hz when the glide phases started (cf. Fig. 6). With decreasing depth, flipper beat frequency also decreased, ceasing altogether for approximately the last third of the dive, excepting what was apparently a flipper beat for orientation just before the birds arrived at the surface (Fig. 8). Maximum flipper downbeat angle decreased from the surface to the point of maximum depth and continued to decrease at a roughly similar rate from this point back to the surface (Fig. 8).

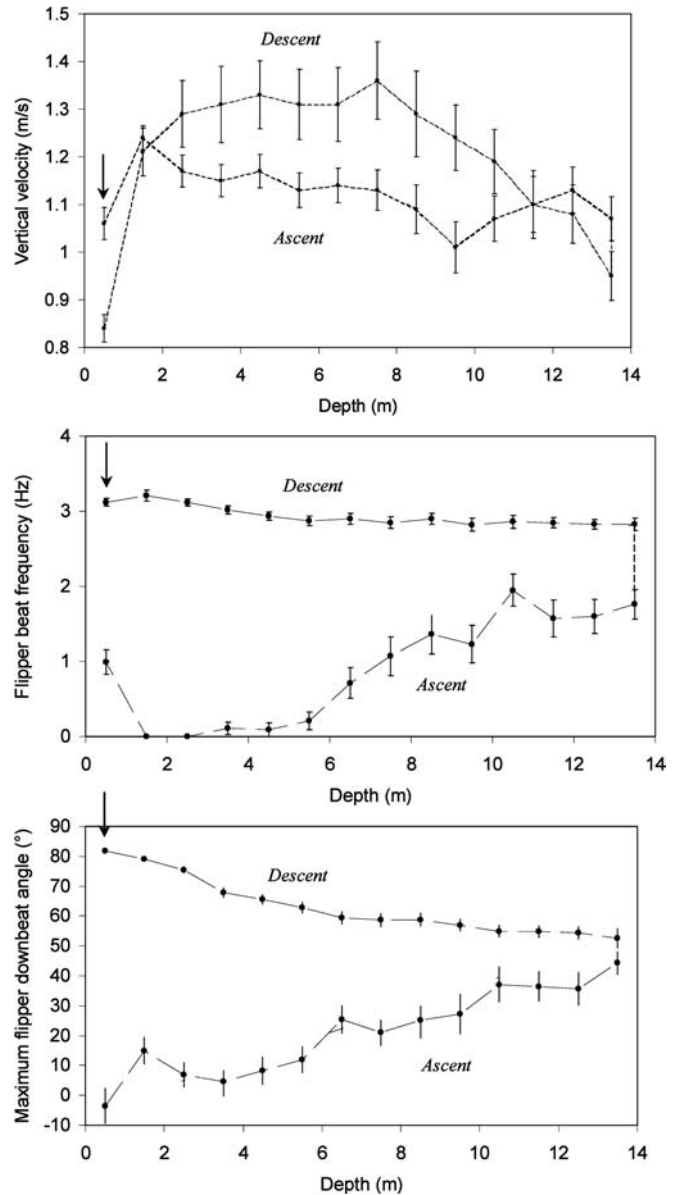


Fig. 8 *Spheniscus magellanicus*. Mean vertical velocity, flipper beat frequency and maximum flipper downbeat angle as a function of depth for 24 dives made by a Magellanic penguin, in cases when dives terminated between 13.5 and 14.2 m. Data are only shown for the descent (upper set of points) and ascent (lower set of points) phases and do not show any extended bottom phase swimming (error bars SE; arrows onset of dives)

These general patterns were modified during prey pursuit. Most pursuits were short, rarely lasting more than a second, and typically consisted of two or three wing beats with high, though highly variable, maximum flipper angles, an unusually high frequency (mean of 30 events was 3.75 Hz, 1.0 SD) and a consequently high flipper angular velocity, often exceeding $2000^\circ \text{ s}^{-1}$ (Fig. 9). Prey ingestion was almost invariably followed by a dramatic reduction in flipper amplitude for a second or so, resulting in angular velocities that rarely exceeded $1000^\circ \text{ s}^{-1}$.

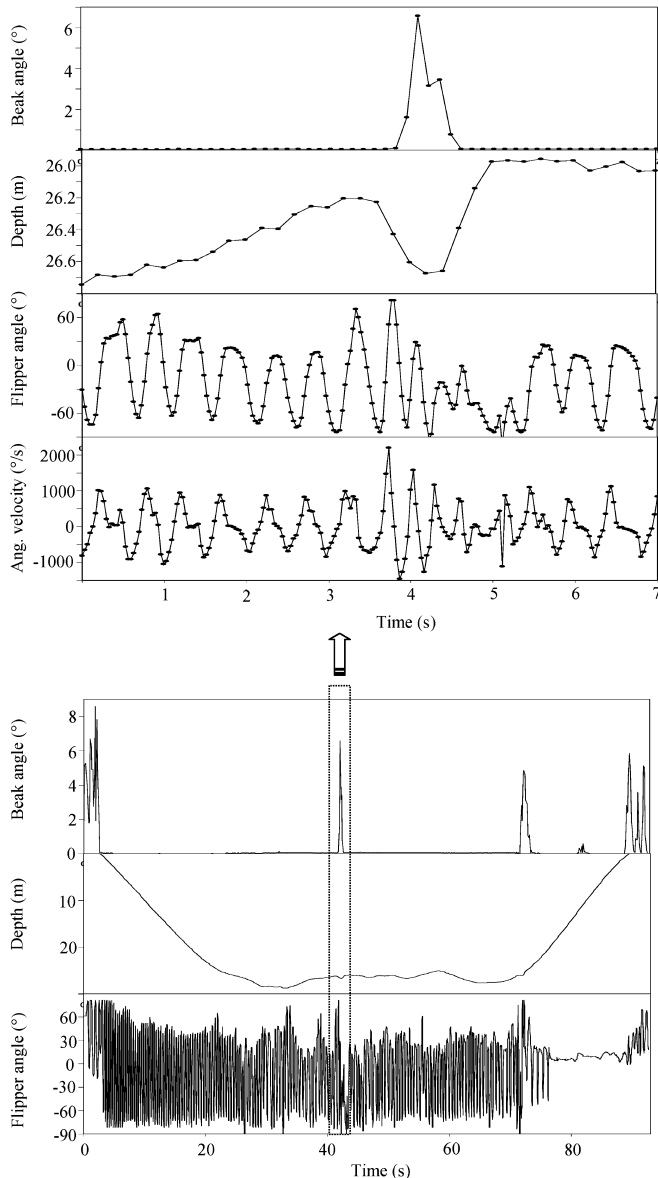


Fig. 9 *Spheniscus magellanicus*. Changes in foraging behaviour as measured by an IMASU attached to a Magellanic penguin during prey pursuit and capture. *Lower graph* shows beak angle, flipper angle (with respect to the bird's body) and dive depth for a full dive lasting some 90 s. The opening of the beak at the beginning and end of the dive corresponds to breathing, while the two peaks during the dive, at ca. 42 and 71 s, respectively, represent prey capture (see Wilson et al. 2002). The changes in depth and flipper movement associated with the 7 s around the first of these prey captures are shown in detail in the *upper graph*. Note the increase in flipper movement amplitude, increase in flipper beat frequency and increase in flipper angular velocity immediately prior to prey capture, as the bird descends to snap at its prey

Discussion

Device effects

The utility of remote-sensing systems attached to free-living animals depends on the extent to which these

systems compromise the animal's well being. Bio-mechanical studies of locomotion may be less influenced by aberrant behaviour, since data need only be examined when the animals travel: travel can only occur when animals are not actively attempting to remove devices or otherwise reacting to them. It should be noted, however, that changes in streamlining can have a profound effect on the mechanics of locomotion (Bannasch et al. 1994). Wilson et al. (1986), for example, found that African penguins (*Spheniscus demersus*) travelled more slowly when carrying larger devices, presumably as a result of increased drag. Quite apart from moral considerations, all aspects of locomotion will be affected by the reduced streamlining caused by the attachment of foreign bodies to aquatic animals, and it is in our best interests, therefore, to minimise these effects and quantify them if possible. In this preliminary work, although we noticed virtually no ill effects of the attached devices, we consider that it would be naive to assume that this was really the case. More critical research is needed on this aspect.

Limitations of the system

The response of the Hall sensor to the magnet over distance is exponential, with signal strength increasing disproportionately as the magnet nears the sensor (Wilson et al. 2002). Assessment of limb movement is further complicated by the simultaneous variation in both distance and angle between the sensor and the magnet. It should be noted though that the larger the surface area of the magnetised face of the magnet, the less the output of the Hall sensor changes in response to changes in angle if distance is held constant (Liebsch 2002). Thus, it is best to use flat magnets magnetised across two major faces, which also facilitates positioning of the Hall sensor with respect to the magnet. The fact that all limb movement is based around an articulation means that the Hall sensor and magnet may be positioned closer or further away from the articulation, as determined by the size of the magnet and the sensitivity of the sensor. In our experiments we erred somewhat in the case of the sea lion in placing the sensor and magnet too far from the articulation so that only part of the motion of the flippers could be resolved (Fig. 2). The data loss resulting from such poor positioning is particularly evident if these data are compared to those obtained from other species (Fig. 2).

When possible, it is important to calibrate limb angle against Hall sensor output, since the exponential relationship between distance and sensor output (Fig. 4) makes interpretation of the raw data difficult (cf. Figs. 3, 5). Limb beat frequency can be easily resolved without a problem using raw data, but, as we have seen, frequency varies less than does amplitude. Although comparison of raw data values for use in derivation of amplitude can show trends, the non-linearity of such data compared to corrected values is likely to lead to problems in statistical assessment (non-normality) and over- as well as

under-emphasise trends within a single stroke, depending on the position of the limb.

The non-linearity of the sensor output also influences the degree of resolution obtained over the limb stroke in that resolution of, for instance, limb angle is less at greater angles, as is particularly evident in the penguin data presented (cf. Figs. 3, 4, 5). This may be partially offset by using 16 bit resolution, which allows finer step resolution, but is best considered critically by looking at skeletons of the study animals before attempting field work.

The physical stability of the Hall sensor and the magnet when deployed on the study animal are important considerations. Since the Hall sensor reacts dramatically to even small changes in sensor–magnet distance, particularly when the inter-unit distance is small (see above); poor attachment, or attachment to surfaces that move appreciably, such as loose skin, can lead to considerable noise in the signal. For this reason, deployments on animals such as turtles, with their scutes, or penguins, with minute feathers on the flippers resembling scales, are less prone to noise of this type than deployments on seals. Careful consideration is warranted before deployment and during fixation of both magnet and sensor to ensure that the glue base is secure and that the site chosen is subject to minimal movement other than that directly involving limbs.

One aspect that can be problematic is that of the sculling motion of animal limbs, i.e. limb movement in more than one plane. This is not really an issue in penguin swimming (Clark and Bemis 1979; Bannasch 1995), nor indeed would it be for most cetacean fluke movement (Coffey 1977) or fish tail beating (Videler 1993), but it is noticeable in the flipper beating of turtles (Fig. 2) and is also likely to occur in otariids (Godfrey 1985). When determination of transverse movement is important, we suggest the use of two or more Hall sensors, which may respond variously to either one magnet, or perhaps even two sensors, one on each flipper, with magnets positioned so as to optimise assessment of movement in each of the planes.

The frequency with which data are measured by the IMASU is important for determination of the parameters associated with movement. Consideration of discussion in Boyd (1993) and Wilson et al. (1995) suggests that a measurement frequency $\leq 10\%$ of the limb beat frequency is adequate for assessment of stroke frequency. Thus, IMASU units measuring at 30 Hz are adequate for measurement of most penguin swimming activities, although they may be non-optimal during prey capture. Current IMASUs can measure up to 100 Hz (manufacturer's specifications, Driesen and Kern), so that stroke frequencies of up to 10 Hz may be assessed using the present technology. Measurement of peak amplitude is more complex. If the amplitude is to be assessed on a beat-by-beat basis, essentially, the interval between measurements has to be short enough so that a record of the magnetic field strength will occur during the time that the limb is within 5% of the peak amplitude (assuming

that an error of 5% is acceptable). The actual time available for this depends on the form and speed of the limb motion, and, in particular, the speed with which the motion is reversed at the end of the stroke. This makes a general-case mathematical formulation difficult. Close inspection of the penguin data shows that values for flipper angle near the peaks are generally only represented by a single point, so that the error is likely to be appreciable. During selection of sampling interval, however, researchers have to consider the length of time over which they wish to record as well as the quality of the definition of the limb movement they require. Higher sampling intervals lead to faster depletion of the memory. Current IMASU models with 8 Mb memories set to record at 100 Hz can only record for just over 11 h.

Potential uses of the system

In this preliminary work the IMASU system has proved itself useful for documenting a number of trends that have already been alluded to in the literature. For example, speed and acceleration appear to be primarily mediated via changes in stroke amplitude rather than stroke frequency (e.g. Lovvorn et al. 1999). The advantage of this is that animals may operate their limbs at an ideal resonant frequency, which is an energy-saving mechanism (Nassar et al. 2001 and references therein). Interestingly, this seems to be a feature of penguin swimming, even though flipper beat frequency apparently changes substantially during the course of a dive (Fig. 8). Here, however, the frequency of the actual movement is relatively constant (cf. Figs. 3, 5), with the apparent overall frequency only changing as a result of glide phases between beats. This is not entirely analogous to the “burst and glide” movement exhibited by a number of animals such as fish and dolphins (Skrovan et al. 1999) and guillemots (Lovvorn et al. 1999), but nonetheless further suggests that marine animals favour economical swimming modes. Substantial departures in real flipper beat frequency, such as occur during prey pursuit (Fig. 9), can be justified since energy gain in this case far exceeds energy expenditure.

Our limited study also indicates that the animals used tend to conform with the general allometric trend in having normal operating limb beat frequencies that are dependent on body size, larger animals having lower beat frequencies (Peters 1983). Further studies using the IMASU could broaden the database considerably.

Buoyancy has been shown to be a major feature influencing the energetics of swimming in marine mammals (Skrovan et al. 1999; Williams et al. 2000), turtles (Minamikawa et al. 1997, 2000) and diving birds (e.g. Lovvorn et al. 1991, 1999; Hustler 1992; Stephenson 1995), as a result of air associated with the body. Predictably, compression effects with depth reduce buoyancy (Wilson et al. 1992) and, thus, result in reduced energy expenditure in many species with increasing depth (Williams et al. 2000). Sato et al. (2002), using

accelerometers on free-living penguins, were able to show this trend clearly. Their bio-mechanical calculations, derived from changes in body acceleration associated with flipper movement involve a number of assumptions. However, our data substantiate their findings, even to the point of detailing flipper angles during penguin gliding phases and the extent to which this might be depth/buoyancy related and therefore involved in correction for upthrust.

It has been suggested that energy expenditure for locomotion may be alluded to by considering both limb beat frequency and movement amplitude; higher amplitudes and frequencies are associated with greater energy expenditure (see Lovvorn et al. 1991; Kooyman and Ponganis 1998). In fact, the data we present are an expanded version of limb angular velocity taken over at least one beat cycle that permit consideration of time-corrected cumulative limb angular velocity, which may prove useful in representing the energetics of movement over both small and large time scales. Such an approach is potentially useful for biomechanical studies and for studies that require energy expenditure to be determined for other reasons, including determination of overall energy budgets and considerations of optimisation (e.g. Williams and Kooyman 1985). In addition, for biomechanical work considerations, limb angular acceleration can also readily be calculated by use of the IMASU, set to record at sufficiently high frequencies. Of particular interest will be the treatment of speed data with which the energetics of limb motion can be equated to animal speed.

Overall, the small size and relative ease with which the IMASU can be deployed means that it may prove to be a particularly useful tool for a variety of reasons. One of the most important advantages, however, is that the device can be deployed on free-living animals, so that movement restrictions imposed by captivity can be circumvented, thus freeing the study animals of their confines, allowing them to move as they wish, and liberating the associated researchers of all the energetic problems, such as wall effects, that such confinement brings.

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