Body composition of the sperm whale, *Physeter catodon*, with special reference to the possible functions of fat depots

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ABSTRACT

Morphometric data collected from sperm whales indicate a relatively thin covering of blubber on the head and thickest blubber in the middle region of the body. The girth of the whale is greatest at the axilla. Body weight at length is heavier than for most baleen whales, and blubber comprises nearly a third of body weight, a greater proportion than in most baleen whales. Biochemical analyses of blubber indicate significant differences between anterior (head) blubber and that elsewhere on the body, the former being highly proteinaceous with very little lipid. The blubber was found to vary in biochemical composition throughout its depth, with the skin-adjacent zone being significantly different in composition to the deeper zones, with generally more protein fibre, water, mineral, and only about half the lipid content of the latter. No heterogeneity of muscle which contained little lipid, was observed over the body, and visceral organs were found to be similar to muscle in composition. Visceral fats contained more lipid (70–80% wet weight) than the most fat-laden blubber (ca 60%), but contained negligible protein. Structurally and biochemically, the anterior (head) blubber appears unimportant as a fat depot, and may function as a flexible exoskeleton for the spermaceti organ. The main lipid class in blubber is wax (sterols and esters), with fairly high levels of triacylglycerol, unlike muscle, where triacylglycerol, polar lipids and free fatty acids are most prominent. The distribution of blubber density over the body is such that it may provide stability in buoyancy. It is speculated that density changes of blubber with temperature over the body during diving could assist in buoyancy control. If liquid-solid phase changes in the lipids occur as well, protection from external pressure at depth through incompressibility may also take place. Other explanations for high wax levels are also discussed in the light of metabolic requirements in comparison with other hyperbaric-living organisms. The fatty acid composition of the triacylglycerol fraction comprises a significant proportion of short-chain acids <C12, and C18:1 and C16:1 are overall the most prominent fatty acids. Over 60% of identified fatty acids were monoenoic.

INTRODUCTION

The sperm whale (*Physeter catodon*) is the largest of the odontocetes, toothed cetaceans, and is characterized by marked sexual dimorphism, the male attaining larger adult sizes than the female: on average, ca 15.9 m compared with ca 10.9 m in length, and more than 43,500 kg. compared with a mere 13,500 kg in weight (Best 1970, 1974; Lockyer 1981a). Differences between the sexes also encompass geographic ranges and distribution; only the males, generally adult bulls of potential breeding status penetrate polar waters in each hemisphere, the females and young remaining in tropical to temperate waters (Gambell 1972; Best 1979). The sperm whale has been the quarry of the whaling industry throughout history in many parts of the world's oceans. During the years up until 1975, sperm whales were regularly taken off the coast of Natal, South Africa and landed at Durban in latitude 31°S. The catch composition included both

TABLE 1

Record of sperm whale carcases examined and sampled for this study.

Whale no	*Sex*	*Age/Repro. status*	*Location*	*Date worked up*	*Length (m)*	*Girth-G_3 (m)*	*Blubber thickness (mm)*			*Body weight* (kg)*	*Blubber sample for density*
							Dorsal-D_3	*Lateral-L_3*	*Ventral-V_3*		
D104	F	FOETUS	DURBAN	12.03.73	3.43						Samples taken
D89F	M	FOETUS	—	10.03.73	3.33						Samples taken
D8/D6F	M	FOETUS	—	4.03.72	3.61		67	50	74		
D14F	M	FOETUS	—	6.03.72	3.81	2.10	40	50	65		
D8F	M	FOETUS	—	4.03.73	3.99		38	35	48		
D111F	M	FOETUS	—	12.03.73	4.12	2.26	53	47	63		Samples taken
D4/C12	F	CALF	—	4.03.73	4.60	2.60	63	63	78	1,450	
D63/C14	M	CALF	—	8.03.73	3.94					1,000	Samples taken
D28/C13	M	CALF	—	7.03.73	4.22	2.52	58	44	69	1,050	
D40	F	SUB-ADULT	—	7.03.73	9.15		63	90	145		
D68	M	JUVENILE	—	9.03.73	8.54	4.60	160	104	117		Samples taken
D97	M	JUVENILE	—	10.03.73	8.84	4.80	144	90	134		
D5	M	JUVENILE	—	4.03.72	10.06		114	112	148		
D11	M	JUVENILE	—	4.03.72	10.37		110	119	146		
D102	M	JUVENILE	—	12.03.73	10.67						Samples taken
D6	F	PREGNANT	—	4.03.72	10.06		112	145	143		
D60	F	MATURE	—	8.03.73	10.06						Samples taken
D14	F	PREGNANT	—	6.03.72	10.37	5.74	160	105	155		
D43	F	ADULT	—	10.03.72	10.67	6.40	120	130	140		
D17	F	ADULT	—	6.03.72	10.67	6.31	75	135	170		
D12	F	LACTATING	—	6.03.72	10.67	5.79	114	160	123		
D103	F	ADULT	—	12.03.73	10.67						Samples taken
D16	F	LACTATING	—	6.03.72	11.28	6.37	167	150	160		
D118	F	ADULT	—	12.03.73	11.51	6.40	129	107	190	15,260 (13,006)	Samples taken
D11.1	M	ADULT	—	6.03.73	12.50	7.64	233	203	170		
D13	M	ADULT	—	6.03.73	13.11						
Gib.Pt	M	ADULT	GT BRITAIN	3.03.85	14.50	8.80					
213	M	ADULT	ICELAND	30.07.81	15.24	8.23	250	140	205		

*Whole body weights given; weights in parentheses are in pieces totalled

sexes and all age classes of adults as well as juveniles. Facilities for collecting biological data and samples from these catches were available to scientists during the whaling season, through the courtesy of the *Union Whaling Company*. As recently as 1981 (their last operational season for sperm whales), Iceland caught this species up to 200 n.mi. west and northwest of the country in the North East Atlantic, in the latitude between 62–67° N, just below the Artic circle. The bulk of the catch originated off Snæfellsnes peninsula and Vestfirðir in 64–66° N, and consisted only of males, mostly large adults. Through the courtesy and co-operation of the Icelandic whaling company, *Hvalur h.f.*, and the *Marine Research Institute, Reykjavík* laboratory facilities were regularly made available to scientists at the whaling station in Hvalfjörður each summer, facilitating collection of material and data from the catch.

AIMS

Access to the carcases of sperm whales at both the Durban and at the Hvalfjörður whaling station permitted various morphometric data to be collected as well as specimens of

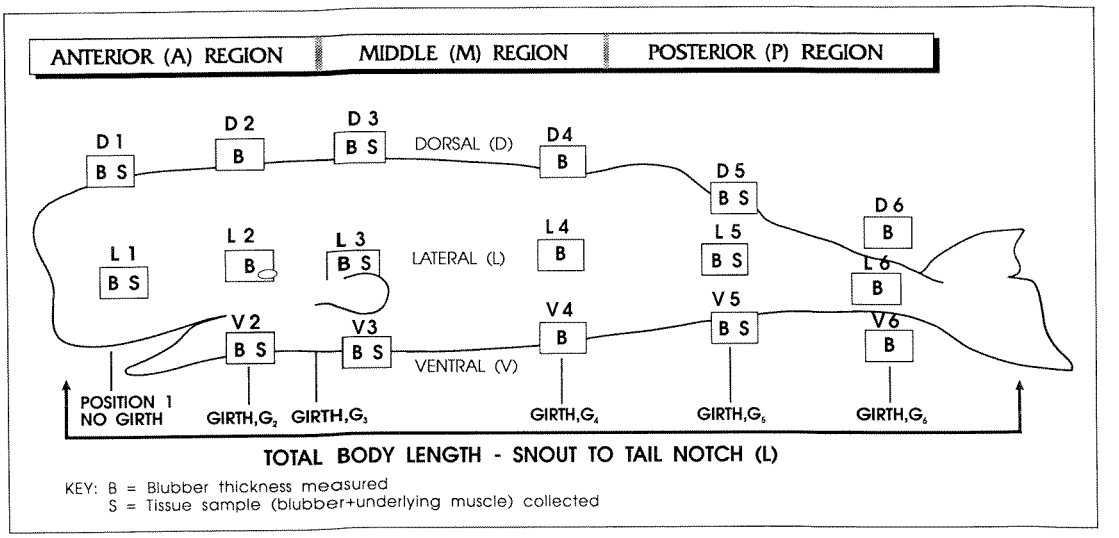

Fig. 1. Diagram of the sperm whale body showing sites of length, girth and blubber thickness measurement, and tissue sampling. Key: B = blubber thickness site; S = tissue sample site (blubber and underlying muscle collected).

body tissues for biochemical analysis. Post-morten time for the sperm whale carcases averaged 28.4 hr on arrival for flensing at the Icelandic whaling station, and, although carcases were not sufficiently fresh for enzymatic studies, they were adequate for analyses of basic composition. Off Durban, the usual post-mortem time was between 20–25 hrs when flensing commenced.

The purpose of this study was to attempt an assessment of the morphological and biochemical composition of the sperm whale body, in comparison with other cetacean species; to identify particular fat energy depots in the body; and to evaluate the possible roles of blubber as an energy store, buoyancy regulator and exoskeleton.

MATERIAL AND METHODS

Between 1972 and 1973, a total of 26 sperm whale carcases were examined at Durban, mostly from the commercial catch, but also including a few undersized and lactating whales taken under special permit issued by the South African Goverment (Best *et al.* 1984). The carcases included foetuses, calves, anoestrous, lactating and pregnant females, adult males, and several juveniles and sub-adults of both sexes. Details of these whales are presented in Table 1.

A single male of 15.2 m (50 ft) in length, taken in the commercial catch, was examined and sampled on 30 July 1981 at Hvalfjörður, Southwest Iceland. The whale appeared in good body condition, and was landed 22.05 hrs after the kill. This is also listed in Table 1 together with a single British stranded adult male. Only the Icelandic whale samples were analysed biochemically.

Morphometry

The whales were measured for total body length, girth and blubber thickness in the positions indicated in Figure 1. Measurements were taken in a similar manner to those for fin whales, as described in detail by Lockyer (1987a) and Lockyer *et al.* (1985): length was determined as total length taken in a straight line alongside the carcase, girths were measured as half-girths, and blubber was measured perpendicularly from skin to the base, excluding any connective tissue adhering, mostly *in situ*. In addition, at the Durban station, intact body weights were obtained for an adult fe-

male using a railway wagon at a weigh station facility, and two calves using a suspended weigh scale. Weight by tissue and organ parts was also undertaken for a few whales, using a suspended balance, including the adult female mentioned above. The weighing procedure was similar to that described by Gambell (1970).

Tissue sample

Samples of complete core-depth blubber of ca 30–100 g from nine sites over the body, were excised from the carcases examined at Durban. These sites corresponded with dorsal head, trunk and tail; lateral head, trunk and tail; and, ventral head, trunk and tail regions (Fig. 1). These were removed to an on-site laboratory where tissue density by volume displacement on total immersion (weighted if necessary) in a graduated cylinder of water of known temperature was determined. The temperature of the air and the blubber sample was also recorded. Overall temperature range varied between 23–30°C.

Nine samples of ca 100 g of blubber and underlying muscle were taken as indicated in Figure 1, for all animals sampled (Table 1). In addition, samples of liver, kidney, heart, visceral fat from the mesenteries, thorax and cardiac fat, as well as stomach contents were taken from the Icelandic-caught whale for biochemical analysis. All samples were fast-frozen in resealable zip-lock polyethylene bags from which most air had been evacuated, and maintained at −26°C prior to, during and after shipment to England for analysis.

The Icelandic blubber samples were collected in a core of several cm^2 in cross-section, through from skin to underlying connective tissue between blubber and muscle interface. These blubber cores were divided into three sections: top – adjacent to skin, middle, base – adjacent to the blubber/muscle interface. Each section was defined by macroscopic appearance and texture: i.e. the density of fibres, fat-load, etc., but no microscopic or histologic study was undertaken. Generally, the top section appeared more fibrous and denser in texture, the middle section which was usually the largest section, was less fibrous and more amorphous in appearance, and the base section which was more similar in appearance to the middle section, contained some fibres. This gross stratification is crude, but the criteria have been strictly adhered to in defining sections for all blubber samples and have not raised practical problems on tissue definition. The skin was removed from the top layer prior to analysis. The nine muscle samples collected were not sub-sectioned. Prior to biochemical analysis, all sample tissues were prepared for analyses in the semi-frozen state in order to minimise loss of any fluids, and the specimen to be analysed was subsampled from the centre of the original in order to minimise errors due to chemical changes at the air/tissue interface at the time of collection and contamination during the subsequent handling and processing.

Biochemical analysis

1) Water and mineral. All sub-sampled specimens were analysed for water content by drying a known-weight of 1–2 g at 40°C for about 48 hr in a Gallenkamp drying oven fitted with a vacuum pump. The dried specimens were transferred to a vacuum chamber, cooled, and reweighed. These dried specimens were then reduced to mineral ash in a muffle furnace at 550°C for 24 hr, cooled, and transferred to a vacuum chamber and then reweighed.

2) Protein content. Specimens of about 1 g wet weight were analysed by semi-automatic Kjeltec apparatus for total-N (Kjeldahl), using a similar technique as described in Lockyer *et al.* (1984).

3) Lipid. For lipid analysis, specimens of about 1 g were chopped roughly with a scalpel, and then homogenized using a pneumatic-powered Ultra Turrax 18N homogenizer, and cloroform/methanol extracted (Bligh and Dyer 1959) using a similar technique as described in Lockyer (1987a) and Lockyer *et al.* (1984). The subsequent extractions were

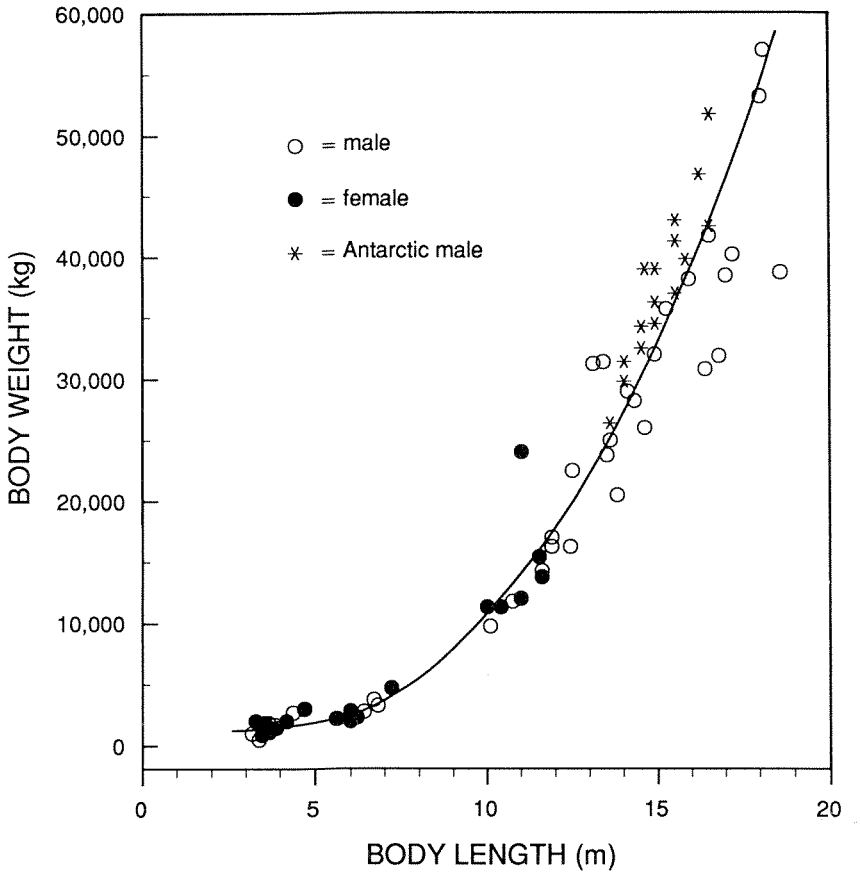

Fig. 2. Body weight (kg) at length (metres) for sperm whales, including published data of Best, Canham and Macleod (1984), Bjarnason and Lingaas (1954), Crile (1941), Gambell (1970), Lockyer (1976, 1981a), Ohno and Fujino (1952), Omura (1950), Sleet, *et al.* (1981), Tomlin (1967) and Zenkovich (1937). The predictive curve of body weight (W) in tons at length (L) in metres, from Lockyer (1976):

$W = 0.0196\ L^{2.74}$, for weight by parts.

Weights are unadjusted for fluid loss.

stored under nitrogen in a frozen state at −50°C, and the solid residue retained for carbohydrate analysis.

Some lipid extracts were selected for lipid class investigation using thin layer chromatography (TLC-plate) and of these, a few lipid extracts were prepared for fatty acid analysis using capillary gas-liquid chromatography (GLC). For TLC analysis the methodology is described in Clarke (1977) and in Lockyer *et al.* (1984). The component lipid classes were quantified using a Camag densitometer. The separated lipid class fractions from TLC analysis were eluted in chloroform, and then prepared as methyl esters according to the method of Clarke (1977) for triacylglycerides. The samples were run on a Hewlett Packard GC 5790A gas chromatograph (GC) with helium carrier, using similar methods to those described in Lockyer *et al.* (1984). The results of peak traces from GC runs were analysed using a Hewlett Packard 3390A integrator (Clarke and Wickins 1980). Total integrator response was in the chain length range C_{12} to C_{24}. Discrimination between short-chain fatty acids was therefore not possible.

4) Carbohydrate. The residue from the lipid extraction (see above) was digested in 30 ml of 10% trichloroacetic acid (TCA) for 30 min. The digest was then diluted to 60 ml. Four 2 ml subsamples were then taken and centrifuged. Subsamples of 200, 300, 400 and 500 μl, made up to 1 ml in distilled water, were taken. To these were added 1 ml of 5% phenol and 5 ml of concentrated sulphuric

acid (H_2SO_4), and the solution left to stand for 10 min. They were then transferred to a water bath at 30°C for 20 min. to cool. The subsequent samples were then read on a spectrophotometer at wave length 490 nm, using 1 g in 100 ml distilled water D-glucose solution diluted to 100 μg ml^{-1} standard stock solution for calibration.

Calorimetric analysis. Samples of known weight dried tissue were pelletised and ignited in a Perkin Elmer adiabatic bomb calorimeter. The resulting heat of combustion was calibrated using benzoic acids as standard.

All the above analyses were performed in duplicate.

RESULTS

Body and tissue weights

Body weights (unadjusted for fluid loss) at length are plotted together with many data from previously published sources in Figure 2, and the predicted weight from length curve (after Lockyer 1976), again unadjusted for fluid losses during flensing. Gambell (1970) calculated a fluid loss of 12% during flensing, while the difference for D118 (Table 1) between whole body weight and weight in parts amounts to 14.8%. Lockyer (1976) estimated that weight by parts represented only 90% of whole body weight, so that a predictive formula for whole body weight (W) in metric tons from length (L) in m, would require the following modification of the formula used in Figure 2,

$$W = 0.0218\ L^{2.74}$$

Sleet *et al.* (1981) experimentally determined a blood volume *in vitro* of 20.13% for a female sperm whale stranded off Oregon, so that 10% fluid loss during flensing may be conservative.

Table 2 summarises the overall body composition from present and published sources.

TABLE 2

Body organ and tissue weights as percentage of total body weight for cetaceans.

Species of whale	*Geographic region*	*Body size range (length in m)*	*Sample Size*	*Percentage body weight of tissue*			*Reference*
				Blubber	*Muscle*	*Viscera*	
Eubalaena glacialis siebaldii (Right)	N.Pacific	12.4–17.4	14	43	31	13	Lockyer 1976
Physeter catodon (Sperm)	N.Hemisphere	10.1–18.6	16	31	30	9	—
	S. Hemisphere	11.0–16.5	18	32	22.5	9	—
Globicephala melas (Pilot)	N.Atlantic	juvenile	15	23	23.5	11	Lockyer, in press
	—	adult, <6.0	15	30	23.5	11	
Balaenoptera musculus (Blue)	S.Hemisphere	20.3–27.6	38	27	39	12	Lockyer 1976
Balaenoptera musculus brevicauda (Pygmy blue)	—	16.0–21.8	5	29.5	40	15	—
Balaenoptera physalus (Fin)	N.E.Atlantic	15.8–20.5	11	18.5	45	10	Lockyer & Waters 1986; Lockyer 1976
	S.Hemisphere	17.4–22.9	33	23.5	46	10.5	
Balaenoptera brydei (Bryde)	N.Pacific	11.3–13.8	27	23	46	10	Lockyer 1976
Balaenoptera borealis (Sei)	N.E.Atlantic	12.2–14.6	4	18	51.5	11.5	Lockyer & Waters 1986; Lockyer 1976
	N.Pacific	9.1–14.7	16	18	58	10	
Balaenoptera acutorostrata (Minke)	S.Hemisphere	7.1–13.8	9	15	62	8	Lockyer 1976

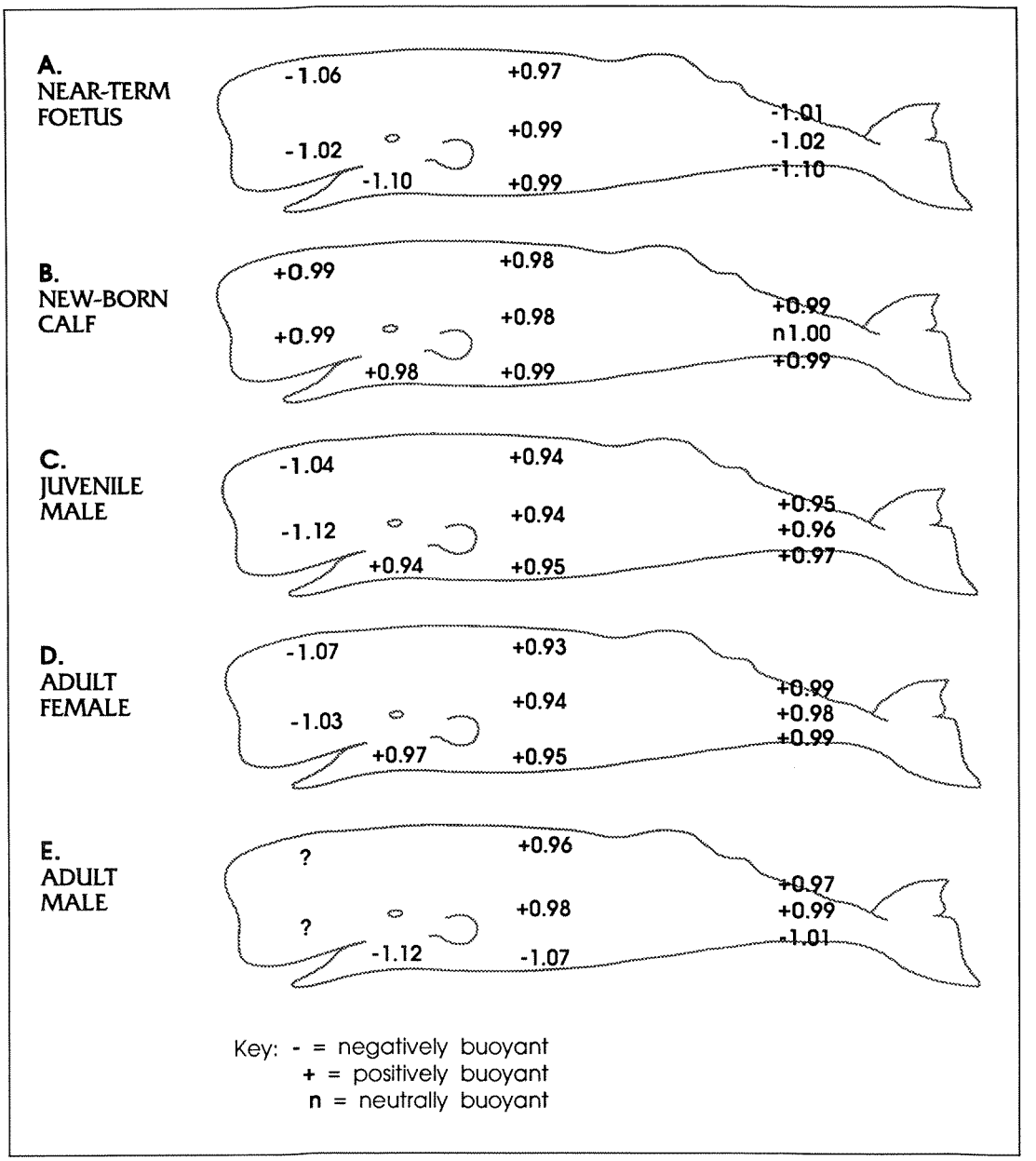

Fig. 3. Blubber density (g cm^{-3} at 23–30°C distribution over the body of the sperm whale, with relative buoyancy of the blubber tissue indicated. A. Near-term foetus, N = 2, male and female; B. New-born calf, n = 1, male; C. Juvenile male, n = 2; D. Adult female, n = 3; E. Adult male, n = 1.

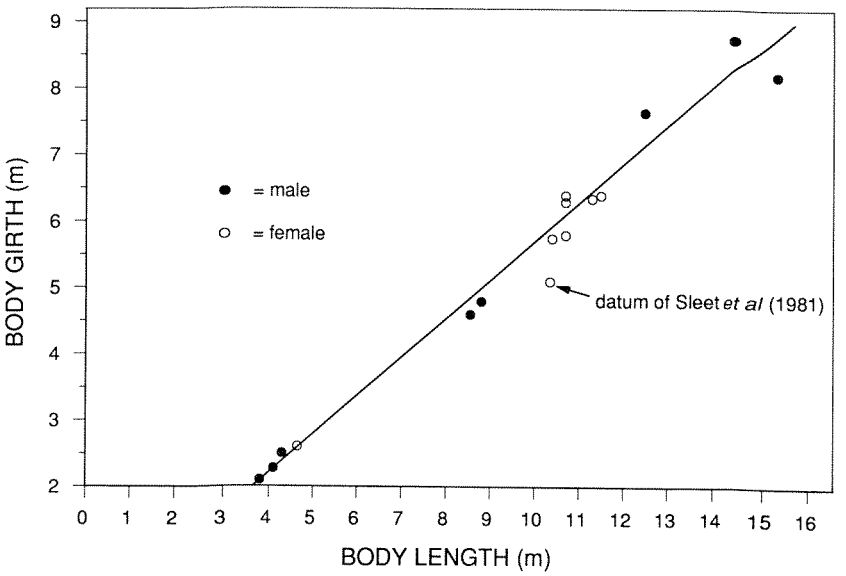

Fig. 4. Body girth (metres) at the stoutest position, G_3, with length (metres), and calculation of the linear regression:

$G = 0.583\ L - 0.139$, where G = girth G_3, L = length.

The data for sperm whales have been taken from Lockyer's Appendix (1976) but include only animals for which total body weights of blubber and muscle have been recorded.

The density of the blubber from various parts of the body at temperatures 23–30°C is shown in Figure 3 for whales of different sex and maturity status. The relative buoyancy of the blubber in seawater at these temperatures is also indicated.

Morphometry

The results of girth and blubber thickness at length are detailed in Figures 4 and 5, respectively. The stoutest region of the whale body is at the flipper insertion (axilla). The girth appears to be directly correlated with length. The blubber thickness is least in the region around the head, where the blubber is intensely fibrous and rigid, and quite different in texture to the more fat-laden and less fibrous blubber over the remainder of the body. However, the blubber appears to be the thickest in the middle region of the body, attaining as much as 250 mm dorsal to the flipper region (position D5 in Fig. 5) in the largest male. The blubber thickness appears to be correlated with length, over most of the body.

Basic Biochemistry

The results of the different biochemical analyses have been integrated and are presented separately for each tissue type. Comparisons between samples have been made using an ANOVA randomised/one treatment model.

1) Blubber – Whole core

The results of 36 duplicate samples of blubber (nine body sites, each analysed as whole core, top, middle and base section, for lipid, protein, carbohydrate, water and mineral contents) are graphically displayed in Figure 6. The results for the nine whole core samples are discussed below, by body region.

(1) Protein. The pattern emerging is that protein fibre matrix of the blubber ranges between 10 and 35% wet weight of tissue. The greatest amount of protein is found in the anterior region, especially on the head, which confirms the macroscopic observation on blubber texture and tissue fibre density.

(2) Lipid. The content ranges between 3 and 58%, the lowest, almost negligible amounts being located in the anterior dorsal and ven-

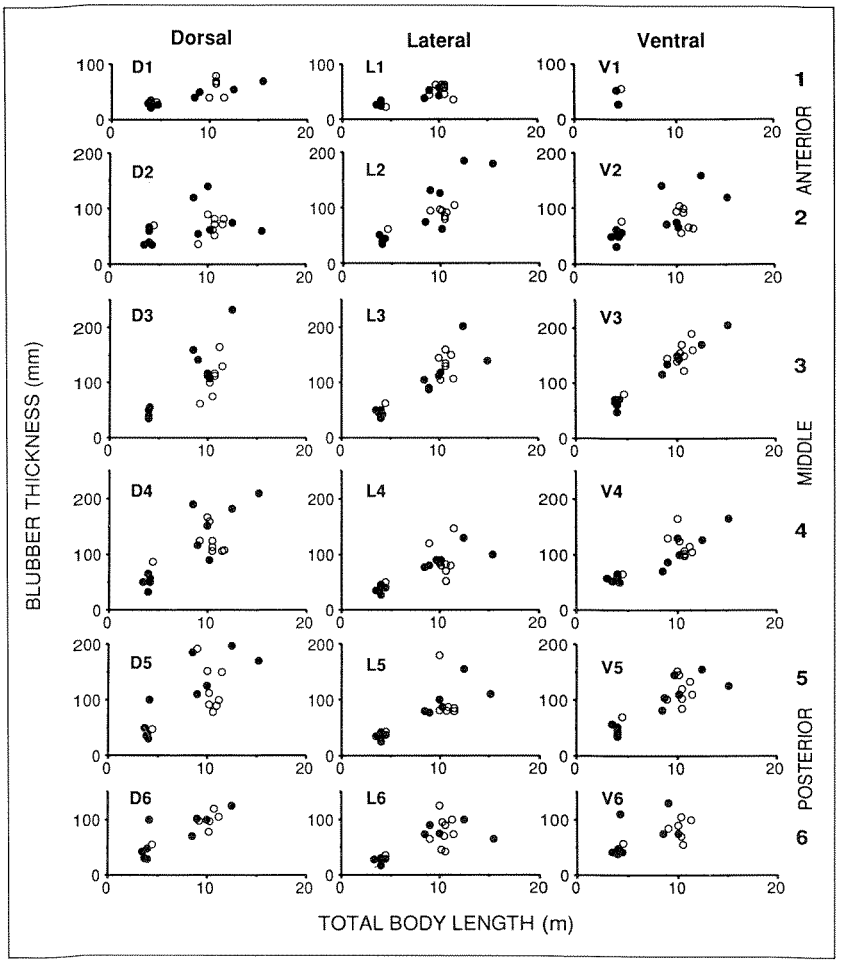

Fig. 5. Blubber thickness (mm) with body length (metres) in six different regions of the body, from anterior to posterior: (D) dorsal; (L) lateral; (V) ventral. Position codes indicated are from Fig. 1.
● = male; ○ = female.

tral regions (the head). The next lowest lipid region is the posterior ventral, where the level is 21.5%. One-way ANOVA (Zar 1984) indicates that there is a significant difference ($p<.05$) between anterior, middle and posterior body regions (d.f. 2/4, F-ratio=10.48) with mean % of 10.91 ± 7.26 SE, 47.64 ± 2.31 SE and 40.28 ± 10.40 SE, respectively. There is, however, no significant dorso-ventral difference.

(3) Water. In general, the most prominent component of the blubber is water which comprises up to 62% wet weight of tissue in the head region, and not less than 18% anywhere.

(4) Carbohydrate. Carbohydrate which has been directly assessed (not deduced by substraction of other components from total weight of sample) is significant in amount, reaching levels in the range 8–30%, except in the anterior dorsal and ventral regions (head) where levels are 6% and <1%, respectively.

(5) Ash. The ash residues are very small compared with other components of the blubber and the values found are given in Table 3. The mineral levels for whole blubber core range between 0.2 and >0.5%.

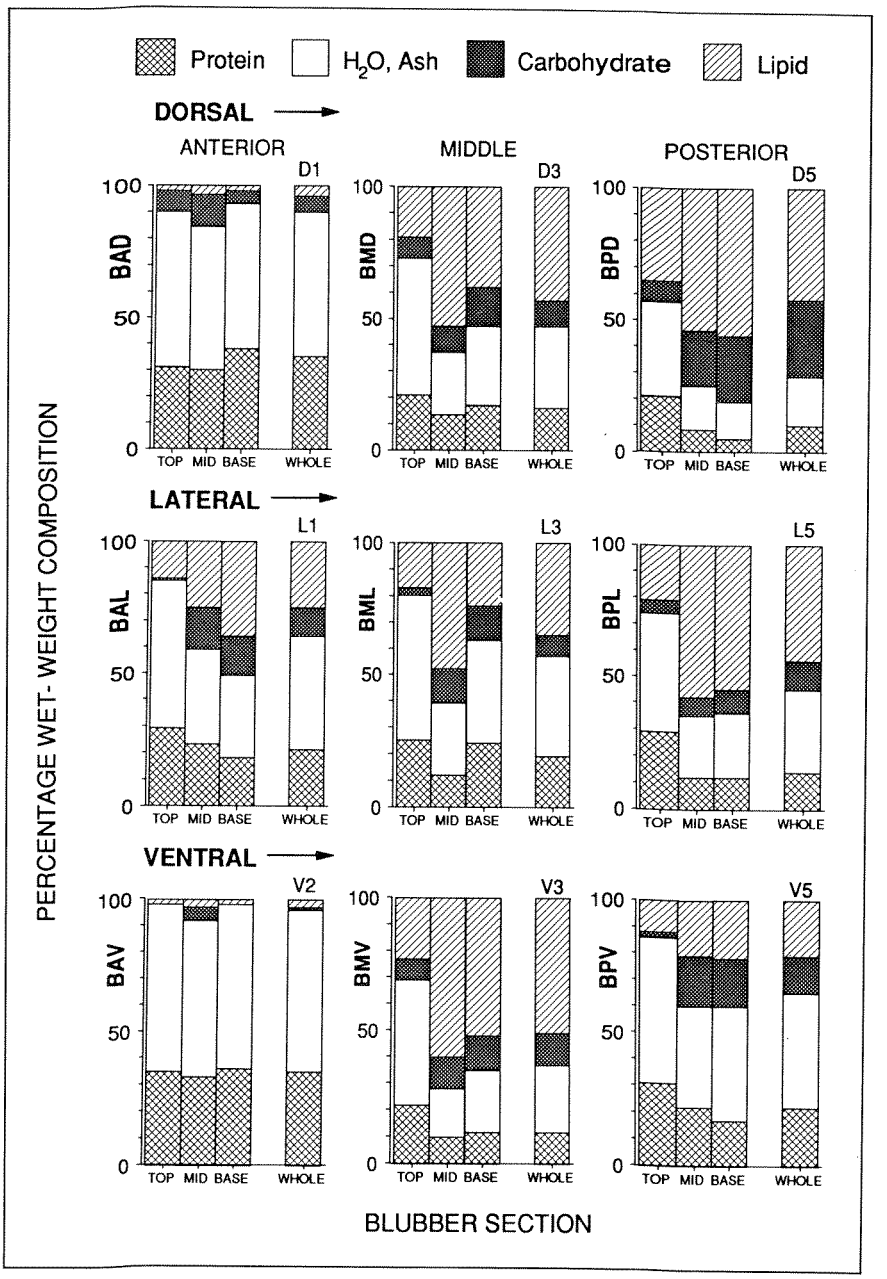

Fig. 6. Biochemical composition of the blubber of sperm whale: whole core sample; top, middle and base sections of core.

Key: BAD = anterior dorsal (D1);
BAL = anterior lateral (L1);
BAV = anterior ventral (V2);
BMD = mid dorsal (D3);
BML = mid lateral (L3);
BMV = mid ventral (V3);
BPD = posterior dorsal (D5);
BPL = posterior lateral (L5);
BPV = posterior ventral (V5).

TABLE 3
Mineral ash residues in sperm whales tissues.

Tissue sample and body region	Ash content as % wet weight of tissue			
	Whole tissue	Top section	Middle section	Base section
Blubber				
anterior dorsal	0.51	0.44	0.28	0.56
anterior lateral	0.32	0.44	0.27	0.25
anterior ventral . . .	0.38	0.38	0.50	0.27
mid-dorsal	0.33	0.43	0.17	0.41
mid-lateral	0.35	0.72	0.34	0.30
mid-ventral	0.38	0.58	0.30	0.29
posterior dorsal . . .	0.20	0.37	0.05	0.06
posterior lateral . . .	0.39	0.43	0.29	0.38
posterior ventral . . .	0.41	0.59	0.26	0.38
Muscle				
anterior dorsal	1.19			
anterior lateral	1.04			
anterior ventral . . .	1.31			
mid-dorsal	1.05			
mid-lateral	1.29			
mid-ventral	1.10			
posterior dorsal . . .	1.12			
posterior lateral . . .	1.02			
posterior ventral . . .	0.98			

(6) Summary. The largest component of the blubber, regardless of body site, is usually either water or lipid. The water component is higher in the anterior sites, whilst the lipid is often greater in the middle and posterior sites, the maximum content of either component being about 60%. Protein is an important component, and attains up to 35% in the anterior blubber of the head, and rather less elsewhere. Carbohydrate level appears to be very significant throughout most of the body blubber. Mineral ash residue is low everywhere.

2) Blubber – Stratified core

Comparison of the three sectional blubber regions, stratified by depth from the skin through to muscle interface (top, middle and base), show that, in general (see Fig. 6), the sections vary considerably in relative composition. Essentially, in the comparisons, there are nine body regions (sites of sampling) and three blubber sections at each site.

(1) Protein. The protein content is often highest in the top section, ranging from 20–35% wet weight of tissue. However, in the anterior dorsal and ventral regions of the body, there appears to be an almost uniform distribution of protein fibre throughout the blubber depth, ranging from 30–38% wet weight of tissue. In other regions, the middle and basal sections contain only 9–23% protein. One-way ANOVA indicates that there are significant differences in the protein content of the sections from top to base ($p<.001$, d.f. 2/16, F-ratio=9.39) and also by body region ($p<.001$, d.f. 8/16; F-ratio=10.08).

(2) Lipid. The lipid analyses, however, indicate that the middle and/or basal section contain more lipid than the top section, regardless of the region of the body. In the anterior dorsal and ventral regions of the body (head), the lipid content is almost negligible in all three sections, ranging from <2–4%. One-way ANOVA gives significant differences by section top to base: $p<.001$ (d.f. 2/16, F-ratio=13.07) and body region: $p<.001$ (d.f. 8/16, F-ratio=11.80).

(3) Water. The water content is frequently similar in all sections, although the top section consistently contains more, ranging from 35–66% wet weight of tissue, compared with a range of 14–64% in the middle and basal section. One-way ANOVA indicates significant differences both by stratification of blubber ($p<.001$, d.f. 2/16, F-ratio 33.41) and region of the body ($p<.001$, d.f. 8/16, F-ratio= 15.34).

(4) Carbohydrate. The carbohydrate content is consistently least in the top section, excluding the anterior dorsal and ventral regions, where the situation seems variable with respect to the top and basal section; in the anterior ventral region, carbohydrate is undetectable in the top and basal section.

(5) Ash. The ash residues are generally highest in the top and/or basal sections, except in the anterior dorsal and ventral regions where levels are variable. Levels in the top range from <0.4–>0.7%, middle from 0.05–0.5%,

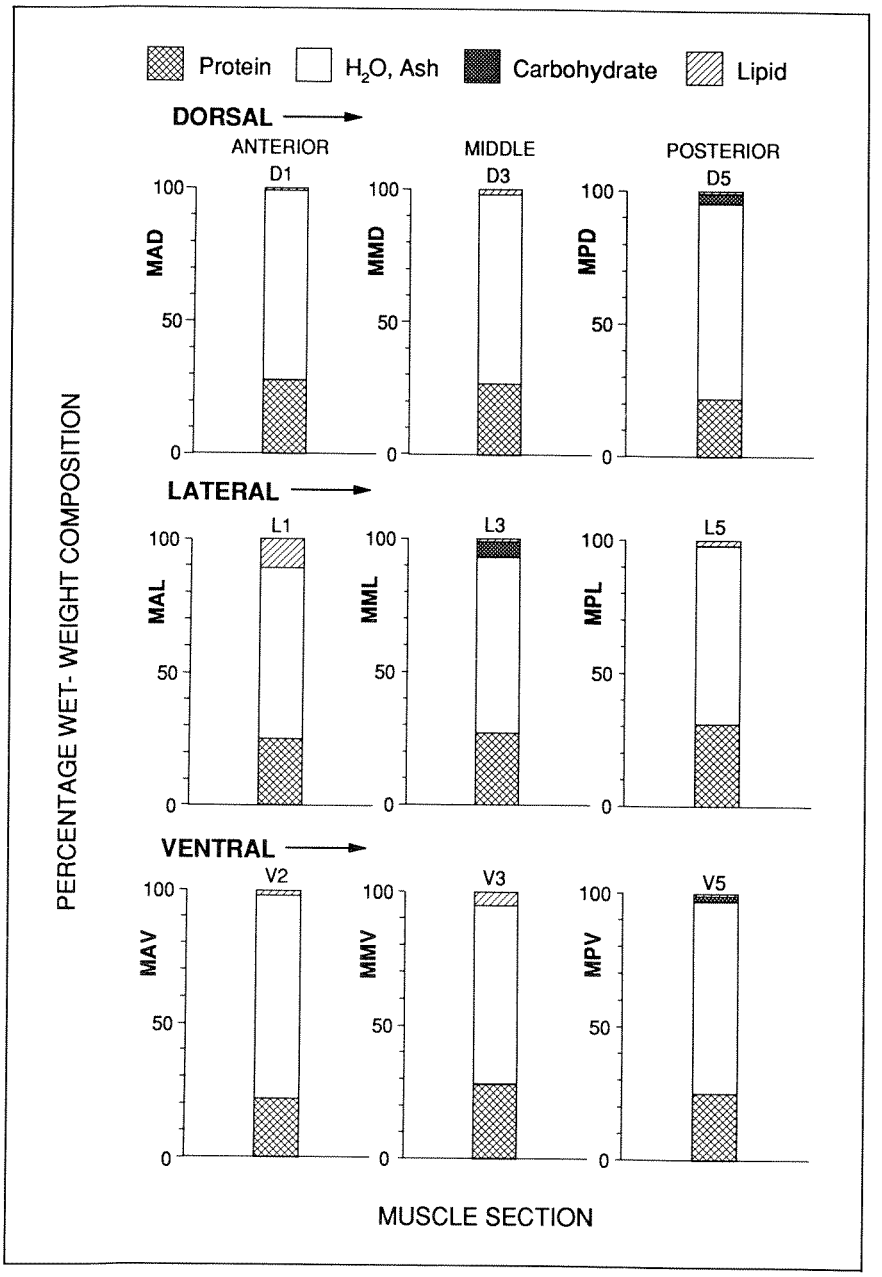

Fig. 7. Biochemical composition of muscle of sperm whale:

Key: MAD = anterior dorsal (D1);
MAL = anterior lateral (L1);
MAV = anterior ventral (V2);
MMD = mid dorsal (D3);
MML = mid lateral (L3);
MMV = mid ventral (V3);
MPD = posterior dorsal (D5);
MPL = posterior lateral (L5);
MPV = posterior ventral (V5).

and base from <0.2–0.6% wet weight of tissue (Table 3). One-way ANOVA indicates that there are significant differences between sections top to base ($p<.005$, d.f. 2/16, F-ratio=9.23), but that there is no significant difference by body region. Furthermore, a series of Newman-Keuls' multiple range tests (Zar 1984) on the means and SE values of the top, middle and base section results indicate that the top section is consistently significantly different from the middle and basal section which are similar for all components.

(6) Summary. Percentage lipid means from top through to base are 15.97±3.43 SE, 36.40±7.76 SE and 31.98±7.07 SE, respectively with $p<0.01$; % protein means are 26.48±1.66 SE, 18.02±3.04 SE, and 20.01±3.63 SE, respectively with $p<.01$; % water content means are 53.20±2.87 SE, 32.84±5.12 SE and 35.56±5.37 SE, respectively with $p<.01$; % ash residue means are 0.49±0.04 SE, 0.27±0.04 SE and 0.32±0.04 SE, respectively with $p<.01$. In summary, the top section generally contains more protein, less lipid, more water and more minerals than the middle and base section, and appears to be distinct from the rest of the blubber in composition.

3) Locomotory muscle

The composition of the muscle (Fig. 7) appears to be more homogeneous throughout the body than blubber. Statistical testing, using ANOVA, indicates no significant differences in the components by body region. The mean % values for the components are 26.29±0.86 SE protein, 2.88±1.14 SE lipid, 71.72±0.82 SE water, 0.97±0.66 SE carbohydrate, and 1.12±0.04 SE mineral residues. The muscle from the anterior lateral region (near to the flipper insertion) contains the most lipid, >11%, but generally the muscle does not appear to contain much fat. Mineral ash residues are higher than for blubber (Table 3).

4) Visceral fats and organs

The result of analyses for fats and liver, kidney and heart muscle are given in Table 4. Protein levels are very small in visceral fat. The lipid levels in these fatty tissues are in the approximate range 70–80%, higher than in blubber. The water content is not considered reliable, and carbohydrate tests were inconclusive. Mineral ash residue is almost negligible for these fatty tissues. In general, the composition of the visceral organs is more similar to locomotory muscle (see above), although the protein component is lower kidney and heart. The carbohydrate component was not reliably tested.

TABLE 4
Biochemical composition of visceral tissues of sperm whale and food items.

	Content as % wet weight of body tissue			
Tissue sample	*Lipid*	*Protein*	*Water*	*Ash*
Liver	3.38	21.46	70.13	1.23
Kidney	2.35	16.05	(69.64)	0.92
Heart	4.38	17.70	77.64	1.13
Visceral facts				
Mesenteric	69.44	1.67	(7.64)	0.07
Thoracic	72.73	no test	(11.47)	0.08
Cardiac	80.43	1.61	(11.67)	0.02
Stomach contents				
Lumpfish	14.78	11.08	70.70	1.63

Note: The above values have been obtained from analyses on separate subsamples and indicate non-homogeneity of some tissues, especially fats and kidney, where totals are substantially less than 100%. The deficit is not expected to be made up from carbohydrate, and the cause is most likely to be attached connective tissue and water loss from cell-damaged tissues due to thawing. The water values are thus in parentheses where suspect.

5) Stomach contents

The analysis of fresh food from the first stomach of sperm whale is shown in Table 4. The diet was lumpfish, *Cyclopterus lumpus*, and the analysis was performed on muscle from the fish, although the fish were ingested whole. The diet appears to be relatively high in lipid, >14% wet weight of tissue.

Detailed lipid biochemistry

1) TLC-analysis

The results of TLC-analysis for different tissues are presented in Table 5. The blubber

TABLE 5
Lipid components of sperm whale tissues, as determined by TLC analysis, expressed as percentage of total lipid components.

	Tissue sample							
	Blubber-posterior dorsal				*Blubber-anterior*	*Visceral*	*Muscle-Posterior*	
Lipid type	*top*	*middle*	*base*	*whole*	*dorsal whole*	*fat-cardiac*	*dorsal*	*Liver*
Polar lipids	0.35	0.33	0.33	0.33	0.48	1.53	22.35	24.11
Free fatty acids	0.39	0.30	0.36	0.36	0.67	0.64	9.13	3.44
Tryacylglycerol	19.46	18.23	20.54	20.18	17.96	32.13	35.21	30.65
Waxes – sterols and esters	62.35	63.94	61.19	61.27	62.47	45.08	15.40	17.36
Hydrocarbons, monacylglycerol and unidentified . .	16.24	14.35	15.74	15.75	16.14	18.31	14.21	22.33

lipid appears to be fairly homogeneous, both by body region and throughout its depth. The major component lipid classes appear to be waxes and triacylglycerol, comprising >61% and >18%, respectively, of all lipids. A large part of the lipids remained undifferentiated (ca 15%). The lipid of the visceral fats also is high in both waxes (45%) and triacylglycerol (32%). However, although waxes comprise >15% of lipids in the muscle, tryacylglycerol is the predominant lipid class (35%), and polar lipids also comprise a significant 22% of the lipids. The lipid components of liver lipid are similar to those in the muscle, with less free fatty acids, and a very high proportion (>22%) of unidentified components.

2) GLC-analysis

The fatty acid analysis by weight composition of methyl esters in the triacylglycerol fraction (mean of four analyses) is presented in Table 6. The most important finding is that >19% of the total components were outside the sensitivity range of the gas chromatograph, thus limiting the discussion and conclusion which can be inferred from this analysis. Of these fatty acids, the majority were short-chain. Of the identified fatty acids, 60% were monoenoic, 1% dioenoic, and 18% saturated; the ratio of unsaturated: saturated was approximately 3.4.

Calorimetry

Results of calorimetry are presented in Table 7 for a variety of sperm whale tissues, including the dietary component, lumpfish. Generally, the observed values were in accord with the anticipated values predicted from proximate analysis, using conversion factors of approximately 39.5 kJ g^{-1} for lipid, 23.6 kJ g^{-1} for protein and 16.7 kJ g^{-1} for carbohydrate (after Brody 1968).

DISCUSSION AND CONCLUSIONS

Morphology

Among the large whales, the weight at length of sperm whales is heavier than for balaenopterids, but less than for balaenids (Lockyer 1976). The proportion of blubber tissue in sperm whale is higher than in other large whales except balaenid whales (Table 2). The proportion of muscle tissue in sperm whale is correspondingly less than in other large whales except the balaenids. Tissue weight distribution appears similar to that in the adult pilot whale, *Globicephala melas* (Table 2). Generally, the more active and swift-swimming cetaceans carry less blubber and more muscle. The overall relative blubber volume in sperm whale is considerably higher than in balaenopterid whales for which the

TABLE 6
Identified triacylglycerol fatty acids in sperm whale and *Tursiops gilli *blubber.*

Fatty acid	Percentage of total components				Fatty acid	Percentage of total components			
	This study	Mori et al. 1965	Hansen & Cheah 1969	*Varanasi & Malins 1971		This study	Mori et al. 1965	Hansen & Cheah 1969	*Varanasi & Malins 1971
5:0	—	—	—	8.7	19:1	—	—	0.3	—
10:0	?	0.1	trace	—	20:1	(7.22)	15.2	9.1	1.6
11:0	?	0.1	—	0.7	20:1w9	2.13			
12:0	?	1.0	0.3	1.6	20:1w7	5.09			
13:0	—	0.1	—	1.7	22:1	(5.56)	12.1	1.8	1.8
14:0	6.21	3.7	3.8	4.8	22:1w11	3.93			
15:0	0.30	0.2	0.4	2.2	22:1w9	1.63			
16:0	9.84	9.1	12.7	7.1	24:1	—	—	0.1	—
17:0	0.91	0.2	0.2	1.3	14:2	—	2.0	—	—
18:0	0.95	1.3	1.3	1.5	16:2	—	1.9	0.2	—
14:1	(1.63)	0.3	(1.6)	2.0	18:2	(1.05)	1.2	0.8	—
14:1w9	—		1.6		18:2w6	1.05			
14:1w5	1.63		—		20:2	—	—	0.3	—
15:1	—	0.2	0.3		17:3	—	—	1.0	—
16:1	(18.30)	18.7	22.4	22.5	24:4	?		0.2	—
16:1w9	4.08				20.5	(1.10)	—	1.8	—
16:1w7	14.22				20:5w6	1.10			
17:1	—	0.8	1.2	2.2	22:5	—	—	0.9	—
18:1	(27.26)	31.4	35.9	35.0	22:6	(0.52)	—	2.3	—
18:1w9	25.28				22:6w3	0.52			
18:1w7	1.98				**Unidentified	19.15			

**Including mainly <C12 and a few >C24

blubber has a demonstrated role in energy storage (Lockyer 1981b, 1987a,b). However, the actual value of the blubber as a potential energy store in sperm whales depends on the lipid content, which is discussed below.

The blubber thickness of the sperm whale is very great (Fig. 5) compared with that of fin whales (Lockyer *et al.* 1985). Considering the much greater relative size of the fin whale at 19–20 m compared with the largest (15.2 m) sperm whale here, not only the proportional but the actual thickness of the sperm whale blubber is greater than that of the fin whale.

The density of the blubber over the body (Fig. 3), which is a crude measure of lipid level, shows a progressive trend from high to low density relative to water from pre- to post-natal: the near-term foetus having predominantly high density blubber whereas the newborn calf is mostly low density. The transition is slight, but overall will affect both the insulation and buoyancy properties of the animal, and in turn affect energy expenditure in the

TABLE 7
Calorific values (kJ g^{-1} wet weight) of sperm whale tissues and dietary items.

Tissue sample and body region	Calorific value, kJ g^{-1}			
	Whole tissue	Top section	Middle section	Base section
Blubber				
anterior dorsal	11.17			
anterior lateral	19.12	10.63	19.63	23.18
anterior ventral	10.04	8.58	11.84	8.66
mid-ventral	26.32	12.93	32.56	31.05
posterior dorsal	23.60			
posterior lateral	27.91	16.91	31.89	30.34
posterior ventral	14.52	13.01	17.03	14.48
Muscle				
anterior lateral	10.92			
anterior ventral	6.86			
posterior ventral	7.16			
Visceral fats				
cardiac	37.87			
Food (lumpfish)				
whole-ground up . . .	6.57			
muscle only	11.63			
skin only	2.74			
gonad only	6.18			

calf. The pattern of density in juveniles and adults is variable, but the head blubber appears to be consistently of higher density, with lower density on the dorsal and lateral blubber over the trunk and tail. The adult male has high density blubber on the ventral surface, unlike the female. In all cases, however, the blubber appears to be of lower density and thickest on the dorsal parts of the body, excluding the head. Berzin (1972) reported a mean body density of 0.95 g cm^{-3} for sperm whale, which would render the animal positively buoyant in surface seawater. Mori *et al.* (1965) reported a density (at 40°C) of waxes from head oil, blubber and muscle of sperm whale at 0.848–0.859 g cm^{-3}. Clarke (1978b) reported density of spermaceti oil between 0.853–0.937 g cm^{-3} at temperatures 37–0°C and pressures 2–210 atmospheres. All these data indicate that lipid-filled tissues such as blubber will usually have a low density, which in turn will affect overall body density.

Biochemistry

The basic biochemical composition of blubber over the body follows a similar pattern of protein, lipid, water and ash residue, to that reported by Watanabe and Suzuki (1950a) for sperm whale, although they found lipid levels as high as 78% along the mid-posterior back, rather higher than the greatest value here of 62%. However, in their study, Watanabe and Suzuki did not sample systematically from the same individual, but combined several samples from many different whales. The blubber from the top of the head had virtually no lipid and about 60% water content, similar to results reported here. However, no carbohydrate was reported, and it is unclear if analysis for this was omitted, or that none was observed in the Watanabe and Suzuki study. In comparison with other cetaceans, the overall range of lipid level of the blubber appears relatively low. For example, Lockyer (in press) reports lipid levels of 70–85% wet weight of tissue for long-finned pilot whale over the body. For baleen whales such as blue (*Balaenoptera musculus*), fin (*B. physalus*) and sei (*B. borealis*), lipid levels may be variable according to season and reproductive condition (Lockyer 1987a,b), but frequently fall in the range 65–88%, excluding the ventral groove blubber (Ackman *et al.* 1975a; Ackman *et al.* 1975b; Feltmann *et al.*1948; Heyerdahl 1932; Lockyer 1986, 1987a,b; Lockyer *et al.* 1984, 1985; Víkingsson 1990; Watanabe and Suzuki 1950b).

An interesting finding is that the component lipids are in the same proportion in both anterior and posterior dorsal blubbers, as well as throughout the blubber depth (Table 5), indicating that there is no special lipid component "mix" in the head region blubber despite the low overall lipid content of this region. Morris (1973, 1975) reported that the spermaceti (including the junk region) comprised mostly (45–>95%) wax esters, and 8–54% triglycerides. Hansen and Cheah (1969) similarly reported 84.2% waxes and 15.8% triglycerides for the head oil, and 79.2% waxes and 20.8% triglycerides in the blubber (Table 8). These findings suggest that, with reference to the results in Table 5, the proportion of blubber lipid components may be similar to those of the spermaceti. However, the actual fatty acid composition of the waxes and triacylglycerols are reportedly somewhat different in the head oils and blubber as will be discussed below.

Despite low levels of lipid in muscle (see also Watanabe and Suzuki 1950a) and liver of the sperm whale, both contain a relatively high proportion of waxes (>15%), but the main lipid class component is triacylglycerol (Table 5). This is very different from the blubber. The high percentage of polar lipids in the muscle are a reflection of the different microhistological cell structure of metabolically active tissue to fat tissue. However, the different and relatively higher proportions of free fatty acids and triacylglycerols in muscle and liver indicate perhaps a different type of energy reserve. Either the type of lipids reflect the tissue's need to meet different energy requirements and patterns of energy mobilisation, or merely reflect the different respiratory capabilities of various body tissues during

TABLE 8

Comparison of component blubber lipids in different cetacean species. Lipids are expressed as percentage of total component lipids.

	Species of cetacean											
	Family – Physeteridae				*Family – Ziphidae*			*Family – Platanistidae*		*Del-phinidae*	*Family – Balaenopteridae*	
	Sperm whale											
Lipid type	*this study (post. dorsal)*	*Mori et al. (1965)*	*Hansen & Cheah (1969)*	*Dwarf sperm whale*[1]	*Baird's beaked whale*[2] *(post. dorsal)*	*Bottlenose whale*[3]	*Blainville's beaked whale*[4]	*Ganges river dolphin*[5] *(post. dorsal)*	*Amazon river dolphin*[6] *(ventral)*	*False killer whale*[7]	*Fin whale*[8]	*Sei whale*[9]
Polar lipids	0.3	0.53	—	—	—	—	—	4.9	—	—	5.4	3.3
Free fatty acids	0.4	?	—	—	—	—	—	} 80.6	—	—	26.3	10.6
Tryacylglycerol	20.2	8.81	20.8	58.0	3.0	6.0	?		99.0	96.0	61.3	59.8
Waxes – sterols and esters	61.3	85.48	79.2	42.0	97.0	94.0	99.0	—	?	4.0	—	—
Other – hydrocarbons, sterols, mono- and di-acylglycerols, unknown	17.8	0.05	—	trace	—	—	—	14.5	—	trace	7.0	26.3

[1] *Kogia simus* (Litchfield *et al.* 1975)
[2] *Berardius bairdi* (Litchfield *et al.* 1975)
[3] *Hyperoodon ampullatus* (Litchfield *et al.* 1975)
[4] *Mesoplodon densirostris* (Litchfield *et al.* 1975)
[5] *Platanista gangetica* (Tsuyuki and Itoh 1971)
[6] *Inia geoffrensis* (Litchfield *et al.* 1975)
[7] *Pseudorca crassidens* (Litchfield *et al.* 1975)
[8] *Balaenoptera physalus* (Lockyer *et al.* 1984)
[9] *B.borealis* (Bottino 1978)

deep dives. During deep dives wax lipids may be deposited in tissues forced into anaerobic conditions because they are tissues with low metabolic output (i.e. blubber) and not targetted for regular blood supply during prolonged diving (i.e. muscle, liver).

Morris and Culkin (1976) mention that marine wax esters usually occur in animals living at depth. Sargent and McIntosh (1974) state that wax ester biosynthesis appears to be "an adaption to a partly anaerobic environment where oxidative respiration is limited, or a means of enhancing fatty acid biosynthesis and the rate of lipid deposition from an excess of dietary constituents through elimination of the normal respiratory-dependent rate control". These statements were made of invertebrates, but it is nevertheless interesting to speculate on the deep and long-duration diving habits (Clarke 1976; Heezen 1957; Lockyer 1977) and potentially anaerobic capabilities (Lockyer 1981a) of the sperm whale. In addition, the highest levels of wax esters are reported for members of the two deepest and longest diving families *Physeteridae* and *Ziphidae*. The biosynthesis of wax esters rather than neutral lipids e. g. triacylglycerols, may be energetically more efficient under prolonged periods of diving and anaerobic conditions. However, this is only a theory, but could explain the relatively high wax levels in deep divers and also the lower wax levels in more metabolically active tissues.

Watanabe and Suzuki (1950a) reported finding lipid levels of 14–47% in bone tissue, ranging from sternum (low) to vertebrae and skull (high). Although no such studies were made here, the published findings indicate further means of affecting buoyancy, with the replacement of water by lipid.

In Table 8 the component lipid classes in sperm whale blubber are compared with those reported for other species' blubber. The members of the family *Physeteridae* (sperm and dwarf sperm whales) and *Ziphidae*

(bottlenose and beaked whales) feature waxes as a prominent if not major lipid component. However, for the families *Balaenopteridae, Delphinidae, Platanistidae, Phocoenidae* and *Monodontidae* (Table 8 and Litchfield *et al.* 1975) triacylglycerol is the exclusive or major component lipid form. Significant amounts of waxes have been reported in the head (melon and spermaceti) of the pygmy sperm whale, *Kogia breviceps* (Karol *et al.* 1978), >28% in the melon and up to 6% in the blubber of *Stenella coeruleoalba* (Morii 1982). In these cases, the other major lipid component was triacylglycerol. Wedmid, *et al.* (1973) reported up to 33% wax esters in the inner melon of pilot whale, *Globicephala melas,* and 67% triglycerides. Wax esters have also been reported in the melon, jaw and blubber of *Tursiops gilli* (Varanasi and Malins 1970, 1971). Here there were differences reported in the proportion of unsaturated straight-chain and saturated branched-chain fatty acids and alcohols in acoustic and non-acoustic "type" tissues, possibly associated with acoustic function.

Morris (1975) reported significant levels of fatty acids <14: – up to 11% 10:0, 8–39% 12:0, and up to 7.5% 12:1 in samples taken throughout the spermaceti of sperm whales. Other major fatty acids, ranging from >3–24.5% by weight, reported by Morris in spermaceti were 14:0, 14:1, 16:0, 16:1, 18:1 and 20:1, although the exact proportion of these varied according to the part of the head sampled. Apart from 14:1, these are also the most prominent fatty acids found in this study (Table 6). Data of Hansen and Cheah (1969) and Mori *et al.* (1965) indicate that in head oils, 10:0, 12:0, 14:0 and 14:1 feature more strongly than in blubber, whilst 16:1, 18:1, 20:1 and 22:1 are more strongly featured in blubber (Table 6). These trends exist regardless of fraction (i.e. wax ester acid, alcohol or triglyceride acid). However, 16:0 is common in both head and blubber. The pattern is thus for predominantly shorter chain fatty acids in the spermaceti, and longer ones in the blubber. It would appear that shorter chain (10:, 12:) fatty acids feature in the blubber, but cannot be accurately determined here (Table 6).

In comparison with other cetaceans, specifically baleen whales, the dominant fatty acids in blubber common to these and sperm whales (Table 6) are 16:0, 16:1, 18:1, 20:1 and 22:1 (Ackman *et al.* 1965; Ackman *et al.* 1971; Lockyer *et al.* 1984). The rorqual also has a significant 22:6 component lipid. The bottlenose dolphin, however, along with sperm whale, features strongly on 14:0, 16:0, 16:1 and 18:1. However, the bottlenose has significant 5:0 component lipid. The two fatty acids of greatest prominence in the blubber lipid of sperm whales, 18:1 – >27% and 16:1 – >18%, are also reported as the most prominent in blubber of other odontocetes including *Tursiops* sp. at 35% and 22.5%, respectively (Varanasi and Malins 1971), *Platanista gangetica* (Tsuyuki and Itoh 1972), *Inia geoffrensis* (Tsuyuki and Itoh 1973), *Neophocaena phocaenoides* (Tsuyuki and Itoh 1969), and are also the main component fatty acids in mysticete blubber (Ackman *et al.* 1965; Lockyer *et al.* 1984; Tsuyuki and Itoh 1970).

The fatty acid composition in mammal lipids has usually been ascribed in part to the dietary composition (Garton *et al.* 1952; Hansen and Cheah 1969; Morris and Culkin 1976; Reidinger *et al.* 1985), so that it is perhaps not so surprising that many cetacean species have similarities, being in the same marine environment and trophic system. The usual diet of sperm whale is squid (Berzin 1972), and Hansen and Cheah (1969) reported that despite only about 4% wet weight of lipid in squid tissue, the lipid contained 48.6% wax ester and 25.7% triacylglycerol. Furthermore, inspection of the fatty acids supported their belief that the lipids in dietary squid were a direct source of the whale wax esters. The lumpfish reported here as one of the main dietary item of sperm whales off Iceland, was not analysed in detail. However, the food is relatively high in lipid (Table 4) and in calories (Table 7). From this point of view, the nutritional value would be high.

Function

All the findings on basic biochemistry imply that the blubber around the top of the head and adjacent to the lower jaw in sperm whale are not typical in the sense of usual definition of blubber tissue. The blubber here is not an important region of fat storage, and unlike the elastic, rather soft and supple tissue elsewhere on the body, it is very hard and rigid. The colouration of these anterior blubber samples is reddish-pink, unlike the creamy colouration of blubber elsewhere, and frequently bleeds from the profuse capillary network permeating its structure when cut. The blubber of the head region, around the spermaceti organ and case, thus appears to be very tough, resilient and fibrous in texture. Such tissue could perform as a flexible exoskeleton (the blubber behaving like a rubber casing on a pressure depth guge) for the spermaceti apparatus which is believed to change in shape and in physical properties of the component lipid, in response to pressure with depth of dive of the whale. The spermaceti organ then acts in the capacity of a buoyancy aid (Clarke 1970, 1978a,b,c), and also in the capacity of an acoustic lens (Morris 1973, 1974, 1975). The former function also requires good blood supply and hence capillary network around the spermaceti organ to effect rapid heat exchange (cooling and reheating) in bringing about the physical state changes of lipid from liquid to solid waxes, which create the density changes affecting buoyancy.

We may speculate that liquid-solid phase changes are possible in blubber as a result of diving depth and temperature change, although fatty acid composition varies between head and blubber. If such physical changes in the outer integument of the whale affecting density were feasible, the blubber would thus also aid buoyancy control of the body during diving, as well as form an incompressible shell around the animal. The combined blubber and head oils/waxes in the spermaceti case and junk, comprise almost 50% body weight, based on data of Gambell (1970), representing an enormous potential capacity for effecting buoyancy changes. The possibility of blubber having a buoyancy function has been tentatively suggested by Clarke (1978c), although no consideration of the effect of possible phase changes in the lipid on the buoyancy have been examined before. If such changes were to occur, depth during diving could be very precisely controlled with minimal muscular exertion, merely by altering buoyancy, thus assisting speeds of descent and ascent as well as conserving energy and prolonging dive time. Such fine buoyancy control would certainly help explain the variable rates of ascent with depth and duration observed for sperm whales (Lockyer 1977). It is worth noting that the sperm whale is not an especially fast swimmer, rarely topping 14–15 knots for brief spurts when seriously alarmed, usual speeds being 3–8 knots (Lockyer 1981b). The body and flipper shape do not enhance swimming performance which does not match that of the balaenopterids or that of many other toothed cetaceans. Thus buoyancy control would greatly enhance diving ascent and descent which may be from or to depths of 1,200–2,500 m (Clarke 1970; Lockyer 1977).

Regardless of this theory on buoyancy control, two points can be made. Firstly, the variation in density of the blubber together with the variation in thickness automatically renders the animal dorsal surface uppermost in the water in a stable posture. The head which is large and full of spermaceti oil with a density of about 0.85–0.87 g cm^{-3} at normal body temperature (Clarke 1978b), is encased in blubber of high density, which may help counteract excessive buoyancy at the anterior end at the surface and upon diving. Secondly, the relative buoyancy of the whale could be trimmed by increasing blood flow and changing the temperature gradient across the blubber according to the external temperature without any actual liquid/solid phase changes.

Seawater is of course of higher density than freshwater, and temperature affects the relative buoyancy of objects in water. The sea surface temperature between 20°S and 40°S is usually in the range 17°–28°C, whereas off Iceland, the range is −1°–12°C. Within these

temperature limits, the density of seawater ranges from 1.02 to 1.04 g cm^{-3} depending upon the salinity and pressure (depth) in question (Sverdrup *et al.* 1946). During deep diving the whale will frequently encounter severe temperature gradients within a few minutes (Clarke 1978c) after leaving the sea surface. Furthermore, deep bottom temperatures are similarly low and fairly stable in all latitudes of all world oceans, regardless of surface temperatures. Clearly, the density of blubber (excluding the head region) at temperatures of 23°–30°C is less than that of seawater, regardless of temperature, and practical evidence of this comes from the necessity to weight blubber samples in the density determined in freshwater. However, the blubber density can be increased with drop in temperature, thus making it less buoyant. The blubber may thus perform as a usual means of buoyancy control under highly variable circumstances. The sperm whale frequently surfaces close to the position it dove, indicating that the whale may be fairly stationary at the bottom. Complete mastery of its buoyancy would enable the whale to remain relatively motionless if required at almost any depth.

The rorqual whale stores fat mainly in the form of triacylglycerol (Lockyer *et al.* 1984), as does the bottlenose dolphin exclusively (Litchfield *et al.* 1975), and the sperm whale in wax form (Table 8), being very different in component lipids, as noted above. Neither the rorqual nor the bottlenose dolphin is a deep or prolonged diver, and furthermore, the rorqual regularly and seasonally stores fat for migratory and winter energy reserves. There is no evidence that food supply is intermittent for sperm whales, so that energy reserves are not required for periods of food scarcity. Lockyer (in press) has determined that seasonal fat energy stores in long-finned pilot whales are most likely linked to repoductive demands. The sperm whale will thus most probably utilise fat stores for reproduction. The distribution of fat throughout the body is also very different in rorquals, pilot whales and sperm whales: the first mentioned accumulates vast reserves of primarily triacylglycerols in the muscle as well as in visceral fats and blubber; the pilot whale accumulates lipid in the muscle, fat tissue within the visceral cavities and around organs, and blubber (Lockyer, in press); while the sperm whale has a vast wax lipid store in the blubber yet virtually no lipid in muscle and visceral organs, and what is stored there is mostly triacylglycerol rather than wax (Table 5). It is worth noting that Mori *et al.* (1965) found that muscle contained as much as 60.38% wax, unlike findings here (15.4%), although the triacylglycerol component was similar (31.53%) to results here (Table 5). The polar lipid component found by Mori *et al.* was 4.41%, far less than found here. The two differences seem very great, and I have no explanation for them. The visceral fats in sperm are a mixture of wax and triacylglycerol, not similar to blubber. The blubber of the sperm whale does not appear to be as high in caloric density (Table 7) as that measured for the fin whale at 33 kJ g^{-1} (Lockyer *et al.* 1984), so that quantity of lipid appears to be made up by volume of tissue in sperm whale, this fact alone suggesting that energy storage is not the primary function. The metabolically active tissues studied here (locomotory muscle and liver), both appear to be characterised by relatively high triacylglycerol and low wax levels in comparison with blubber. The shift in balance between these two lipid forms in the fat and muscle tissues may be linked to the mode of energy utilisation and respiration. However, the high wax component in blubber may have some other physical function as discussed above with respect to buoyancy control. The significant levels of carbohydrate, probably mostly in the form of glycogen, in both blubber and muscle, may represent an instant form of energy for diving via anaerobic glycolysis. It is interesting that such a carbohydrate reserve has not previously been reported for sperm whale nor indeed for any other whale so far examined.

One further point of interest in the structure of the blubber tissue itself is that the outermost layer adjacent to the skin is more fibrous and contains less lipid than the middle

and basal layers, regardless of body region. This suggests that an important function might be to render some rigidity as an exoskeleton, leaving the inner layers with the function of storing energy and transferring it to the muscle.

The lipid composition of different tissues, whether it is in tissue distribution, lipid components or fatty acids, almost certainly reflects specific function. This may be primarily for long- or short-term energy storage, buoyancy regulation, acoustic focusing (Litchfield and Greenberg 1974), insulation (Kanwisher and Sundnes 1966; Parry 1949; Ridgway 1972) or as a pressure resistant buffer from the environment, depending on the chemical and physical properties of the tissue. There are distinct differences between tissues and species, but the exact explanation of these differences is open to speculation and further research.

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