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# Sound velocity in the head of the dwarf sperm whale, *Kogia sima*, with anatomical and functional discussion

John C. Goold* and Malcolm R. Clarke†

*Institute of Environmental Science, University of Wales Bangor, Robinson Building, Deiniol Road, Bangor, Gwynedd, LL57 2UW. E-mail: j.c.goold@bangor.ac.uk
†'Ancarva', Southdown, Millbrook, Torpoint, Cornwall, PL10 1EZ

The velocity of sound through spermaceti oil from the melon of two *Kogia sima* specimens, stranded in Florida in 1995, was determined across a range of temperatures between 7 and 38°C and at pressures between 0 and 90 atm. Sound velocity values ranged between 1395–1669 m $s^{-1}$, increasing linearly with increasing pressure but decreasing non-linearly with increasing temperature. Polynomials were generated to describe sound velocity as a function of temperature and pressure for the core and peripheral lipids of the melon. The results suggest that, at normal body temperature, sound travelling from the back to the front of the melon would have a tendency to focus during dives to any depth, largely due to heat exchange across the periphery of the melon. Effects of changes in ambient temperature and pressure are described and discussed in relation to anatomy.

## INTRODUCTION

The nasal passages and surrounding fatty tissues in the foreheads of many Cetacea are now known to have functional significance in the production and conduction of sound (Au, 1993; Cranford et al., 1996). Wood (1964) first suggested that the fatty deposits called the 'melon' in the forehead of delphiniids may act as a transducer to couple sound travelling from the head with the sea water. Norris & Harvey (1974) advanced this idea by showing that sound travelling through the forehead had a greater velocity towards the outside than through the central core of the melon. This they suggested curved the sound peripherally so that the sound was focused and this effect would be enhanced by sound channelling through the curved blubber layer around the melon. They also suggested that the velocity of sound, passing forwards, increased to match acoustic impedance across the lipid/seawater interface, thereby coupling sound energy to the surrounding seawater more efficiently. The melon was shown to contain different lipids to those in the surrounding blubber (Varanesi & Malin, 1972) and these have sometimes been referred to as 'acoustic fats'. Within the melon, its core also differs from its outer layers in lipid content and the lipid structure has been related to ultrasonic velocity, density and compressibility and suggested as the basis of an acoustic lens in *Tursiops* (Litchfield et al., 1973; Varanasi et al., 1975) and in *Globicephala* (Blomberg & Lindholm, 1976). The lens effect almost certainly contributes, with the curve of the cetacean's head, to produce the observed directionality of the beam emitted (Au, 1993). The sound velocities vary with temperature (Litchfield et al., 1979) and the effect of the temperature of ambient seawater against the cetacean's surface must also be influential in altering acoustic impedance (i.e. velocity and density) near the forehead. Another factor influencing sound velocity values is hydrostatic pressure and this must be important in any cetacean but is most important in the deep-diving species.

In the three species of the Physeteridae, *Physeter macrocephalus*, *Kogia sima* and *K. breviceps*, sound also passes through the fatty tissues of the forehead (Norris & Harvey, 1972). However, in these, the structure of the forehead is different from that in the dolphins (Raven & Gregory, 1933; Schenkkan & Purves, 1973; Clarke, 1978b; Cranford et al., 1996). The lipids of the forehead, in these animals, solidify at relatively higher temperatures and have often been called 'spermaceti oil or wax' (Clarke, 1978a). They were first chemically analysed in *Physeter macrocephalus* by Morris (1973, 1975) and later in *Kogia* (Karol et al., 1978) and a difference between the core and the peripheral lipids was demonstrated. The lipids consisted of a mixture of triglycerides and wax esters. Velocity of sound in samples taken from various positions in the forehead of *Physeter* showed inverse correlation between wax esters and sound velocity (Flewellen & Morris, 1978). As the core has a higher proportion of wax esters than peripheral tissues, sound velocity is slower in the core and hence it is likely that a sound focusing effect will occur through the whale's head. However, the structure of the forehead and the distribution of the lipids is very complex and is different in the two genera, *Physeter* and *Kogia*. For example, it is very probable, from their structure, that the sound is produced at the anterior end of the forehead in *Physeter* (Norris & Harvey, 1972) but at the posterior end in *Kogia* (Karol et al., 1978).

All the above sound velocity measurements were made at atmospheric pressure but did not take account of the fact that *P. macrocephalus* dives to great depths (Clarke, 1976, 1978c; Lockyer, 1977; Watkins et al., 1993). It therefore remained to find the effect of pressure upon the sound velocity through the lipid tissues (Goold et al.,

1996) and to find how the relationship between samples from the core and the peripheral spermaceti might change during a dive.

Another factor, is that there is good reason to suppose, from the complex structure of the forehead in *P. macrocephalus*, that it does not merely act as a passive conductor of sound but also acts as an organ for buoyancy control (Clarke, 1978c). As this control depends on manipulation of the temperature of the spermaceti, an understanding of the relationship between sound velocity and temperature is relevant to understanding the potential dual function of the organ.

*Kogia* has been less well studied than *Physeter* in many respects and the present work is part of an attempt to rectify this position. The considerable anatomical and size differences between *Kogia* and *Physeter* suggest that the functions of their foreheads and spermaceti organs may be different from one another. The object of the sampling was intended to provide data comparable with sound velocity measurements obtained previously from *P. macrocephalus* (Goold et al., 1996) and to see whether there are, in *Kogia*, clear differences between the sound propagation of the central core tissues of the melon and the more peripheral tissues around it, as chemical analyses suggest (Karol et al., 1978). In addition, the relationship between sound velocity, temperature and pressure during deep dives should provide a firmer basis for relating function with diving and echolocating behaviour.

## MATERIALS AND METHODS

### *Anatomy and sample collection*

Samples of tissue for these determinations were removed from the foreheads of two *Kogia sima* (Owen, 1866) specimens which became stranded on the coast of Florida in 1995. Ks25 was stranded on Cocoa beach (28°21′30″N 80°35′18″W) on 20 July 1995, and was a mature male having a length of 222 cm and a weight of 30.85 kg. It was alive and intact when first examined but died upon being towed to sea. Apart from a heavy load of *Phyllobothrium cestodes*, necropsy showed nothing remarkable although the outer skin had largely sloughed off as if it had been badly damaged during stranding. Only the head was examined by one of the authors (M.R.C.). Unfortunately, few details of Ks16 are available; it was stranded in Florida and had been kept alive for some time in an oceanarium. Only the head had been preserved and, from its weight (14.7 kg) and linear dimensions (forehead tip to blowhole, etc.), the animal was probably close to 200 cm in length. Both heads had been deep frozen soon after death and kept until they were thawed and samples were taken, in January 1996, by an author (M.R.C.). They were refrozen and finally examined in the UK in April 1996.

In January 1996 the head of Ks25 was cut into 5 cm thick horizontal sections with a bandsaw. From the largest section, several chunks of fat were taken from positions along the centre of the melon core (Figure 1). As about 100 ml of oil was required for the sound velocity measurements and the samples were smaller than this, the oil from these was combined; the measurements are considered a useful check on the core sample from Ks16.

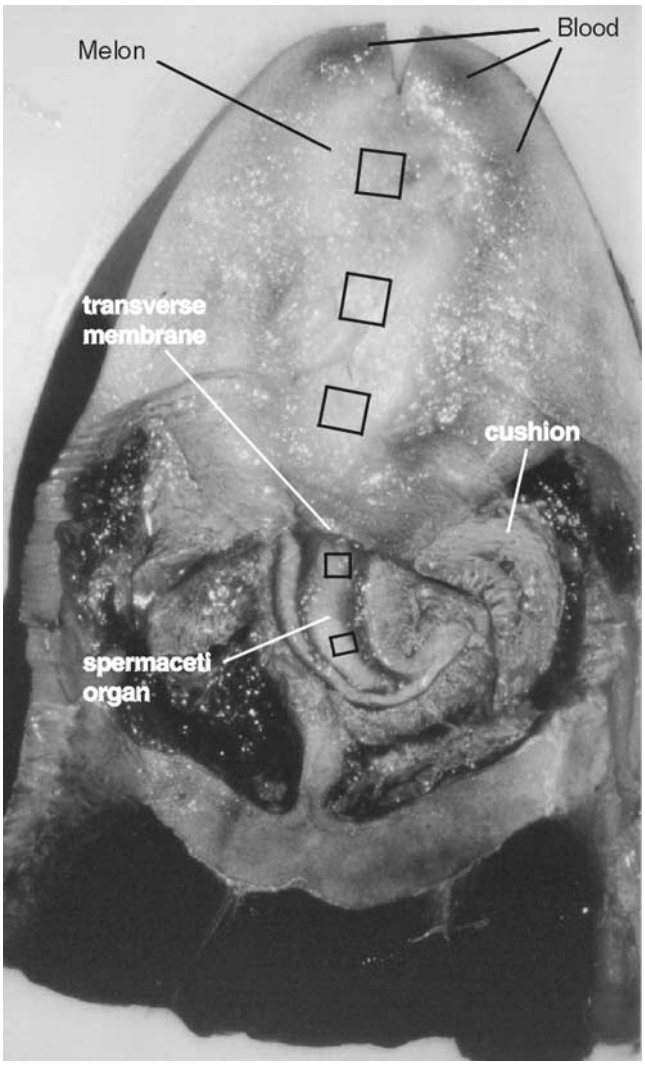


**Figure 1.** Horizontal section of the forehead of *Kogia sima* no. 25 viewed from the dorsal side. Approximate positions of the samples of tissue from which lipids were squeezed and combined are shown.

The head of Ks16 was thawed and 3 cm longitudinal–vertical sections were made. Samples were taken from the core of the sagittal section and the periphery of the section to the right of the sagittal section for sound velocity measurements (Figure 2). The internal tissues of both animals seemed in good condition when examined and tissues of Ks16 were differentially stained yellow, possibly as a result of drugs or food administered during captivity. Immediately prior to the experiment in the UK, the tissue samples were squeezed at room temperature to deliver their oil. [Oil from the foreheads of physeterids has historically been referred to as spermaceti oil. In this paper we continue with this convention, and draw the readers attention to the fact that the 'spermaceti oil' referred to in this manuscript is extracted from both the melon and the spermaceti organ as illustrated in Figures 1 & 2.]

### *Sound velocity*

Sound velocity was measured through the samples at discrete temperatures across the range 7–38°C, and at



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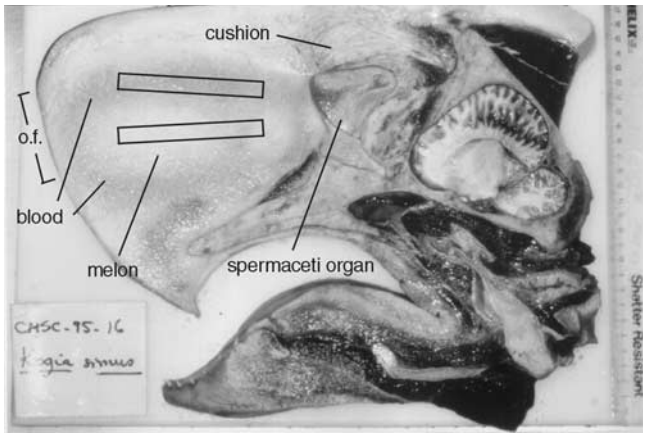


**Figure 2.** Vertical section of the forehead of *Kogia sima* no. 16 viewed from the left side showing the positions from which the two tissue samples were taken for lipid removal. The abbreviation 'o.f.' denotes the oval face.

discrete pressures across the range 0–90 atm (atmospheres, 1 atm=1.01325×10$^5$ Pascals) above ambient atmospheric pressure for each temperature. The velocimeter was essentially a hydraulic ram/cylinder assembly semi-immersed in a temperature regulated water jacket. The apparatus and experimental setup are detailed in Goold et al. (1996) but a brief account will be given here. The cylinder bore held the fluid samples through which sound velocity was to be measured. The ram fitted into the cylinder bore to complete the fluid enclosure and all trapped air was expelled through a bleed vent. The experimental sound source was an ultrasonic transducer embedded in the front face of the ram, with sound reception through a similar ultrasonic transducer in the base of the cylinder. Sound velocity was measured by 'time of flight' of individual sound pulses through a known column length of spermaceti oil (i.e. distance over time). The pulse firing rate was 50 s$^{-1}$, with the received pulses displayed on a digital storage oscilloscope. Each pulse firing triggered a sweep on the oscilloscope, and the fast repetition produced a stable display of the received sound pulse waveform. Time elapsed from trigger event to waveform reception was measured from the oscilloscope timebase (to a precision of ±0.05 μs) using the scopes' timebase cursor. Spermaceti sample length was measured to a precision of ±0.01 mm from the exterior length of the exposed ram using a pair of digital callipers. Total precision of sound velocity measurement was better than ±4 m s$^{-1}$. Sample temperature was held constant by the water jacket as the internal cell pressure was increased to 90 atm above atmospheric, in steps of 15 atm. Pressure was applied to the fluid sample using a modified oedometer and calibrated weights, which applied the necessary load onto the top of the ram. A sound pulse time of flight measurement was made at each discrete pressure value for a given temperature plateau. Once

**Table 1.** *Sound velocity m s$^{-1}$ in lipids extracted from the melon core of* Kogia sima *no. 16 at various temperatures and pressures.*

| | Ksl6 Melon Core Spermaceti | | | | | | |
|---|---|---|---|---|---|---|---|
| Temp (°C) | 0 atm | 15 atm | 30 atm | 45 atm | 60 atm | 75 atm | 90 atm |
| 37.9 | 1411 | 1415 | 1418 | 1423 | 1426 | 1433 | 1433 |
| 36.4 | 1404 | 1409 | 1417 | 1419 | 1424 | 1428 | 1432 |
| 34.4 | 1413 | 1419 | 1425 | 1428 | 1437 | 1447 | 1436 |
| 30.9 | 1418 | 1424 | 1430 | 1442 | 1437 | 1441 | 1445 |
| 28.9 | 1420 | 1426 | 1432 | 1441 | 1433 | 1440 | 1446 |
| 26.9 | 1427 | 1432 | 1437 | 1447 | 1443 | 1447 | 1449 |
| 25.0 | 1461 | 1465 | 1461 | 1470 | 1474 | 1480 | |
| 23.2 | 1484 | 1491 | 1488 | 1495 | 1495 | 1498 | 1503 |
| 21.1 | | 1496 | 1495 | 1508 | 1510 | 1517 | 1519 |
| 18.9 | | 1516 | 1516 | 1523 | 1529 | 1536 | 1537 |
| 16.9 | | 1547 | 1550 | 1554 | 1558 | 1563 | 1564 |

**Table 2.** *Sound velocity m s$^{-1}$ in lipids extracted from the melon cortex of* Kogia sima *no. 16 at various temperatures and pressures.*

| | Ksl6 Melon Peripheral (cortex) Spermaceti | | | | | | |
|---|---|---|---|---|---|---|---|
| Temp (°C) | 0 atm | 15 atm | 30 atm | 45 atm | 60 atm | 75 atm | 90 atm |
| 37.9 | 1429 | 1433 | 1439 | 1447 | 1452 | 1456 | 1460 |
| 35.6 | | 1435 | 1440 | 1444 | 1451 | 1458 | 1461 |
| 33.0 | 1427 | 1437 | 1442 | 1444 | 1450 | 1457 | 1459 |
| 30.9 | 1429 | 1436 | 1441 | 1445 | 1453 | 1457 | 1459 |
| 28.9 | 1426 | 1434 | 1440 | 1444 | 1450 | | |
| 26.9 | 1423 | 1435 | 1439 | 1442 | 1448 | 1451 | 1454 |
| 24.9 | 1428 | 1436 | 1438 | 1444 | 1446 | 1453 | 1453 |
| 22.9 | 1429 | 1436 | 1439 | 1445 | 1450 | 1456 | 1457 |
| 20.9 | 1431 | 1436 | 1442 | 1446 | 1453 | 1452 | 1456 |
| 19.1 | 1447 | 1450 | 1455 | 1459 | 1464 | 1467 | 1470 |
| 17.0 | 1447 | 1452 | 1460 | 1463 | 1465 | 1468 | 1476 |
| 15.0 | 1456 | 1460 | 1468 | 1473 | 1477 | 1480 | 1483 |
| 13.0 | 1463 | 1471 | 1476 | 1479 | 1483 | 1487 | 1490 |
| 10.9 | 1465 | 1477 | 1481 | 1487 | 1489 | 1491 | 1496 |
| 9.0 | | 1482 | 1489 | 1494 | 1495 | 1501 | 1503 |
| 6.9 | | 1491 | 1495 | 1498 | 1501 | 1503 | 1507 |

**Table 3.** *Sound velocity m s$^{-1}$ in lipids extracted from the spermaceti organ and melon core of* Kogia sima *no. 25 at various temperatures and pressures.*

| | Ks25 Melon Core Spermaceti | | | | | | |
|---|---|---|---|---|---|---|---|
| Temp (°C) | 0 atm | 15 atm | 30 atm | 45 atm | 60 atm | 75 atm | 90 atm |
| 38.3 | 1395 | 1399 | 1405 | 1410 | 1415 | 1419 | 1424 |
| 35.2 | 1401 | 1406 | 1411 | 1416 | 1420 | 1425 | 1429 |
| 32.2 | 1408 | 1412 | 1418 | 1423 | 1427 | 1430 | 1435 |
| 29.8 | 1413 | 1417 | 1423 | 1427 | 1431 | 1436 | 1439 |
| 27.2 | 1416 | 1420 | 1425 | 1430 | 1434 | 1438 | 1443 |
| 24.8 | 1428 | 1432 | 1436 | 1440 | 1445 | 1449 | 1453 |
| 22.2 | 1450 | 1448 | 1452 | 1456 | 1460 | 1464 | 1469 |
| 20.0 | 1467 | | 1476 | 1483 | 1488 | 1492 | 1498 |
| 17.9 | 1494 | 1492 | 1496 | 1497 | 1501 | 1505 | 1509 |
| 15.1 | 1515 | 1518 | 1518 | 1519 | 1520 | 1523 | 1525 |
| 11.8 | | 1573 | 1576 | 1578 | 1579 | 1579 | 1580 |
| 9.2 | 1646 | 1642 | 1646 | 1653 | 1660 | 1668 | 1669 |



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measurements had been made across the pressure range at a given temperature, the water jacket temperature was lowered by approximately 2°C and the apparatus left to reach thermal equilibrium before the next set of measurements.

The raw time of flight readings were corrected against a distilled water medium and these data were compared to tabulated standards for distilled water (Bark et al., 1964). A calibration was thereby obtained to convert raw time of flight sound velocities into true sound velocity. Once corrected sound velocity data had been generated for the three samples of spermaceti oil, multivariant regression analysis was applied to the data sets using the parameters P (pressure), T (temperature) and $T^2$ to obtain least squares best fit. This analysis produced polynomials for the description of sound velocity in *Kogia* spermaceti oil between prescribed pressure and temperature limits.

## RESULTS

### *Anatomy*

To understand the significance of the sound velocity measurements and discussion it is useful to describe the structure of the melon in greater detail than has been previously attempted. Details of structure of the region behind the melon show that sound produced by the 'museu de singe' or 'monkey's mouth' travels along the broadening funnel-like tube called the spermaceti organ and enters the posterior end of the 'melon' at a thin transverse membrane (clearly seen in these specimens but not found in all specimens, possibly due to post-mortem degeneration). The core of this funnel is white fat but it is surrounded by a red, jelly-like tissue, rich in fine capillaries (this is black in the figures). The spermaceti organ is cut through the middle in Figure 1 but, in Figure 2, it is cut through the side so that more of the jelly layer is visible. The fatty tissues anterior to the transverse membrane, form a broad 'sausage' which is less fibrous than the more peripheral blubber fatty tissues from which it is clearly separated by a continuation of the jelly-like, red tissue of the spermaceti organ but which is thicker and less well defined. This outer layer of the sound-conducting tissue, which we shall call the 'cortex' (called 'a brown outer-melon zone' by Karol et al., 1978), is particularly well provided with blood vessels towards the anterior end (black in Figure 1). In this position the front of the head is flat over an oval area which we shall call the 'oval face'. This has the usual fine transparent epidermis overlying the black dermis containing vascular papillae. Instead of this dermis overlying a tough, fibrous blubber layer, as is found outside the rest of the melon and in almost all other regions of the body surface, under the oval face, the fatty core of the melon comes directly against the dermis and is particularly rich in capillaries in that region (the flat nature of the oval face is clear in uncut heads but tends to bulge in sections, particularly where the centre line is cut as in Figure 1—its position is indicated in Figure 2). In view of the high body temperature of the *Kogia* (probably close to 37–38°C) and the low water temperatures in which the *Kogia* almost certainly lives (<10–27°C) this anatomical arrangement would appear to be very prone to losing body heat. Indeed, it would act as a heat-exchanger and its presence suggests that temperature of the forehead, is not only variable, but is under control of the blood circulation and that such control has particular significance to the *Kogia*.

### *Sound velocity*

Tables 1–3 detail sound velocity at various temperatures and pressures for the three samples Ksl6 core, Ksl6

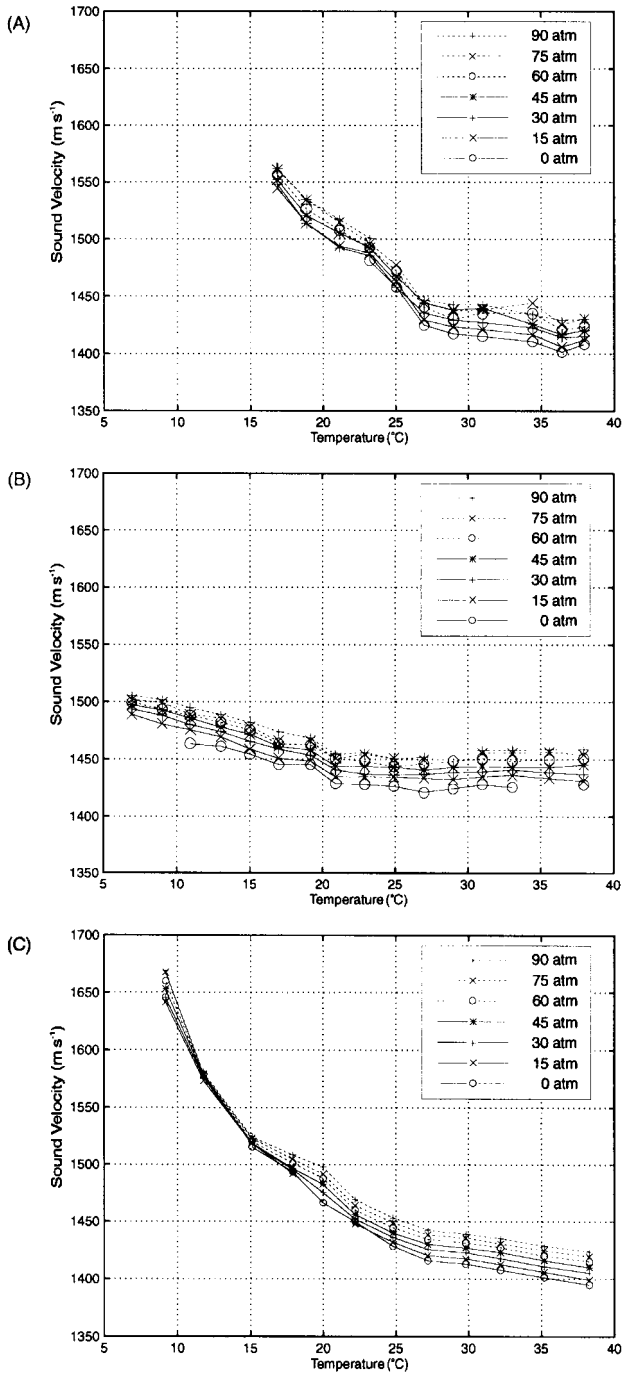


**Figure 3.** (A) Sound velocity measurements of the core lipids of *Kogia sima* no. 16 at various temperatures and pressures; (B) sound velocity measurements of the cortex lipids of *K. sima* no. 16 at various temperatures and pressures; and (C) sound velocity measurements of the core lipids of *K. sima* no. 25 at various temperatures and pressures.



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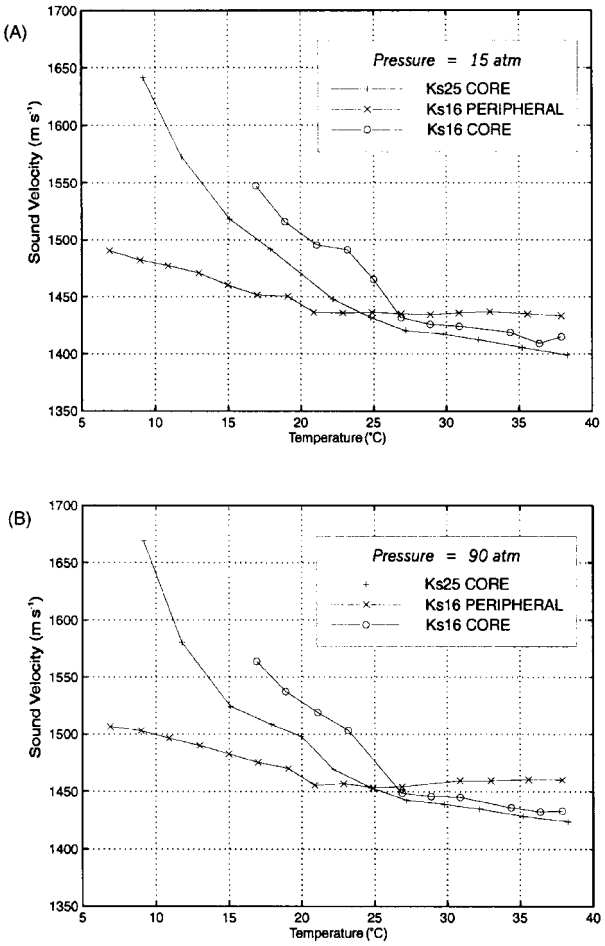


**Figure 4.** (A) Sound velocity measurements of the three samples of lipid from *Kogia sima* at various temperatures and 15 atm pressure; (B) the same samples at 90 atm pressure.

peripheral (cortex) and Ks25 core respectively. Figure 3 illustrates the trends contained within these data. It is clear that in all cases an inverse non-linear relationship exists between temperature and sound velocity, the gradient of a given tangent to the curve generally becoming steeper at low temperature, and particularly so in melon core samples. The relationship between velocity and pressure can be seen to be approximately linear. In general, sound velocity in all samples increases linearly with increasing pressure, but decreases non linearly with increasing temperature, across the ranges measured. In the case of peripheral spermaceti (Figure 3B) velocity-temperature curves essentially 'level out' above approximately 22°C, in fact it is arguable that the curves show a slight increase in sound velocity towards the higher temperatures.

An interesting comparison can be made by superimposing the temperature–velocity curves from different samples. Figure 4A shows the superimposition of temperature–velocity curves of all three samples at a uniform pressure of 15 atm. The peripheral (cortex) oil has the shallowest gradient, with velocities ranging between approximately 1490 and 1435 m s$^{-1}$ (between 7 and 38°C). The core samples have the steepest gradients with velocities ranging between approximately 1550 and 1410 m s$^{-1}$ (between 17 and 38°C) for Ks16 core oil, and

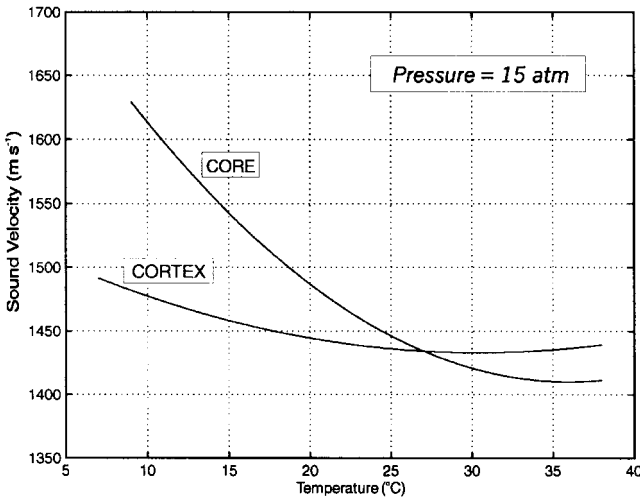


**Figure 5.** Derived curves of sound velocity vs temperature in *Kogia sima* spermaceti at 15 atm pressure. The core curve is derived from the combined measurements of the two core samples.

between approximately 1645 and 1400 m s$^{-1}$ (between 9 and 38°C) for Ks25 core oil. It is also notable that both of the core velocity curves cross the cortex curve between 25 and 27°C. At temperatures below 25–27°C sound velocity is faster in core spermaceti oil than it is in cortex spermaceti oil. At temperatures above 25–27°C sound velocity in peripheral spermaceti oil is faster than that in core spermaceti. At the body temperature of *Kogia sima* (38°C) this difference appears to be in the range 20–35 m s$^{-1}$ (1.4–2.4% of the higher velocity). Figure 4B shows a similar set of curves for all three samples, but this time at the elevated pressure of 90 atm. As expected, the trends and interactions are the same, with all curves simply displaced upwards by some 20–25 m s$^{-1}$.

Eqn 1 is a polynomial generated from the combined datasets of Ks16 and Ks25 melon core oil. Eqn 2 is a polynomial generated from the data set of Ks16 cortex oil.

$$C_{core} = 1796 + 0.27P - 21.7T + 0.302T^2 \quad (1)$$
$$9 < T < 38$$
$$0 < P < 90$$

$$C_{cortex} = 1527 + 0.31P - 6.5T + 0.107T^2 \quad (2)$$
$$7 < T < 38$$
$$0 < P < 90$$

where C=sound velocity (m s$^{-1}$), P=pressure (atm), T=temperature (°C).

Eqns 1 & 2 can be used to derive sound velocity in *Kogia* melon core spermaceti and melon cortex spermaceti, given values of T and P within the prescribed limits. Combining the data sets of Ks16 core and Ks25 core to produce eqn 1 gives a more general estimate of core velocity, given that both curves were similar in shape but slightly displaced from one another (Figure 3). Figure 5 shows polynomial generated curves at 15 atm pressure for melon core and cortex spermaceti, derived from the outputs of eqns 1 & 2.



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## DISCUSSION

We have no direct measurements of the depth to which *Kogia sima* dives but it is widespread in tropical and temperate seas and its diet includes many deep-living cephalopod species (Ross, 1979; Clarke, 1996). Further, Willis & Baird (1998) refer to literature on *K. sima* stomach content, which details shrimp typically occurring between 500 and 1300 m and bottom dwelling fish typically found in water of 450–1500 m depth. Other observations suggest habitual feeding by *K. sima* at depths in excess of 250 m (Willis & Baird, 1998). From these it seems probable they dive to feed within the 500–1000 m horizon. Such dives lead to considerable and rapid changes in the ambient temperature and pressure experienced. For example, a drop in ambient temperature may be as much as 20°C and the rise in pressure may be over 100 atm, possibly in less than 20 min. Clearly, any discussion of the difference in the relationship between the velocity of sound in the core and peripheral regions of the melon must take these effects into account.

In the dolphin, both the graded sound velocity of the melon fat and the curvature of the head surface probably contribute to the observed focussing of sound ahead of the animal. The shape of the melon in *Kogia* (Figures 1 & 2) shows that much of the sound issuing from the front end of the spermaceti organ will have a direct and unimpeded passage to the oval face where it will pass through at close to right angles to the skin/water interface. Sound straying to the side of the direct path will mainly strike the front half of the cortex and its comparatively higher velocity will help to flatten the wavefront and guide it towards the oval face. It is in this region that most blood vessels are evident in sections (Figure 1). Differential sound velocities might be required to both curve the sound round towards the front and to synchronize the arrival of sound at the oval face on the anterior forehead surface. If velocities were uniform, sound following a central path from the spermaceti organ would arrive slightly before sound travelling round the periphery of the core. The distance travelled can be measured on Figures 1 & 2 although the section in Figure 2 is slightly to the side of the centre line and exaggerates the width of the cortex. From Figure 1, the sound entering the cortex has to travel 9.5% further, than the direct route, on the right side and 2.7% further on the left side. From Figure 2, dorsally the sound would travel 16.6% more and ventrally it would travel 12.6% more. These values are higher than the percentage differences in sound velocity between the core and peripheral fat. From eqns 1 & 2, at the sea surface (0 atm), if the whole forehead is near 38°C (blood temperature) sound will travel 27 m s$^{-1}$ [P=0, $C_{core(T=38)}$=1407.5, $C_{cortex(T=38)}$=1434.5] faster through the periphery than through the core, i.e. a 1.9% increase. However, it must be remembered that the concentration of lipids within the tissues is not taken into account in any studies on extracted lipids. The appearance of the tissues certainly suggests that there is more lipid in the core than in the cortex and this would emphasize the difference in sound velocity shown by the lipid composition. More structural tissue and more blood in the tissues would lead to higher velocities.

Deep diving will take the animal into much colder water anywhere in its wide range of distribution in tropical and temperate seas; in the tropics the surface water temperature may be over 25°C while it may be less than 5°C at 900 m and, even in middle latitudes in Winter, it may drop 10°C, from 17°C at the surface to 7°C at 900 m (Fuglister, 1960). During a drop of 20°C in ambient temperature, possibly over less than the same number of minutes, it is likely that the animal will have some difficulty in preventing its forehead from cooling. It is therefore of considerable interest that, even if the cortex cooled to 25°C, providing the core kept to normal blood temperature, the difference in sound velocity would still be a very similar 27.5 m s$^{-1}$ [P=90, $C_{core(T=38)}$=1431.8, $C_{cortex(T=25)}$=1459.3]. If, however, the core dropped to 25°C as well, there would be a slight inversion of the sound velocity profile with the core 7.3 m s$^{-1}$ [P=90, $C_{core(T=25)}$=1466.6, $C_{cortex(T=25)}$=1459.3] faster than the periphery at 900 m.

Bearing in mind the low temperature of the ambient water, there is a possibility that the periphery might drop to lower than 25°C and then we see that, if the core stayed at 38°C, the difference would be increased; at a cortex temperature of 9°C the velocity difference would be more than doubled to 73.3 m s$^{-1}$ [P=90, $C_{core(T=38)}$=1431.8, $C_{cortex(T=9)}$=1505.1]. Conversely, if the core temperature also dropped to below about 20°C with a cortex temperature of 9°C [P=90, $C_{core(T=20)}$=1507.1, $C_{cortex(T=9)}$=1505.1], sound velocity would become greater in the core than in the cortex and the wavefront would diverge rather than be focused.

As stated above, when near the surface, if the whole forehead is near 38°C (blood temperature) sound will travel 27 m s$^{-1}$ faster through the cortex than through the core. If the *Kogia* were to dive to 900 m, this difference would be much the same (30.6 m s$^{-1}$). Thus, at the depths at which *K. sima* probably feeds and spends much of its time, the ambient sea temperatures and the blood circulation provide a mechanism by which the sound produced could be focused or spread out ahead of the animal. If such manipulation is of selective value to the animal it seems possible that this facility has developed. Focusing of the sound is almost certainly of value to optimize echolocation off prey, particularly off gelatinous or low density cephalopods with high water content and close impedance matching to seawater (i.e. poor sound reflectors); these form a high proportion of their food. Wavefront divergence could be useful for wide beam echo location, e.g. off bottom contours, which would give strong echoes relative to cephalopods.

It has previously been held that the anatomy of the blood system in the forehead of *Physeter macrocephalus* suggests it provides a method for cooling the spermaceti wax (Clarke, 1978c). Although the anatomy in *Kogia* is very different, the parallel development in *Kogia* to utilize physical properties of similar lipids might be expected.

Of course, because we required relatively large lipid samples, the present experiment compares only the core with the cortex and multiple samples across the forehead would probably show a gradual change in sound velocity as chemical analyses suggest. Indeed, as indicated in Figure 2, the Ksl6 sample is slightly to the side of the midline and the difference in velocities between the core



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of Ks25 and Ksl6 may well reflect this slightly more peripheral position of the Ksl6 sample. Further, it should be noted that our restricted sample size inevitably means that the relationships and equations derived here should be taken as broad generalisations for *Kogia*.

In work on delphiniids the gradual transition in velocity values from the core to the extreme outer layers of the melon indicated by the lowering of the triacylglycerols and wax esters towards the outside, has been suggested as a feature facilitating passage of sound from the forehead into the water (Au, 1993). Our sampling could not check this, but clearly there would be a downward gradient in temperature towards the oval face which would have the same effect as the proposed lipid differences. Also, in the dolphin, the curved surface of the melon probably contributes to focusing the sound emanating through its surface (Au, 1993). Similar functions of the melon of *Kogia* are most unlikely since the tip of the forehead over the melon is flat. The arrangement shows that any focussing must be by internal velocity differences. Incidentally, the flat nature of the oval face, unlike the curved surfaces in many of the delphiniids, would have virtually no effect on sound waves at close to normal angles of incidence. In addition, its lack of heat insulation layers between water and core would allow the cooling effects of ambient water at depth to be quickly experienced by the core. In fact, the general shape of the insulating blubber layer, which noticeably begins to thin two-thirds along the forehead length, suggests that cooling right across the front part of the forehead can take place with the core possibly cooling faster than the periphery near the anterior end (Figure 1). Another feature supporting this is that there appear to be more blood vessels in the tip of the core which could regulate heat loss and gain of the anterior melon and periphery (in the region of the most anterior sample shown in Figure 1).

The effect on the tissues and their sound conduction of any heat exchange at the flat oval face must depend upon the direction in which the circulation moves the blood. If blood of high temperature enters the cortex at the posterior end and travels forwards round the core, is cooled at the oval window and moves back through the core, the core would be cooled relative to the cortex. The opposite would be true if the opposite route were taken. However, most of the core appears to have very few blood vessels and the low heat conductivity of the core may insulate against temperature fluctuation on a short timescale. The length of dives by *Kogia* has been observed only infrequently but is commonly believed to be long, as is the case for *Physeter* (Lockyer, 1977). Breese & Tershy (1993) report dive times between 14 and 30 min for *K. sima* in the central Gulf of California. Willis & Baird (1998) report that dive times of up to 25 min seem fairly common. To judge from the blood round the front of the core, which is generally seen in dead specimens, the circulation appears to deliver blood to and from the oval face via the cortex. Such a configuration could be used to vary the temperature of the cortex, particularly towards the anterior end, without changing the core temperature too much.

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