

Compositional Topography of Melon Lipids in the Atlantic Bottlenosed Dolphin *Tursiops truncatus*: Implications for Echo-Location

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Abstract

Major variations in lipid composition exist within the fatty melon tissue of the Atlantic bottlenosed dolphin *Tursiops truncatus*. Topographical lipid analyses indicate a central "inner melon" core surrounded by distinctive "outer melon", "under melon", and blubber tissues. Acoustical considerations suggest that this melon-lipid topography may aid in collimation of the ultrasonic pulses used by the dolphin for echo-location.

Introduction

The fatty melon tissue found in the head of all Odontoceti (dolphins, porpoises, and toothed whales) has been postulated to serve as an acoustical transducer and sonic lens for transmitting the ultrasonic pulses used by these animals for echo-location (Evans and Prescott, 1962; Norris, 1968; Wood, *in* Norris, 1968). The unique occurrence of large amounts of isovaleric acid in the wax esters and triglycerides found in Delphinidae and Phocoenidae melon fats (Varanasi and Malins, 1971, 1972; Litchfield and Greenberg, 1973) has led Varanasi and Malins (1971) to speculate that these unusual melon lipids may have special acoustical properties aiding sound transmission during echo-location.

Visual inspection of frozen melon sections from various species reveals that the melon is not sharply defined, but exhibits gradations of color and blends into the surrounding blubber tissue. Recent studies on the chemical composition of odontocete melon tissues (Wedmid *et al.*, 1971; Blomberg, 1972) have shown that the lipid composition varies with location within the melon of a single animal. To determine whether this melon nonhomogeneity might refract and possibly focus odontocete echo-location pulses, we have made a detailed examination of the compositional topography of melon lipids in the Atlantic bottlenosed dolphin *Tursiops truncatus*. Our results show distinct regions of different lipid composition within the melon, which would cause refraction of sound waves passing through the melon tissue.

Materials and Methods

The frozen head of a 2.27 m male *Tursiops truncatus* (MLF-230) was obtained from Marineland of Flo-

rida (USA) through the courtesy of Mrs. M. C. Caldwell and Dr. D. K. Caldwell. The dolphin had been captured in April, 1968, near Cedar Key, Florida, and had been maintained in captivity until its death from unknown causes in March, 1972. The fatty melon and adjacent muscular tissue was serially sectioned into 13 transverse slices, each ~20 mm thick (Fig. 1). After refreezing, appropriate sample cores were cut from every other section using a 6 mm inner-diameter cork borer. Each core (~500 mg) was extracted with 2/1

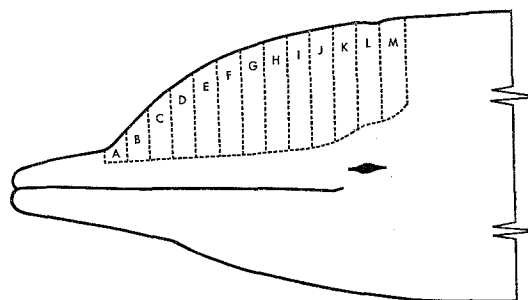
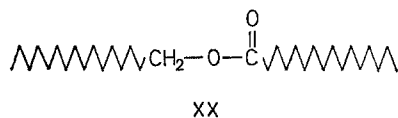
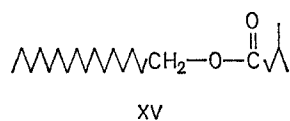


Fig. 1. *Tursiops truncatus*. Side view of head, showing locations of the 13 transverse melon slices taken for analysis. Each slice is ~20 mm thick

$\text{CHCl}_3/\text{CH}_3\text{OH}$, following the technique of Bligh and Dyer (1959), and the percent lipid recorded.

Previous analyses of *Tursiops truncatus* melon, jaw, and blubber fats (Ackman *et al.*, 1973; Litchfield and Greenberg, 1973) have revealed only two major (>1%) lipid classes, wax esters and triglycerides, which can be further subdivided according to their long (X) and short (V) chain moieties (Fig. 2). Gas-liquid chromatography (GLC) (Litchfield *et al.*, 1965, 1971; Ackman *et al.*, 1973) of intact *T. truncatus* melon lipids on a 0.50 m \times 3 mm inner-diameter column packed with 3% JXR on 100/120 Gas-Chrom Q with rapid temperature programming (135° \rightarrow 360 °C at 10 C°/min) resolved 4 distinct groups of peaks: XV, XX+ VXV, XXV, and XXX. Separation and re-

Wax esters



Triglycerides

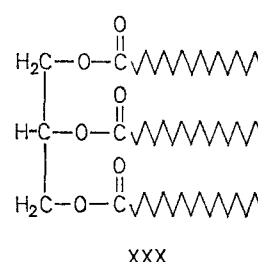
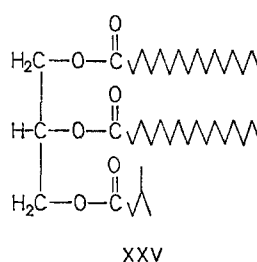
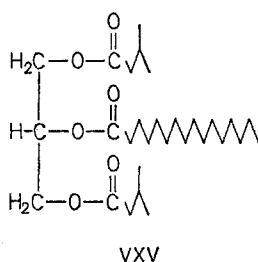


Fig. 2. *Tursiops truncatus*. Major lipid components found in melon fat are wax esters and triglycerides containing long (X) and short (V) chain moieties. Wax-ester Subclass XV has a long-chain alcohol (C₁₄ - C₁₈) esterified to a short-chain acid (C₄ or C₅), and Subclass XX has a long-chain alcohol esterified to a long-chain acid (C₁₂ - C₂₂). The 3 triglyceride subclasses VXV, XXV, and XXX contain, respectively, 2 short and 1 long, 1 short and 2 long, and 3 long-chain acids esterified to glycerol (Litchfield *et al.*, 1971; Ackman *et al.*, 1973; Litchfield and Greenberg, 1973)

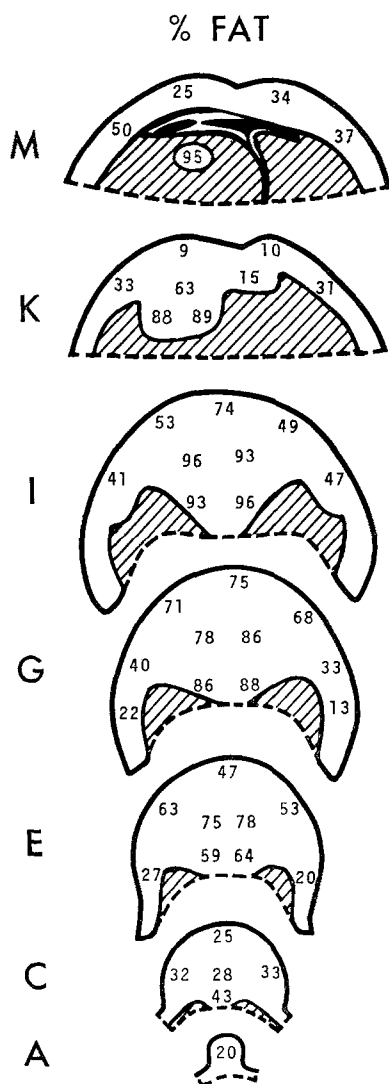


Fig. 3. *Tursiops truncatus*. Compositional topography of fat content (% weight) in melon of Atlantic bottlenosed dolphin. Surfaces shown are rear views of Slices A, C, E, G, I, and K and the front view of Slice M in Fig. 1. Hatched area is muscular tissue. Note that front part of melon has bilateral symmetry, while rear half is canted toward right side of head

covery of the wax-ester fraction by preparative thin-layer chromatography (Ackman *et al.*, 1973), followed by GLC under the same conditions as before, gave the relative amounts of XV and XX. Both runs were quantitated based on appropriate weight-calibration factors (Litchfield *et al.*, 1965) obtained using a known-composition mixture of hexadecyl isovalerate, hexadecyl palmitate, trioctanoin, trilaurin, and tripalmitin. Cross calculation between the two GLC runs with XV as the common component gave the percentage weight of all 5 subclasses present.

Results

Fat content of the melon ranged from 9 to 96%, depending on location (Fig. 3). Samples containing <47% fat were all located in peripheral blubber-like tissues. Results for % XV, % VXV, % XXV, and % XXX in the total lipid at specific points in the melon are given in Fig. 4. Since very little XX wax ester (0 to 4%) was found in any of the samples, these data are not given, but can be easily calculated by difference if desired.

Visual inspection of the middle melon (Slices F—I in Fig. 1) immediately after dissection revealed 3 distinctive types of fatty tissue (see Fig. 5): a light brown, translucent “inner melon” in the center; a paler, translucent “under melon” beneath; and a white subcutaneous layer which we assumed to be blubber. Our analyses indicate that the inner melon and the under melon have distinctive lipid compositions, which vary only slightly within each region (Table 1, Figs. 3 and 4). However, the white subcutaneous tissue can be divided into 2 distinct regions on the basis of lipid composition: an “outer melon” of high VXV content, and a characteristic “blubber” tissue with a high level of XXX. A gradient change of lipid composition occurs at the juncture of the outer melon with the blubber, but the outer melon/inner melon boundary is more clearly defined.

Another distinguishing feature of the 4 types of fatty melon tissue is their fat content (Table 1, Fig. 3).

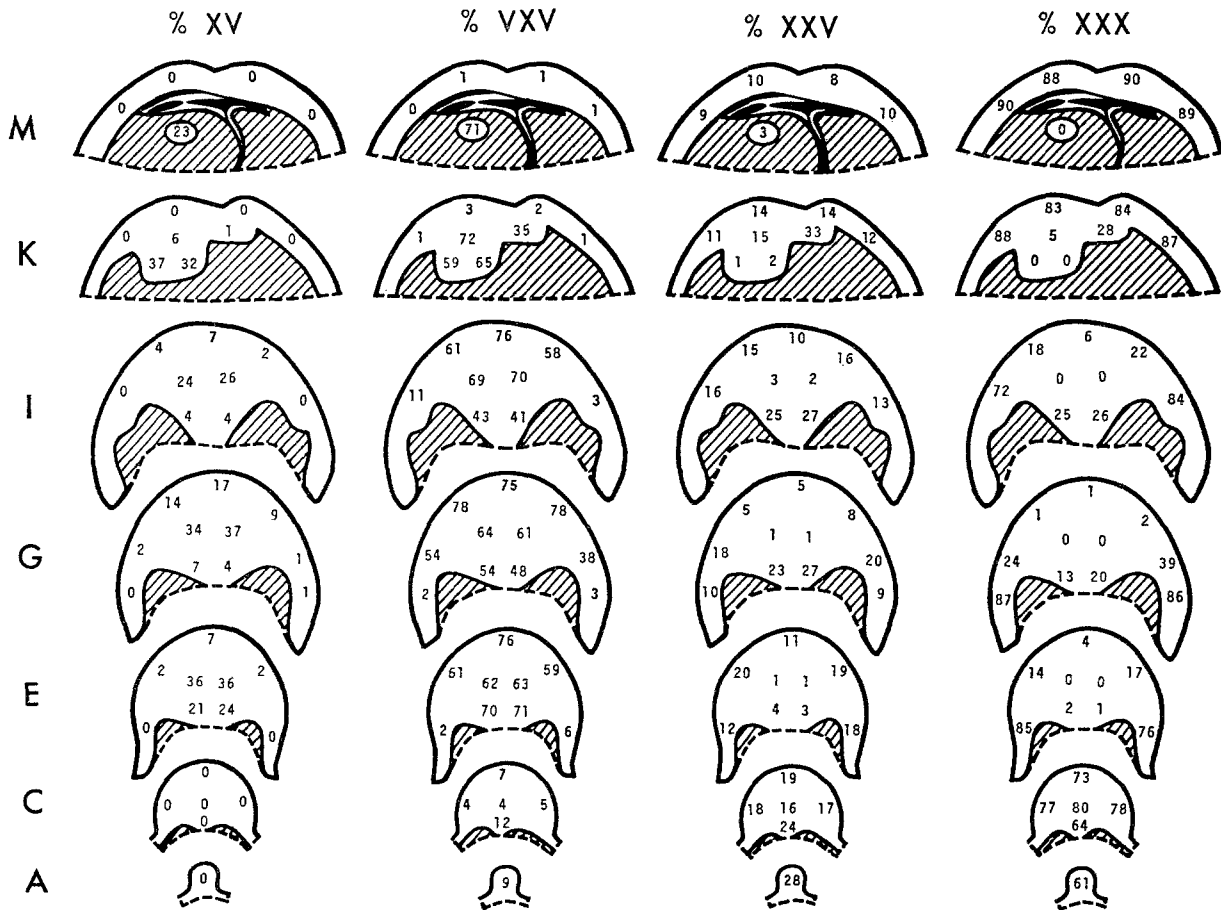


Fig. 4. *Tursiops truncatus*. Compositional topography of lipid composition in melon of Atlantic bottlenosed dolphin, showing weight % XV wax ester, and % VXX, % XXV, and % XXX triglycerides present in total lipid at each sampling point. A small amount (0 to 4%) of XX wax ester is also present; the precise value at any point can be calculated by difference. Surfaces shown same as Fig. 3; hatched area is muscular tissue

The inner melon and the under melon have a very high (mostly > 75%) fat content, suggesting that lipid composition has a major influence on acoustical properties there. The outer melon is not quite so fat-rich (47 to 75%); and the blubber region has a low (9 to 50%) fat content, indicating that lipids are not the major determinant of acoustical properties in the blubber.

Discussion

For the purpose of acoustical analysis, the *Tursiops truncatus* melon can be thought of as a central core of fatty tissue (inner melon), surrounded at various points by other fatty tissues (under melon, blubber, outer melon), by muscular tissues, and by bone (Fig. 5). Experiments with live dolphins have shown that the ultrasonic waves used for echo-location form a highly directional beam directly in front of the melon (Norris *et al.*, 1961; Norris and Evans, 1967). A likely model for achieving this result would visualize the inner

melon as the major carrier for straight-through passage of ultrasonic waves. The surrounding tissues would then serve to either reflect or refract divergent sound waves, so as to collimate them with the central beam through the inner melon.

The posterior part of the inner melon (behind Slice K) has a conical shape and is completely surrounded by muscular tissue. Its apex lies at a node in the right nasal plug. Norris (1968) has postulated that this node is the sound producer for echo-location. Norris and Harvey (1973) have also shown that sound waves are strongly reflected at a blubber-muscle interface in dolphins. Analogous reflection by the muscular tissue surrounding the posterior inner melon should play an important role in directing a narrow sound beam forward from the rear node. One might compare this cone of fat-rich inner melon surrounded by muscle to the action of a megaphone.

Additional muscular tissue underlies the middle and forward parts of the melon (Slices A to K). This

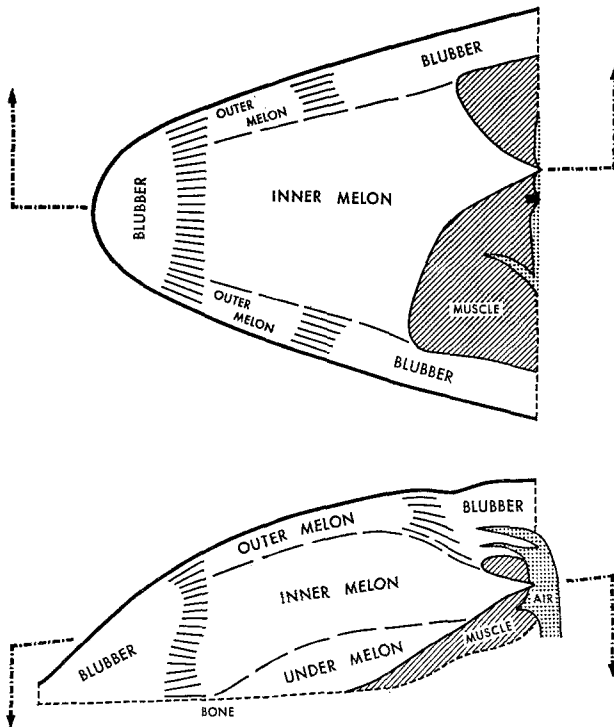


Fig. 5. *Tursiops truncatus*. Horizontal and vertical cross-sections through center of melon, showing locations of the 4 major types of fatty tissue as defined by lipid composition and anatomical morphology. Melon areas with parallel lines indicate gradient changes in lipid composition. External arrowed, broken lines indicate positions of sectional views taken; vertical section follows approximate center of melon, and does not bisect head

Table 1. *Tursiops truncatus*. Range of lipid compositions (% weight) found in the 4 major types of fatty melon tissue

| Region | Lipid content (%) | Wax-ester subclass XV ^a (%) | Triglyceride subclass ^b | | |
|-------------|-------------------|--|------------------------------------|---------|---------|
| | | | VXV (%) | XXV (%) | XXX (%) |
| Outer melon | 47–75 | 2–17 | 58–78 | 5–20 | 1–22 |
| Inner melon | 59–96 | 21–37 | 61–71 | 1–4 | 0–2 |
| Under melon | 86–96 | 4–7 | 41–54 | 23–27 | 13–26 |
| Blubber | 9–50 | 0–1 | 0–11 | 8–33 | 61–90 |

^a XV: Wax esters having a long-chain (X) alcohol esterified to a short-chain (V) acid.

^b VXV, XXV, XXX: Triglyceride subclasses containing short-chain (V) and long-chain (X) acids. (See Fig. 2 for structural formulas).

would also be an important sound-reflecting surface, which aids in collimation of the sound waves. Moreover, those bone and cartilage surfaces of the upper jaw bone which contact the bottom of the melon would be effective sound reflectors also (Norris, 1968).

Similar collimation of the forward-moving sound waves by refraction in the fatty tissues surrounding the inner melon seems likely. Such inward-bending of divergent sound waves requires that the velocity of sound in these surrounding tissues be greater than the velocity in the inner melon. Norris and Harvey (1973) have made sound-velocity measurements through transverse slices of *Stenella melon* tissue, and found a low-velocity core surrounded by a shell of higher-velocity tissue. Since *Stenella* and *Tursiops truncatus* are closely related delphinids, and their melons are morphologically similar, it seems likely that this low-velocity core might correspond to the inner melon that we have defined here on the basis of its lipid composition.

Lipid compositional variations between the inner melon and the surrounding under melon and blubber tissues are clearly large enough to cause inward refraction of the sound waves radiating from the posterior tip of the melon, but the amount of that refraction can only be roughly estimated. It is known (Gouw and Vlugter, 1967; Husted *et al.*, 1974) that low molecular-weight triglycerides such as VXV will transmit sound at a substantially lower velocity than high molecular weights such as XXX. However, no comparable data are available on the velocity of sound in fatty wax esters of the XV or XX type. Empirical relationships (Bergmann, 1954) indicate that the velocity of sound in straight-chain organic esters decreases as the molecular weight or the number of ester groups decreases. Assuming this trend applies here, then the relative sound velocities in the 4 major lipid classes would be XXX > XXV > VXV ≥ XV; and one would estimate the relative sound velocities through the lipids of the 4 types of fatty melon tissue to be blubber > under melon > outer melon ≥ inner melon. If this estimate is correct, then the compositional topography of melon lipids in *Tursiops truncatus* indicates a low-velocity core (inner melon) surrounded by higher-velocity fatty tissues (under melon, blubber, and possibly outer melon) as found in *Stenella* (Norris and Harvey, 1973). This would produce inward refraction of the divergent sound waves in the higher-velocity tissues, resulting in collimation of the emitted sound beam.

Clearly, further data on the velocity of sound through actual *Tursiops truncatus* melon lipids must be acquired before an accurate acoustical model defining the exact contribution of melon lipids to sound refraction can be constructed. Such a model must also take into account any temperature gradient across the melon (Hart *et al.*, 1959; McGinnis *et al.*, 1972) which will influence sound refraction by the melon tissue. (*T. truncatus* inner body temperature is 36.9 °C — Ridgeway, 1965 — much higher than the seawater in which it swims.) Experiments to acquire this necessary acoustical and thermal data are now underway in our laboratory.

Summary

1. The compositional topography of melon lipids in the Atlantic bottlenosed dolphin *Tursiops truncatus* has been examined in detail. Analytical data indicate 4 distinctive regions: a central "inner melon" core surrounded by "outer melon", "under melon", and blubber tissues.

2. Acoustical considerations suggest that this melon-lipid topography may aid in collimation of the ultrasonic pulses used by these dolphins for echolocation.

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