Functional analysis of the surfacing behaviour in the harbour porpoise, *Phocoena phocoena* (L.)

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Introduction

The most well-known behaviour of porpoises is their smooth, rolling way of surfacing when they breath. Observations made by Spencer et. al. (1966) on the Killer whale, *Orcinus orca,* indicates that the respiratory act includes "orienting movements of a dorsal flexure of the thorax, and integrated flipper, fluke and body movements brought together in a complex involuntary act preceding the movement of air".

Such movements are seen in beached animals (Spencer et al. 1966), in surface sleeping ones (McGormick 1969), and according to the latter author, the absence of the tail movements are used to indicate depth of anesthesia, being the last movements to disappear before surgical plane is reached.

Spencer et. al. (1966) also investigated the duration of a blow (expiration and inhalation) and the action of the blowhole in the Killer whale. They found a mean expiratory duration of 0.38 seconds, and a mean inspiratory duration of 0.78 seconds. The expiration was performed through a pursed blowhole, while it was fully open during the inhalation.

This study was conducted to give a more detailed description of the movements referred to above.

Most studies of dolphin behaviour — and quite an impressive bulk of knowledge has been gathered — have been of a descriptive character, and the endpoint of such studies is a so called ethogram. This ethogram must not be considered as a final end, but only as a base for analytic work bringing about an understanding of the behaviour of these animals. Unfortunately, very little analytic work has been done up to date, possibly in part due to the very special, and rather ununiform "dolphin terminology", quite remote from that used on other animals.

Therefore it would be very desirable for a future comparative analysis if students of dolphin behaviour would adopt the ethological methods and terminology.

Materials and methods

The study is based on 8-mm movie pictures, drawn step by step. The time indications in the figures are given in seconds, and are calculated from the number of frames. The film speed was 18 frames per second. As the figures are prepared from different film sequences, there is some variation in the duration of the phases in the behaviour.

The animals were kept in a 40 m² pool with a water depth of 1 m. They were at the occasion around one year old and was captured about one month prior to filming.

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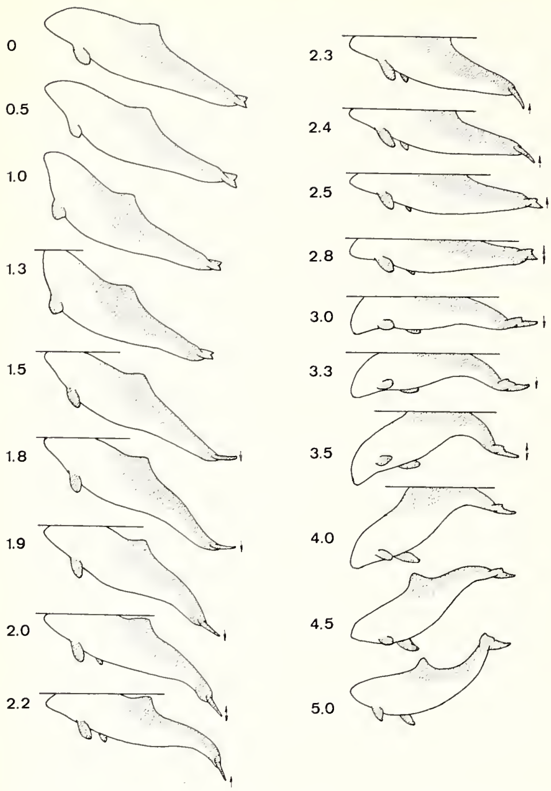

Fig. 1. A normal porpoise surfacing roll. (Explanations to the figures are given in the text. The time base is given in seconds.)

Results

Body movements during a normal roll

Several interesting features can be seen in fig. 1, where the normal porpoise roll is followed step by step. It is seen that the initial part consists of a pronounced bending up of the thorax (0.5—1.3 seconds). When the surface is reached, the tail is struck down, and the head resumes its normal position, why the thorax levels out (1.5—2.0 seconds). Then follows a powerful upward tail-stroke, where after the animal lies parallel to the surface (2.2—2.8 seconds). To support the ensuing bending down of the thorax, the tail is arched downwards, wich raises the tailstock above the water. This constitutes the last part of the roll, and after the short downstroke, the tail is held passive until it is well under the surface.

Blowhole operation

Fig. 2 shows the synchronization of the tail beats and the opening of the blowhole. Between 1.6 and 1.7 seconds, during the downstroke with the tailfin (cf 1.5—2.0 seconds in fig. 1), the lungs are emptied. The succeeding upstroke with the tail is accompanied with the inhalation (2.1—2.7 seconds, cf 2.2–2.8 seconds in fig. 1), and the closure of the blowhole is effected when this tail beat is finished (around 2.7 seconds). Then the head is bent down, and the blowhole becomes submerged.

As seen in fig. 3, the expiration is performed with the blowhole only partly open. During the inhalation the blowhole is wide open and also somewhat "sucked inward".

Pectoral fin movements

Indicated in fig. 1, although not especially clear, are the movements of the pectorals. These movements are very minute, why a closer film sequence had to be taken. This sequence is shown in fig. 4.

The upward flexure of the head (0.9—1,4 seconds, cf 0.3—1.3 seconds in fig. 1), is, partly, effected with a steering of the pectoral fins, i. e. the tip of the fin is moved downward and the trailing edges are turned forward, towards each other, thus putting an upward pressure upon the body.

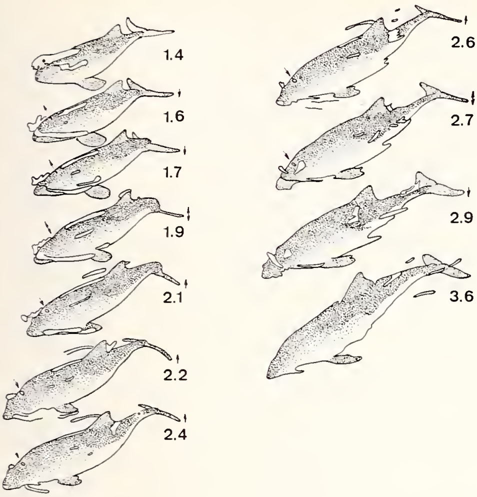

Fig. 3. Close view of the blowhole, showing the difference between the expiratory (above) and inhalatory phase

Fig. 2. Sequence showing the synchronization of the tail-beats and breathing. The pictures are distorted because the original film was taken from above, partly through the water surface. The arrow at the blowhole show direction of air-flow

During the downstroke with the tailfin (cf 1.5—2.0 seconds in fig. 1), the tip and trailing edge of the pectoral fin are turned upward (1.4–2.0 seconds), and the resulting downward pressure assists the leveling out of the body. During the upstroke (2.2–2.9 seconds, cf 2.2—2.8 seconds in fig. 1), the pectorals are adjusted in approximately the same way as during the initial part, i. e. they steer upwards, lifting the head above the water when the animal inhales (cf 2.1—2.7 seconds in fig. 2).

In order to find out how important a role the pectorals played, an approximately half-year-old animal was let loose in the pool with his fins tied tightly against the body. However, this did not make much difference, but the animal was able to surface quite normally.

Discussion

Functional analysis

The results presented here reveale a beautifully coordinated sequence of movements, typical of the gracious dolphin behaviour.

The synchronization of blowhole opening and tail movements are no coincidence, but ensures that the blowhole is above the water at the breathing. Besides that, it is rather natural that the expiration is accompanied with a downward flexure, because of the contraction of the diaphragm and the abdominal muscles. Likewise the inhalation, i. e. the muscular expansion of the lungs, causes an upward flexure of the body.

The downward tail stroke has two functions; firstly it initiates the leveling out of the body, secondly, it put the tailfin in a position that makes the succeeding upstroke possible. Bearing in mind that the thrust is provided by the upstroke (Purves 1968; van Heel 1968), the angle of the tailfin during the downstroke can be understood as being an upward steering with the tail.

The upstroke hat several functions. It completes the leveling out (with the aid of the pectorals), it provides thrust, ensuring "steering speed" to the pectoral fins, and creating a bow wave in front of the melon — vital at least in calm weather — that

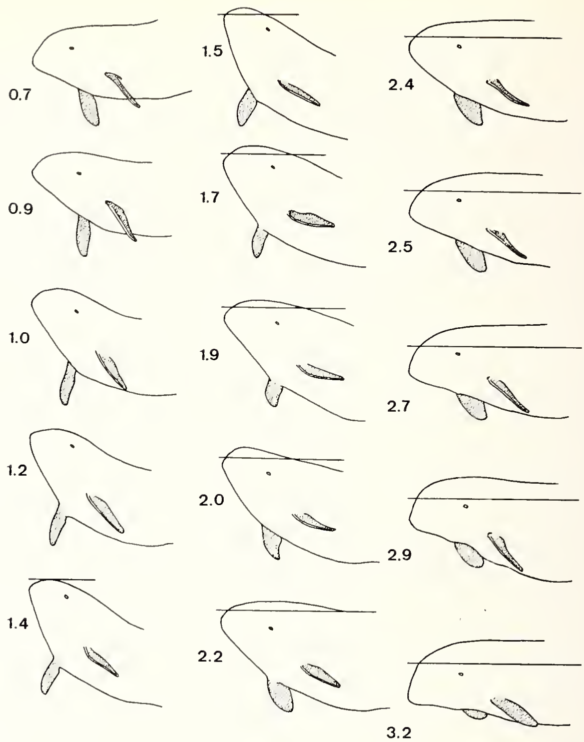

Fig. 4. The movements of the pectoral fins during the first part of the surfacing roll

keeps the blowhole dry during the inhalation. The speed also facilitates submerging, although it is the tailstock, raised above the water, that actually presses down the body. In many whale species, as well as in human divers, this downward pressure is increased by raising the hole tail and legs respectively above the water.

Breathing time

In fig. 2 can be seen that the blow lasts for about 1.1 seconds. Judged from the tail movements in fig. 1 and 2, the expiration and inhalation can be separated, and average 0.4 and 0.8 seconds respectively. Surprisingly enough this is very close to the measures from the much larger killer whale, *Orcinus orca,* mentioned in the introduction. It should be pointed out, though, that the harbour porpoise measures are confined to rather low level activities. In other situations, e. g. in fright reactions, the whole breathing sequence appears much shorter, and then the amplitude of the tail beats are also smaller.

Chest and throat movements

The peculiar form of the chest and the throat, just at the end of the inhalation (2.9 seconds in fig. 3), is no artifact. At present, however, the exact cause of these are not known, but possibly the "bulb" in the throat region is connected with the larynx action, e. g. when the epiglottal orifice is closed. The bulb in the chest region may be caused by the sternum, that due to the absence of clavicles, has no fixed position, but is rather free to move during the breathing.

The elements of the behaviour

The rigidity of some of the movements in connection with the normal surfacing, together with their presence in sleeping and tranquilized animals (McGormick 1969), as well as beached ones (Spencer et al. 1966) — in the latter case most conspicuously demonstrated by the powerful tailfin upstroke, especially in young animals (pers. obs.) — indicate that these movements are strongly bound together with the breathing, and that they most likely are involuntary.

Not only are they synchronized with the blowhole operation, but they also have to be extremely well timed with the reaching of the surface.

Obviously there are both quite stereotypic movements, i. e. the tailbeats, mixed with orienting ones, taxis', i. e. the dorsal flexure of the thorax and the pectoral fin movements.

The fact that the prevention from steering with the pectoral fins has no effect on the surfacing, indicates that the tailfin movements also includes taxis' (cf the egg-retrieving behaviour in the grey lag goose; Lorenz and Tinbergen 1938), making possible an adjustment of the tailbeats in relation to the surface.

If the stereotypic movements are innate, they are to be termed fixed motor patterns (originally called Erbkoordinationen by Lorenz 1937). Unfortunately it is not possible from the literature to get a description detailed enough of the surfacing behaviour of the newborn porpoise to be able to conclude what parts are innate and what parts are not.

McBride and Kritzler (1951), though, report that newborn bottlenose dolphins, *Tursiops truncatus,* do not perform the adult roll when surfacing, until they are 1—2 months old. Instead they raise their whole head above the water at an approximate angle of 45 degrees, and then simply fall back again. Observations on a free-ranging, approximately 2 months old harbour porpoise, indicate that a learning or maturing process takes place at this age, as this juvenile demonstrated both types of surfacing behaviour in the run of a couple of days (Amundin and Amundin in press).

However, complicating the picture are the observations of Andersen (pers. comm.) of a very young, also free-ranging harbour porpoise – its length was only about 70 cm, and it had a pronounced "neck", indicating that it was very close to newborn. In spite of being so young, the little porpoise performed a perfect, species-typic surfacing behaviour.

There are special problems facing a little porpoise at breathing. Firstly the distance from the tip of the snout to the blowhole is much shorter than in the adult, secondly, due to the lesser mass of the little animal, the bow wave in front of the melon, created during the upstroke with the tailfin, is much smaller. Both these factors increase the risk of inhaling water.

Considering the well developed brain in the newborn porpoise, and the skill with which it follows the adults, even at top speed (McBride and Kritzler 1951; Essapian 1953; Tavolga and Essapian 1957), it is quite likely that many, if not all, components in the surfacing behaviour are present at birth.

However, due to the abovementioned problems for the smaller animal at surfacing, it may be that some of the taxes, especially the dorsal flexure of the thorax, supress the downward tendencies, e. g. the downward steering with the pectorals (cf 1.4—2.0 seconds, fig. 3). Such a dominance of the dorsal flexure was seen in a 2 year old Harbour porpoise, which was coughing several times in rapid succession. At the end of the coughing attack, the animal was in a vertical position, with its head above the water (Amundin in press).

Summary

This study confirms earlier observations of apparently involuntary movements, strongly associated with the breathing. The movements include taxes — a dorsal flexure of the thorax and steering movements with the pectoral fins — and a more stereotypic movements, resembling a fixed motor pattern, with the tailfin. In the latter, a downstroke is paired with the expiration, and a powerful, thrust producing upstroke with the inhalation.

The different components are beautifully coordinated into a smooth and highly functional sequence of movements, ensuring that the blowhole is raised above the water at the breathing. Many of the movements are present in sleeping, tranquilized, and beached animals, thereby giving an indicaton of the strength of association with the breathing.

The duration of an expiration and an inhalation was measured for a couple of blows, and was found to be 0.4 and 0.8 seconds respectively.

Zusammenfassung

Funktionelle Analyse des Auftauch-Verhaltens bei Phocoena phocoena (L.)

Diese Studie bestätigt frühere Beobachtungen von offenbar unfreiwilligen Bewegungen, die mit der Atmung stark verbunden sind. Die Bewegungen beinhalten Taxien — eine Dorsalbeugung des Thorax und Steuerbewegungen mit den Brustflossen — und einige stereotypere Bewegungen mit der Schwanzflosse, die einem „fixed motor pattern" gleichen. Im letzten Fall ist ein abwärtiger Stoß mit der Ausatmung verbunden, und ein kräftiger, Treibkraft produzierender Stoß führt durch Einatmung aufwärts.

Die verschiedenen Komponenten sind schön koordiniert, in einer Reihe von gleichmäßigen und sehr funktionellen Bewegungen, die sichern, daß das Luftloch während der Atmung über dem Wasser ist. Viele der Bewegungen sind während des Schlafs, der Betäubung und auch bei gestrandeten Tieren zu beobachten, und es wird daraus die Verbindung zwischen Atmung und Bewegung deutlich. Die Dauer der Ein- und Ausatmung ist einige Male gemessen worden. Sie betrug 0,4 und 0,8 Sekunden.

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