Ontogenetic allometry and body composition of harbour porpoises (*Phocoena phocoena,* L.) from the western North Atlantic

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Abstract

North Atlantic harbour porpoises *Phocoena phocoena* (L.) face considerable energetic challenges, as they are relatively small marine mammals with an intense reproductive schedule and a cold-water habitat. Post-natal growth of these porpoises was described using ontogenetic allometry and body composition techniques. The cross-sectional sample contained robust calves, immature, and mature porpoises (*n* = 122) incidentally killed in commercial fishing operations between 1992 and 1998. Total mass and the mass of 26 body components were measured using a standard dissection protocol. Most body components grew similarly in female and male porpoises. Blubber, brain and skull were negatively allometric, while muscle and reproductive tissues exhibited positive allometry. Female heart, liver, intestine and mesenteric lymph node grew at significantly higher rates than in males. Male locomotor muscle and pelvic bones grew significantly faster than in females. High growth rates for visceral and reproductive organs in porpoises, relative to other mammals, may underlie their early maturation and support their intensive, annual reproductive schedule. Relative to other cetaceans, porpoises seem to allocate a larger percentage of their total body mass to blubber. This allocation to blubber, which is greatest in calves (37% of body mass), may provide harbour porpoises with the thermal insulation required to live in cold water. The factors influencing growth rates and differential investments in body composition seem to change at various stages of a porpoise's life. Energy allocation in porpoises seems to shift from an emphasis on developing an insulative blubber layer in young animals to preparing the body for annual reproduction at sexual maturity.

Key words: ontogeny, allometry, harbour porpoise, *Phocoena phocoena*, energetics

INTRODUCTION

Cetaceans – whales, dolphins and porpoises – are highly specialized mammals. They possess morphological and physiological adaptations to a fully aquatic lifestyle, including increased breath-hold capabilities, axial loco-motor swimming style, streamlined body, insulative blubber, reduced appendages, and novel feeding and sensory structures (reviewed in Howell, 1930; Slijper, 1979; Gaskin, 1982; Wursig, 1989; Pabst, Rommel & McLellan, 1999). Cetaceans also display a large range in body mass, spanning four orders of magnitude (Slijper, 1979; Pabst, et al., 1999). Interestingly, the largest cetacean, the blue whale *Balaenoptera musculus* (100 000 kg), and one of the smallest cetaceans, the

harbour porpoise *Phocoena phocoena* (50 kg), both inhabit the cold, temperate waters of the northern hemi-sphere (Gaskin, 1982).

Although harbour porpoises possess insulative blubber (Worthy & Edwards, 1990), their small body size means that they have a relatively large surface area for heat loss. The surface area to volume ratio for neonatal porpoises, which are born at just 5 kg (Lockyer, 1995*a,b*), is particularly disadvantageous for maintaining mammalian high core temperatures in a medium that can conduct heat from a body 25 times faster than air at the same temperature.

While meeting the energetic demands of homeo-thermy in a cold-water environment, female harbour porpoises in the north-west Atlantic also mature at just

3 years of age and thereafter maintain an annual reproductive schedule (Read & Hohn, 1995). Female porpoises give birth to a neonate that is large relative to maternal body mass and that displays rapid postnatal growth (Lockyer, 1995a,b). Thus, sexually mature females are simultaneously pregnant and lactating for most of their lives (Read & Hohn, 1995). Mature males seasonally allocate up to 4% of their total body mass to testicular growth (Neimanis et al., 2000).

How do harbour porpoises grow to meet the energy needs of homeothermy, early maturity, and annual reproduction? This question was investigated by systematically dissecting a cross-sectional sample of robust harbour porpoises and measuring postnatal changes in the distribution of constituent tissue mass. Two analytical techniques were used to compare mass distributions across six reproductive classes and between males and females in each class:

(1) Ontogenetic allometry (sensu Stewart & German, 1999) describes growth of individual body components, using the allometric equation $Y = aX^b$, where Y equals the mass of the body component and X equals total body mass (e.g. Schmidt-Nielsen, 1975; Calder, 1996).

(2) The body composition technique (sensu Grand, 1977) reports the mass of each body component as a percentage of total body mass.

These two techniques offer complimentary views of growth. The allometric equations describe changes in the rate of growth of a given body component; the composition data offers a snapshot of how those developmental rates are manifested in the distribution of body mass at any point along an ontogenetic trajectory.

There are few studies that describe growth in body components using the ontogenetic allometric approach for either terrestrial mammals (see review in Stewart & German, 1999) or marine mammals. Bryden's (1969) study, with detailed dissections and allometric analyses of southern elephant seals Mirounga leonina remains the model for growth in pinnipeds. The studies of Perrin & Roberts (1972) and Miyazaki, Fujise & Fujiyama (1981), on Stenella spp., are rare analyses of allometric growth of major body components in cetaceans. Read & Tolley (1997) have described allometric growth of external body features for harbour porpoises, but a similar analysis of the mass of internal body components has not yet been conducted. Although the body composition technique has been used to describe the development of terrestrial (e.g. Grand, 1977, 1991, 1992) and marine mammals (e.g. Slijper, 1958; Bryden, 1969; Read, 1990b, Lockyer, 1991; Lockyer, 1995a,b), such detailed studies of the growth are rare for any mammal.

Our goals were to use both allometric and body composition analyses to gain insights into the function and energetic requirements of specific organ systems during growth and reproduction in females vs males, and to offer detailed descriptions of body condition for different reproductive classes of robust harbour porpoises.

MATERIALS AND METHODS

Specimens examined

Dissections were performed on 122 harbour porpoises (49 females, 73 males) from the Gulf of Maine/Bay of Fundy population. Porpoises were incidentally captured in commercial fishing operations (demersal gill nets ($n = 94$) or herring weirs ($n = 28$)) during July–December 1992–98. Summer samples were collected from the Bay of Fundy, while autumn samples were collected in the Gulf of Maine. Thus, the sample included porpoises collected across seasons from this population (Palka et al., 1996; Read & Westgate, 1997). Only porpoises that were robust (defined by convex epaxial muscle profile and no depression caudal to the blowhole) were included in this analysis (Kastelein & van Battum, 1990; Cox et al., 1998). Porpoises exhibiting sunken epaxial musculature or a pronounced depression caudal to the blowhole, characteristics that indicate poor body condition (Kastelein & van Battum, 1990), were excluded from this study. Only carcasses with little or no scavenger damage were used in this study; if scavenger damage was limited to 1 side of the body, the mass dissection protocol (see description below) was performed on the opposite side only. Carcasses were either frozen when returned to land and thawed before dissection, or dissections were carried out on fresh carcasses.

As a routine part of each dissection, total mass and a series of body morphometrics (Read & Tolley, 1997) were recorded for each porpoise before the dissection began. Porpoises were classified into 6 reproductive classes, based on Read (1990a), Read & Hohn (1995) and Neimanis et al. (2000): calf (unerupted teeth or presence of milk in the stomach, $n = 13$); immature male (testis mass < 100 g, absence of sperm in epididymis, and < 3 years old, $n = 22$); immature female (absence of corpora lutea or albicantia in either ovary, $n = 26$); mature male (presence of sperm in epididymis, all seminal tubes mature, usually $\geq$ 3 years old, $n = 46$); mature, non-lactating female (presence of corpora on the ovaries and absence of milk in mammary gland, $n = 7$); and mature, lactating female (presence of milk in the mammary gland, $n = 8$). Both categories of mature females contained pregnant animals. Sample sizes were too small to further subdivide the lactating females into those that were pregnant and non-pregnant. The dataset did not include neonatal harbour porpoises, which are born in May (Read, 1999).

Dissections

A mass dissection protocol was used to systematically separate the body into discrete anatomical components, including blubber and individual muscles, organs, and bones. The identity of muscle and connective tissues was based upon descriptions by Howell (1930), Slijper (1936) and Pabst (1990). Some of these components were later grouped for analysis (see definitions below).

No components that showed gross lesions or extensive scavenger damage were used in this analysis. Whole carcasses, and large body components, were weighed to the nearest 0.1 kg, on a Dillon ED-2000 dynamometer. Smaller components were weighed to the nearest 0.1 g on either an A&D EK-12 kg (model no. 50010), Ohaus LS2000 or Sartorius PT6 digital scale.

Dissections began by bisecting the blubber along the dorsal and ventral midlines. The pectoral flippers were dissected from the body at the axilla to ensure that no blubber was removed with these appendages. The cranial margin of the blubber was defined at the level of the nuchal crest of the skull and the caudal margin at the level of the insertion of the flukes. The blubber and the associated cutaneous trunci muscle were separated cleanly from the underlying subdermal connective tissue sheath (SDS) (Pabst, 1990, 1996) and ventral muscles. On a subset of animals ($n = 20$), the cutaneous trunci muscle was dissected free and weighed separately to determine its contribution to blubber mass. This analysis revealed that the muscle was 1–2% of the total blubber mass and was considered negligible. Thus, the postcranial blubber mass reported here (referred to simply as blubber from this point on) includes this thin skin muscle. The dorsal fin is included in the mass of the blubber. Over the course of the study, the fin was removed in different ways dependent upon the needs of various researchers. These different dissection techniques required the removal of varying, though small amounts of associated blubber, which could not have been accounted for unless the dorsal fin was included in the blubber mass. The fluke lobes, which were consistently removed at the lateral margins of the caudal vertebrae, were not included in the blubber mass.

All muscles and their associated connective tissues were dissected to their points of origin and insertion, and removed as completely as possible from skeletal elements. This dissection technique required filleting of each skeletal element. Although small bits of muscle tissue remained attached to the bones, their contribution to skeletal mass, although not directly measured, was considered negligible.

Shoulder muscle included all intrinsic muscles of the scapula and extrinsic muscles inserting onto the scapula and humerus including the pectoralis, serratus ventralis, latissimus dorsi, rhomboids, levator scapulae, and mastohumeralis.

Axial locomotor muscle included the epaxial (deep neck muscles, semispinalis, multifidus, longissimus, iliocostalis, dorsal intertransversarius) and hypaxial (hypaxialis lumborum, ventral intertransversarius) muscles and the SDS. These axial muscles were dissected completely from the vertebral column and caudal margins of the skull. Abdominal muscle included the external and internal obliques, transverse abdominal muscle, rectus abdominus, and ischiocaudalis. The dorsal margins of the obliques were defined at their tendinous insertion to the SDS. They were cleanly dissected away from their cranial attachments to the ribs and sternum and from their caudal attachments to the ventral SDS and pelvic bones. The sternomastoid, sternohyoid, and sternothyroid muscles were individually dissected. The dorsal and ventral scalenes and all intercostal muscles were dissected cleanly from the ribs. The ribs (including sternal ribs) were disarticulated from the skeleton and weighed together.

In the thoracic cavity, each lung was dissected free at the level of the principal bronchus, and allowed to drain before being weighed. The heart was removed by severing the dorsal aorta at the cranial-most point of the aortic arch, and other major vessels at their entrance to the heart. The heart was drained of free blood and obvious clots removed before weighing.

The abdominal cavity was opened and the stomach tied at the pyloric sphincter. The oesophagus was tied at a level of the cervical vertebrae, and dissected free from mesenteries and diaphragm. The oesophagus, whole stomach (fore, main, and pyloric chambers) and the duodenum were removed, separated from other viscera, and weighed both full, and after they were emptied of their contents. The intestine was removed from the pyloric sphincter to the colon. The mesenteric lymph nodes were trimmed from their mesenteries; the remaining mesenteries and colonic lymph nodes were included in the intestine mass. The spleen and associated satellite spleens, liver, pancreas, kidneys and adrenals were each dissected cleanly and weighed.

The female reproductive tract included the entire vaginal tract (from the level of the genital slit), uterus, uterine horns, ovaries, and associated vasculature (Pabst et al., 1998). The ovaries were subsequently removed for life-history analyses. In a pregnant female, the uterus was opened and the foetus, placenta, and amniotic fluid were removed and the reproductive tract was re-weighed and used in this analysis.

In males, each testis was removed with its epididymis and ductus deferens, which was severed at its entrance to the prostate (Pabst et al., 1998). The testis was separated from its epididymis and weighed separately. The pelvic bones were removed from the base of the penis, and the prostate, penis, and perineal muscles were weighed together as the male reproductive tract.

The skull, as with all skeletal elements, was cleaned of associated soft tissues. The calvarium was opened with a saw, and the brain removed whole and weighed. The empty skull, including mandibles, was then weighed. The vertebral column mass included the spinal cord and vasculature within the neural canal.

Bilateral symmetry

Depending on the severity of scavenger and net damage to blubber and muscle, detailed mass dissections could not always be performed on both left and right sides of all porpoises. Therefore a subset of pristine porpoises for which masses were recorded on both left and right sides were examined to determine whether blubber mass and axial muscle mass were symmetrical. Data were checked for normality and paired t-tests were used to

compare left and right axial and blubber masses for 25 porpoises. Because these tests demonstrated bilateral symmetry (see Results) all porpoises for which blubber and muscle mass were recorded on 1 side only were pooled in the remaining analyses by multiplying the recorded mass by 2.

Ontogenetic allometry

Typically, allometric growth equations are generated in the form of $Y = aX^b$, where Y is the mass of the component being measured, and X is body mass. However, because of scavenger damage, it was possible to measure an accurate total body mass for only 67 of the 122 porpoises in this analysis. Two options exist to address this problem – either estimate missing body mass for damaged carcasses, or use the cube of standard length (to approximate mass) as the independent variable. This latter method has traditionally been used to maintain dimensional similarity in allometric analyses (e.g. Read, 1990b; see also Stahl, 1962). However, for harbour porpoises, mass does not scale with the cube of length (in the form mass = a*length^b), but rather the exponent b, lies somewhere between 2 and 3 (see below and van Utrecht, 1978; Lockyer, 1995a). Comparative data suggest that the exponent describing the relationship between length and mass in cetaceans is highly variable and species-specific (e.g. Bryden, 1972; Lockyer, 1991; Silva, 1998), and should be calculated for each dataset before data are analysed using assumptions regarding this relationship. The exponent and standard errors for females in this dataset is 2.37 ± 0.077, and for males it is 2.10 ± 0.067. Therefore, it is not appropriate to approximate mass as a function of the cube root of length for harbour porpoises. To maximize the number of animals in this study, missing values for total body mass were estimated from a combination of 2 variables, standard body length and girth anterior to the dorsal fin. Read & Tolley (1997) and Lockyer (1995a,b) estimated that this technique predicted body mass with an accuracy of 95%. From the existing total mass data predictive equations were generated using iterative non-linear regression, with standard length (cm) and girth anterior to the dorsal fin (cm) as dependent variables, and total mass (kg) as the independent variable, separately for each sex. Together, these 2 variables accounted for 99% of the variation in mass in females ($n = 29$), and 95% in males ($n = 36$). The equations used to predict total mass were:

females mass = 0.00008*(length**1.394)*(girth**1.417),
males mass = 0.0003*(length**1.660)*(girth**0.827).

These equations are similar to those derived by Read & Tolley (1997) and Lockyer (1995a,b) for the prediction of total mass of harbour porpoises. Because most of the body components were measured in grams, total body mass (either measured directly or predicted using the above equations) was converted to grams.

Allometric growth equations were generated in the form $Y = aX^b$ for 26 body components. All variables were log-transformed before analysis. Patterns of growth were determined separately for males and females. In some cases, several body components were grouped to create a single variable. The sternohyoid, sternothyroid, and sternomastoid muscles, all muscles that act upon the sternum, were combined into 1 variable (sternos). The diaphragm, scalenes and intercostals were considered to be breathing muscles and were treated as 1 variable (breathe). Total muscle included all measured muscle components, and total bone included skull, hyoids, vertebral column, ribs, sternum, pelvics, scapulae, and pectoral flippers. For males, the reproductive tract, epididymes, and ductus deferens were pooled (male repro) and testes were considered separately. For females, the reproductive tract included the entire vaginal tract (from the level of the genital slit), uterus, uterine horns, and ovaries were pooled (female repro). All porpoises were included in the growth patterns analysis. Missing data points were not estimated; carcasses with missing data were excluded list-wise separately for each test.

For body components exhibiting significant relationships with body mass, slopes (b) were tested to determine if they were significantly different from 1.0 at a critical level of 0.05. A slope not significantly different from 1.0 indicates isometric growth. If b was significantly > 1.0, growth was described as positively allometric (i.e. increasing in mass at a rate faster than that of body mass); if b was significantly < 1.0, growth was described as being negatively allometric (i.e. increasing in mass at a rate slower than that of body mass). Additionally, b values were tested for homogeneity between the sexes at a critical level of 0.05.

Body composition

Because this was the first time such an extensive mass dissection protocol was performed on a large number of harbour porpoises, mean values of mass for most body components are presented for all 6 reproductive classes. To examine changes in the relative contribution of different body components to total mass as a porpoise grows, the relative mass (component mass as a percentage of total mass) of selected body components were calculated and plotted against total body mass. This analysis included blubber, axial muscle, abdominal muscle, total muscle, skull, vertebral column, total bone, pelvis, brain, heart, lungs, liver, stomach, mesenteric lymph nodes, intestines, and kidneys. To compare relative body composition among the reproductive groups, percentage data were arc-sine transformed (Steel & Torrie, 1980) before analysis by ANOVA at a critical level of 0.05. Levene's test was used to determine whether variances of the means of various reproductive classes were equal (Tabachnick & Fidell, 1996). Post-hoc, multiple comparisons among reproductive group means were made using either the Sidak test (if Levene's

Table 1. Growth patterns in 23 body components of female harbour porpoises *Phocoena phocoena*. Growth patterns have been determined in the form of $Y = aX^b$, where Y = body component mass (g) and X = total body mass (g). Values presented are for samples size (n), a (intercept), b (slope), and a test of whether $b = 1.0$ (isometric growth). Slopes significantly > 1.0 indicate positive allometric growth, slopes < 1.0 indicate negative allometric growth

System	Component	n	R^2	a	$b \pm$ SE	$b = 1$?
Blubber		27	0.638	22.59	0.589 ± 0.086	< 1
Muscle	Axial	45	0.954	0.006	1.344 ± 0.045	> 1
	Abdominal	37	0.890	0.004	1.196 ± 0.070	> 1
	Shoulder	34	0.846	0.005	1.067 ± 0.079	$= 1$
	Sternos	31	0.877	0.004	1.044 ± 0.071	$= 1$
	Breathe	33	0.940	0.005	1.176 ± 0.053	> 1
	Total muscle	29	0.967	0.013	1.296 ± 0.045	> 1
Bone	Skull	36	0.740	2.16	0.572 ± 0.057	< 1
	Vertebral column	41	0.961	0.029	1.046 ± 0.033	$= 1$
	Ribs	33	0.904	0.015	0.989 ± 0.057	$= 1$
	Sternum	32	0.855	1.47×10^{-4}	1.204 ± 0.089	> 1
	Scapula	34	0.831	0.0019	1.005 ± 0.079	$= 1$
	Pelvics	32	0.624	5.68×10^{-7}	1.581 ± 0.219	> 1
	Total bone	26	0.967	0.415	0.864 ± 0.032	< 1
Brain		44	0.442	36.48	0.236 ± 0.040	< 1
Thoracic viscera	Heart	48	0.649	0.004	1.068 ± 0.114	$= 1$
	Lungs	47	0.793	0.002	1.236 ± 0.093	> 1
Abdominal viscera	Liver	42	0.805	1.54×10^{-4}	1.498 ± 0.115	> 1
	Pancreas	42	0.663	5.26×10^{-4}	1.150 ± 0.127	$= 1$
	Stomach	37	0.814	3.37×10^{-5}	1.546 ± 0.123	> 1
	Mesenteric lymph	40	0.768	1.08×10^{-5}	1.535 ± 0.135	> 1
	Intestines	43	0.795	0.002	1.305 ± 0.102	> 1
	Spleen	44	0.235	0.001	0.825 ± 0.219	$= 1$
	Kidneys	48	0.828	0.002	1.134 ± 0.075	$= 1$
Reproductive	Female repro	26	0.839	6.05×10^{-13}	3.164 ± 0.276	> 1[a]

[a] b is also > 2 at $\alpha = 0.05$

test revealed that group variances were equal) or the Tamhane's T2 test (group variances were not equal) (Tabachnick & Fidell, 1996).

Reproductive tissues

Changes in the mass of tissues associated with reproduction, specifically testes, mammaries, male and female repro, and pelvic bones, were investigated. Arc-sine transformed percentage data (body component expressed as percentage of total mass) were compared among reproductive classes using ANOVA. SPSS (1998) was used for statistical computations.

RESULTS

Bilateral symmetry

Left and right blubber masses were not significantly different for 25 porpoises examined for bilateral symmetry ($P < 0.05$). Mean left and right blubber masses ($\pm$ SD) were 5309 ± 1091 g and 5289 ± 1004 g, respectively. Similarly, left and right axial muscle masses were not significantly different ($P < 0.05$). The mean masses ($\pm$ SD) of the left and right axial muscles were 4604 ± 1871 g and 4624 ± 1910 g, respectively. Thus, left

and right body component masses of porpoises were bilaterally symmetrical.

Ontogenetic allometry

In females, the most common pattern of growth was positive allometry: axial, abdominal, breathe and total muscle; sternum; pelvics; lungs; liver; empty stomach; mesenteric lymph node; intestines and reproductive tract all increased in mass at rates higher than total body mass. Isometric growth was observed in the shoulder and sternos muscle, vertebral column, ribs, scapula, heart, pancreas, spleen, and kidneys of females. Negatively allometric growth occurred in female porpoises in blubber, skull, total bone, and brain mass (Tables 1 & 2, Fig. 1).

The most common pattern of growth observed in the body compartments of males was isometry: sternos and breathe muscles, vertebral column, ribs, scapula, total bone, lungs, liver, pancreas, mesenteric lymph node, intestines, and kidneys all increased in mass at the same rate as total mass. Positively allometric growth was observed in the axial, abdominal, shoulder and total muscles; sternum; pelvics; empty stomach; reproductive tract and testes. Negatively allometric growth was observed in the blubber, skull, brain and heart masses of males. There was no significant relationship between

Table 2. Growth patterns in 24 body components of male harbour porpoises *Phocoena phocoena*. Growth patterns have been determined in the form of $Y = aX^b$, where $Y =$ body component mass (g) and $X =$ total body mass (g). Values presented are for samples size (n), a (intercept), b (slope), and a test of whether $b = 1.0$ (isometric growth). Slopes significantly > 1.0 indicate positive allometric growth, slopes < 1.0 indicate negative allometric growth. The last column indicates whether the slopes (b) generated from linear equations of log (total body mass) *vs* log (body component mass) for males and females are significantly different at $\alpha = 0.05$ (as indicated by F > M or M > F)

System	Component	n	r^2	a	$b \pm$ SE	$b = 1$?	F = M?
Blubber		29	0.603	18.41	0.607 ± 0.092	$b < 1$	F = M
Muscle	Axial	65	0.933	6.28×10^{-4}	1.554 ± 0.052	$b > 1$	M > F
	Abdominal	50	0.870	3.62×10^{-4}	1.426 ± 0.079	$b > 1$	M > F
	Shoulder	48	0.802	0.002	1.169 ± 0.085	$b > 1$	F = M
	Sternos	41	0.769	0.009	0.969 ± 0.084	$b = 1$	F = M
	Breathe	43	0.763	0.021	1.043 ± 0.089	$b = 1$	F = M
	Total muscle	39	0.925	0.002	1.467 ± 0.068	$b > 1$	M > F
Bone	Skull	47	0.504	0.931	0.649 ± 0.094	$b < 1$	F = M
	Vertebral column	52	0.891	0.025	1.059 ± 0.052	$b = 1$	F = M
	Ribs	45	0.725	0.008	1.039 ± 0.096	$b = 1$	F = M
	Sternum	44	0.776	8.30×10^{-6}	1.474 ± 0.120	$b > 1$	F = M
	Scapula	48	0.739	4.32×10^{74}	1.143 ± 0.099	$b = 1$	F = M
	Pelvics	44	0.757	8.13×10^{-11}	2.513 ± 0.216	$b > 1^a$	M > F
	Total bone	38	0.878	0.198	0.932 ± 0.057	$b = 1$	F = M
Brain		68	0.171	49.20	0.211 ± 0.055	$b < 1$	F = M
Thoracic viscera	Heart	70	0.335	0.143	0.715 ± 0.120	$b < 1$	F > M
	Lungs	71	0.578	0.010	1.103 ± 0.112	$b = 1$	F = M
Abdominal viscera	Liver	52	0.452	0.060	0.932 ± 0.142	$b = 1$	F > M
	Pancreas	53	0.251	0.028	0.766 ± 0.179	$b = 1$	F = M
	Stomach	56	0.617	6.35×10^{-5}	1.491 ± 0.157	$b > 1$	F = M
	Mesenteric lymph	58	0.231	0.015	0.854 ± 0.201	$b = 1$	F > M
	Intestines	59	0.502	0.206	0.870 ± 0.113	$b = 1$	F > M
	Spleen	64	–	NS	NS	NS	–
	Kidneys	70	0.734	0.002	1.137 ± 0.082	$b = 1$	F = M
Reproductive	Male repro	42	0.830	4.24×10^{-11}	2.869 ± 0.202	$b > 1$	–
	Testes	70	0.793	6.61×10^{-22}	5.054 ± 0.311	$b > 1^b$	–

[a] b is also > 2 at $\alpha = 0.05$.
[b] b is also > 4 at $\alpha = 0.05$.

spleen mass and total body mass in males ($P < 0.05$), so a value for the exponent b could not be calculated for this tissue.

Growth patterns of most body components were similar in males and females, with the exception of axial muscle, abdominal muscle, and pelvic bones, for which b values were higher in males, and liver, heart, intestines and mesenteric lymph node, for which b values were higher in females. Growth patterns of the spleen could not be compared between males and females, because a significant value for the exponent b for males could not be calculated.
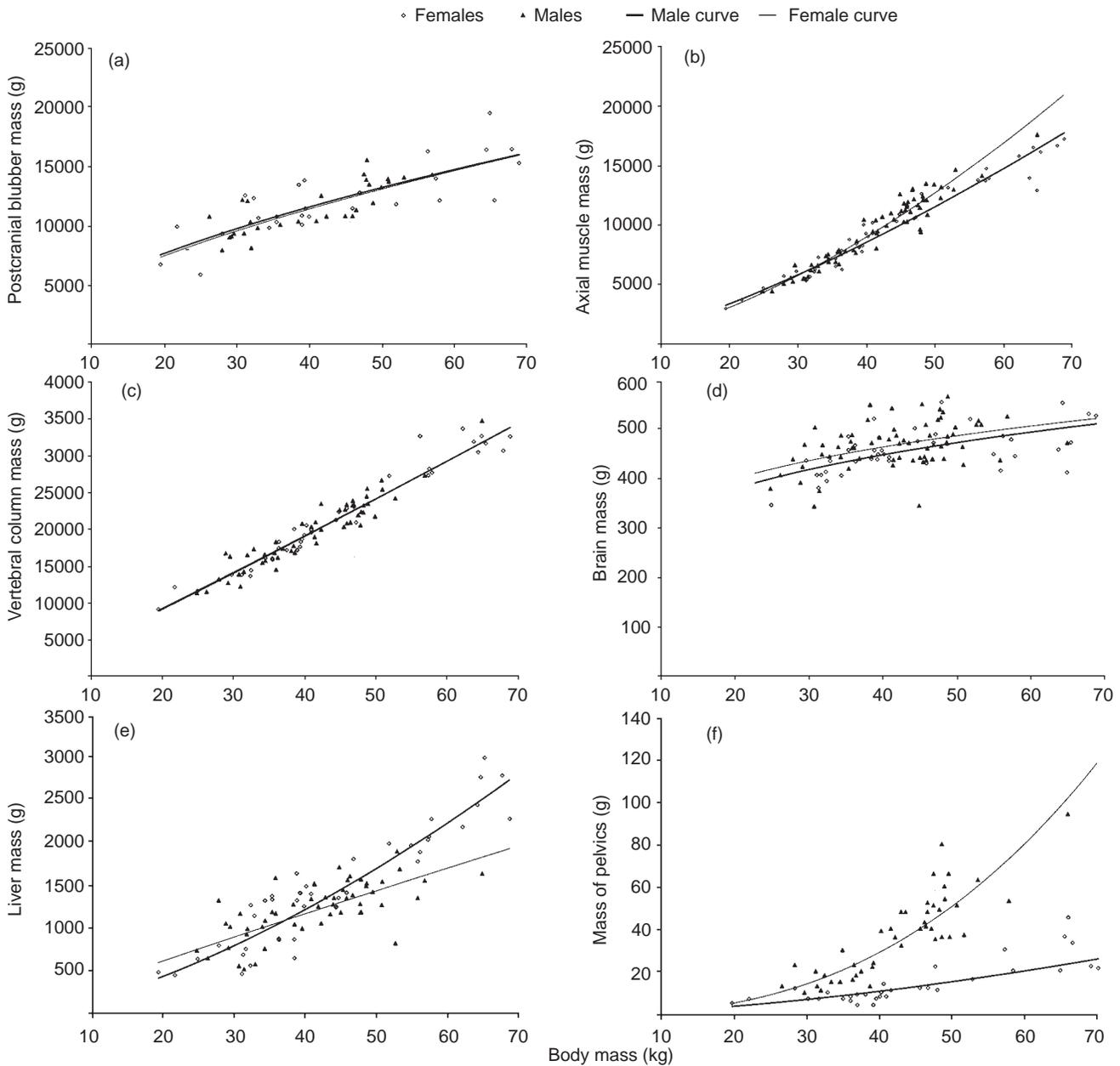
Body composition

Total body mass (Table 3) increased from mean values of 29 kg in calves to 47 kg in mature males (63% increase) and 64 kg in mature, lactating females (121% increase). In all reproductive classes, blubber and muscle contributed 50–60% of the total body mass, but the relative contributions of these components changed significantly with growth. Mean blubber mass increased from 10.7 kg in calves to 12.8 kg in adult males and 15.3 kg in the largest females; the proportion of total body mass allocated to blubber, though, decreased from

37% in calves to 26% in mature males and 24% in the largest females. Muscle mass increased both absolutely and relatively as porpoises grew: calves had 7.8 kg of muscle (representing 26% of total body mass), while mature males possessed 15.8 kg (33% of total body mass) and the largest mature females possessed 21.2 kg of muscle (32.6% of total body mass).

In both sexes, the brain contributed a significantly smaller percentage to body composition in adults, but vertebral column, total bone, heart, spleen and adrenals (not shown in Table 4) did not change as a percentage of body mass across reproductive classes. The skull's contribution to body composition decreased significantly only in mature, lactating females. In both sexes, the lung, liver, empty stomach, mesenteric lymph node, intestines and kidney all significantly increased their percentage contributions to body composition in adult porpoises, relative to calves.

Reproductive tissues

ANOVA of arc-sine transformed percentage data showed that there was considerable investment in reproductive tissues among sexually mature animals. In both sexes, growth of reproductive tissues was strongly,

Fig. 1. Allometric growth curves for body components of harbour porpoises *Phocoena phocoena*. (a) Postcranial blubber growth, which is similar in males and females, is negatively allometric. (b) Axial muscle growth is positively allometric in both males and females although males grow axial muscle at a significantly higher rate. (c) Both female and male vertebral column mass grows isometrically. (d) Brain growth, which is similar in males and females, is negatively allometric. (e) Liver growth in females is positively allometric and isometric in males. (f) Pelvic bone growth in males is extremely positively allometric ($b > 2$) and is significantly higher than the positive allometric growth of female pelvic bones.

positively allometric. The reproductive tracts (male and female repro) increased dramatically in mass: 783% increase in mature, lactating females and 310% increase in mature males, relative to calves. Mammary glands in lactating females were, on average, 10 times heavier than those of non-lactating, mature females, and contributed 1% of total mass in lactating females. Testes mass increased 17-fold from calves to mature males, and contributed 0.7% to body composition in mature males. In both sexes, the pelvic bones increased in mass at rates higher than that of the total body, but contributed a

significantly larger percentage of total mass only in immature and mature males, relative to calves and females.

DISCUSSION

The use of detailed, systematic dissections of a large series of individuals, ranging in age from dependent young to reproductively mature adults, permits a quantitative description of how body components change

Table 3. Mean masses (± sᴅ) of major body components of harbour porpoises *Phocoena phocoena* of different reproductive classes. Also given here are mean standard lengths and mean total body mass (either measured or predicted, see Methods) ± sᴅ. Sample size for each group in parentheses

System	Component	Calf	Immmale	Matmale	Immfem	Pregnonlact	Lact
Blubber (kg)		10.70 ± 2.67 (9)	10.00 ± 1.70 (12)	12.79 ± 1.69 (14)	10.88 ± 1.17 (11)	13.73 ± 1.9 (4)	15.32 ± 2.82 (6)
Muscle	Axial (kg)	5.26 ± 1.40 (12)	6.98 ± 1.19 (22)	11.54 ± 1.76 (39)	8.44 ± 1.94 (24)	13.54 ± 1.76 (6)	15.23 ± 1.68 (7)
	Abdominal (kg)	0.91 ± 0.26 (11)	1.06 ± 0.20 (18)	1.73 ± 0.27 (28)	1.27 ± 0.27 (20)	1.99 ± 0.17 (4)	2.24 ± 0.36 (6)
	Shoulder (g)	278 ± 73 (10)	344 ± 72 (17)	487 ± 85 (28)	428 ± 59 (15)	561 ± 74 (5)	620 ± 73 (7)
	Sternos (g)	179 ± 33 (9)	243 ± 46 (12)	316 ± 37 (26)	268 ± 46 (14)	336 ± 73 (5)	424 ± 25 (6)
	Breathe (kg)	0.97 ± 0.26 (10)	1.19 ± 0.25 (14)	1.58 ± 0.24 (26)	1.31 ± 0.19 (15)	2.10 ± 0.26 (5)	2.25 ± 0.13 (6)
	Total (kg)	7.76 ± 2.08 (9)	10.21 ± 2.11 (11)	15.77 ± 2.40 (25)	12.27 ± 2.01 (14)	19.38 ± 1.55 (4)	21.16 ± 1.79 (5)
Bone	Skull (g)	688 ± 143 (12)	871 ± 110 (16)	995 ± 120 (27)	976 ± 121 (17)	1072 ± 96 (4)	1157 ± 59 (7)
	Vert. column (kg)	1.36 ± 0.30 (12)	1.62 ± 0.20 (19)	2.29 ± 0.32 (29)	1.82 ± 0.26 (20)	2.86 ± 0.39 (6)	3.09 ± 0.17 (7)
	Hyoids (g)	36 ± 11 (11)	44 ± 7 (13)	50 ± 14 (25)	47 ± 7 (15)	59 ± 8 (4)	81 ± 11 (7)
	Ribs (g)	387 ± 91 (10)	446 ± 75 (15)	597 ± 98 (27)	534 ± 80 (15)	780 ± 100 (5)	817 ± 77 (6)
	Sternum (g)	33 ± 9 (11)	40 ± 9 (15)	66 ± 12 (26)	54 ± 10 (14)	79 ± 11 (4)	88 ± 12 (6)
	Scapula (g)	58 ± 14 (10)	68 ± 14 (17)	96 ± 19 (28)	80 ± 15 (15)	121 ± 18 (5)	123 ± 16 (7)
	Total bone (kg)	3.00 ± 0.57 (9)	3.45 ± 0.47 (12)	4.53 ± 0.57 (23)	3.97 ± 0.38 (13)	5.05 ± 0.48 (3)	5.87 ± 0.22 (4)
Brain (g)		392 ± 34 (12)	466 ± 39 (21)	471 ± 41 (43)	452 ± 40 (23)	478 ± 25 (5)	473 ± 53 (8)
Thoracic viscera	Heart (g)	202 ± 47 (12)	256 ± 69 (22)	322 ± 62 (44)	283 ± 78 (25)	482 ± 154 (7)	439 ± 135 (8)
	Lungs (kg)	0.68 ± 0.12 (12)	1.07 ± 0.23 (22)	1.48 ± 0.29 (45)	1.12 ± 0.25 (24)	1.83 ± 0.30 (7)	2.04 ± 0.52 (8)
Abdominal viscera	Liver (kg)	0.59 ± 0.13 (11)	1.07 ± 0.24 (16)	1.38 ± 0.23 (32)	1.22 ± 0.27 (21)	1.99 ± 0.12 (7)	2.47 ± 0.41 (7)
	Pancreas (g)	55 ± 19 (11)	96 ± 25 (17)	108 ± 27 (32)	110 ± 29 (21)	144 ± 34 (7)	176 ± 18 (7)
	Stomach (g)	236 ± 58 (12)	440 ± 145 (16)	598 ± 144 (35)	464 ± 128 (16)	780 ± 201 (6)	886 ± 207 (8)
	Mesenteric lymph (g)	63 ± 21 (11)	148 ± 64 (19)	148 ± 42 (35)	142 ± 49 (20)	197 ± 34 (6)	233 ± 64 (7)
	Intestines (kg)	1.15 ± 0.36 (12)	2.08 ± 0.41 (21)	2.34 ± 0.40 (34)	2.21 ± 0.40 (22)	2.73 ± 0.38 (6)	3.77 ± 0.23 (7)
	Spleen (g)	7 ± 2 (11)	10 ± 4 (21)	9 ± 4 (39)	10 ± 5 (23)	16 ± 5 (6)	12 ± 5 (8)
	Adrenals (g)	5 ± 2 (12)	7 ± 2 (20)	11 ± 3 (35)	8 ± 3 (22)	14 ± 4 (6)	17 ± 2 (7)
	Kidneys (g)	183 ± 29 (12)	271 ± 55 (22)	370 ± 61 (44)	297 ± 60 (25)	432 ± 49 (7)	506 ± 74 (8)
Repro	Female repro (g)	124 ± 21 (6)	– –	– –	196 ± 121 (13)	676 ± 148 (3)	1096 ± 192 (4)
	Male repro (g)	282 ± 11 (3)	401 ± 126 (12)	1156 ± 252 (27)	– –	– –	– –
Length (cm)		111.9 ± 8.4 (13)	122.2 ± 6.4 (22)	140.8 ± 6.5 (46)	128.6 ± 7.6 (26)	149.3 ± 4.9 (7)	157.2 ± 5.2 (8)
Total mass (kg)		28.8 ± 5.5 (13)	34.7 ± 4.5 (22)	47.1 ± 4.9 (46)	38.8 ± 5.2 (26)	55.4 ± 4.9 (7)	63.8 ± 4.5 (8)

Table 4. Mean relative body composition of harbour porpoises *Phocoena phocoena* of different reproductive classes. Values presented are percentage of total body mass represented by a particular body component ± SD. Sample size for each group in parentheses. Significance of ANOVA test to detect differences in arcsine-transformed data is given by *P* value. Mean values with the same letters are not significantly different at α = 0.05

Component	*P* value	Calf	Immmale	Matmale	Immfem	Pregnonlact	Lact
Blubber	< 0.000	37.45 ± 6.13 (9) a	29.62 ± 2.04 (12) b	26.49 ± 2.46 (14) bc	29.47 ± 3.16 (11) b	25.81 ± 2.75 (4) bc	23.54 ± 3.97 (6) c
Axial	< 0.000	17.94 ± 1.73 (12) a	20.06 ± 1.49 (22) ab	24.59 ± 2.03 (39) d	21.65 ± 2.41 (24) bc	24.33 ± 1.19 (6) cd	23.46 ± 2.03 (7) cd
Abdominal	< 0.000	3.05 ± 0.43 (11) a	3.00 ± 0.28 (18) a	3.66 ± 0.43 (28) bc	3.27 ± 0.41 (20) a	3.47 ± 0.21 (4) ac	3.45 ± 0.56 (6) ac
Total muscle	< 0.000	26.01 ± 2.61 (9) a	28.10 ± 2.23 (11) ab	33.43 ± 2.59 (25) d	30.70 ± 2.65 (14) bc	33.77 ± 0.99 (4) cd	32.59 ± 1.29 (5) cd
Skull	< 0.000	2.39 ± 0.33 (12) ac	2.54 ± 0.26 (16) a	2.13 ± 0.31 (27) cd	2.49 ± 0.34 (17) ab	2.02 ± 0.10 (4) bcd	1.79 ± 0.11 (7) d
Vert. column	NS	4.69 ± 0.38 (12)	4.69 ± 0.48 (19)	4.85 ± 0.30 (29)	4.66 ± 0.21 (20)	5.14 ± 0.39 (6)	4.77 ± 0.18 (7)
Total bone	NS	9.79 ± 0.53 (9)	9.77 ± 0.64 (12)	9.56 ± 0.77 (23)	9.89 ± 0.49 (13)	9.68 ± 0.11 (3)	8.85 ± 0.32 (4)
Brain	< 0.000	1.39 ± 0.24 (12) ab	1.35 ± 0.13 (21) a	1.01 ± 0.12 (43) c	1.17 ± 0.11 (23) b	0.90 ± 0.09 (5) cd	0.74 ± 0.06 (8) d
Heart	NS	0.70 ± 0.16 (12)	0.75 ± 0.22 (22)	0.69 ± 0.14 (44)	0.73 ± 0.18 (25)	0.86 ± 0.22 (7)	0.69 ± 0.19 (8)
Lungs	< 0.001	2.40 ± 0.44 (12) a	3.11 ± 0.71 (22) b	3.14 ± 0.47 (45) b	2.92 ± 0.50 (24) ab	3.31 ± 0.50 (7) b	3.17 ± 0.63 (8) b
Liver	< 0.000	2.10 ± 0.48 (11) a	3.18 ± 0.76 (16) bc	2.94 ± 0.46 (32) b	3.21 ± 0.60 (21) bc	3.60 ± 0.18 (7) bc	3.87 ± 0.50 (7) c
Stomach	< 0.000	0.81 ± 0.05 (11) a	1.24 ± 0.33 (16) b	1.26 ± 0.29 (35) b	1.18 ± 0.28 (16) b	1.39 ± 0.25 (6) b	1.38 ± 0.28 (8) b
Mesenteric lymph	< 0.000	0.22 ± 0.04 (11) a	0.42 ± 0.13 (19) b	0.32 ± 0.08 (35) b	0.37 ± 0.10 (20) b	0.35 ± 0.04 (6) b	0.36 ± 0.10 (7) ab
Intestines	< 0.000	3.94 ± 1.04 (12) a	5.99 ± 0.78 (21) c	4.96 ± 0.65 (34) b	5.64 ± 0.67 (22) c	5.03 ± 0.58 (6) bc	5.82 ± 0.37 (7) bc
Kidneys	< 0.002	0.64 ± 0.11 (12) a	0.78 ± 0.12 (22) b	0.78 ± 0.08 (44) b	0.76 ± 0.11 (25) b	0.78 ± 0.10 (7) ab	0.79 ± 0.11 (8) b

during growth in harbour porpoises. It is important to note that this study describes ontogenetic allometries, i.e. how body components change in mass as porpoises grow. These ontogenetic allometries are not comparable to interspecific allometries, which describe how body components contribute to adult form across species.

Relationship between ontogenetic allometry and body composition

Composition of the adult body is determined by the integrated growth of its components. A component's rate and duration of growth will control its ultimate contribution to total mass and determine whether that contribution changes as the animal matures. One would predict, for example, that a body component that grows at a negatively allometric rate would represent an ever-decreasing percentage of total body mass.

In harbour porpoises, a tissue that grows at a strongly negative allometric rate (*b* < 0.5) will account for a smaller percentage of total body mass in the adult. Likewise, a tissue that grows at a strongly positive rate (*b* > 1.4) will represent a larger percentage of the adult body mass. Tissues with intermediate *b* values, however, may not contribute in a predictable manner to adult body composition. For example, the male porpoise heart displays significant negative allometry (*b* = 0.715), yet remains a constant percentage of its total mass throughout growth. Significant differences in ontogenetic allometries between the sexes also do not always

Table 5. Mean ($\pm$ SD) masses and relative body composition of tissues associated with reproduction from harbour porpoises *Phocoena phocoena* of different reproductive classes. Ranges of observed values are given below means. Sample size for each group in parentheses. Significance of ANOVA test to detect differences among arcsine-transformed data is given by *P* value. Mean values with the same letters are not significantly different at $\alpha = 0.05$

Component	*P* value	Calf	Immmale	Matmale	Immfem	Pregnonlact	Lact
Male repro (g)		282 $\pm$ 11 270–290 (3)	401 $\pm$ 126 193–616 (12)	1156 $\pm$ 252 636–1665 (27)	–	–	–
Male repro % body mass	< 0.000	0.96 $\pm$ 0.12 0.86–1.09 a	1.13 $\pm$ 0.26 0.66 $\pm$ 1.60 a	2.46 $\pm$ 0.43 1.53 $\pm$ 3.41 b	–	–	–
Testes mass (g)		19 $\pm$ 5 12–26 (5)	46 $\pm$ 28 11–116 (20)	325 $\pm$ 137 109–718 (45)	–	–	–
Testes mass % body mass	< 0.000	0.07 $\pm$ 0.02 0.05–0.10 a	0.13 $\pm$ 0.07 0.03–0.33 b	0.69 $\pm$ 0.26 0.26–1.47 c	–	–	–
Female repro (g)		124 $\pm$ 20 100–161 (6)	–	–	196 $\pm$ 121 92–471 (13)	676 $\pm$ 148 513–801 (3)	1096 $\pm$ 192 906–1350 (4)
Female repro % body mass		0.39 $\pm$ 0.04 0.33–0.44 a	–	–	0.48 $\pm$ 0.24 0.25–1.02 a	1.29 $\pm$ 0.17 1.09–1.39 b	1.73 $\pm$ 0.27 1.40–2.06 b
Mammaries mass (g)		–	–	–	55 $\pm$ 18 32–87 (8)	74 $\pm$ 23 45–101 (4)	732 $\pm$ 148 527–875 (8)
Mammaries % body mass	< 0.000	–	–	–	0.14 $\pm$ 0.04 0.08–0.19 a	0.14 $\pm$ 0.05 0.07–0.18 a	1.16 $\pm$ 0.26 0.76–1.46 b
Pelvics (g)		9 $\pm$ 5 4–20 (10)	19 $\pm$ 7 10–36 (14)	49 $\pm$ 15 24–94 (27)	10 $\pm$ 2 6–14 (15)	22 $\pm$ 6 16–30 (4)	30 $\pm$ 10 20–45 (6)
Pelvics % body mass	< 0.000	0.03 $\pm$ 0.02 0.01–0.06 a	0.05 $\pm$ 0.02 0.03–0.09 b	0.10 $\pm$ 0.02 0.06–0.17 c	0.02 $\pm$ 0.01 0.02–0.04 a	0.04 $\pm$ 0.01 0.03–0.05 ab	0.04 $\pm$ 0.02 0.03–0.07 ab

result in sexually dimorphic, adult body compositions. Although the direction of growth (i.e. isometry, positive and negative allometry) of a component may not always be predictive of its contribution to adult body composition, it does indicate the rate at which that component must grow to achieve that contribution.

Ontogenetic allometries and body composition patterns shared by female and male porpoises

Both female and male harbour porpoises show: (1) positive allometry in their axial, abdominal and total muscles; sternum and pelvic bones; stomach and reproductive tissues; (2) isometry in sternos muscles, vertebral column, ribs, scapula, kidneys and pancreas; (3) nega-

tive allometry in blubber, brain and skull. Both female and male porpoises also display similar changes in body composition as they grow. In the adults of both sexes, the percentage of total body mass allocated to (1) total muscle, lung, liver, empty stomach, mesenteric lymph node and reproductive tissues increase, (2) vertebral column, total bone and heart remain constant, and (3) blubber and brain, decrease. These patterns of growth for major body components are discussed in more detail later.

Blubber

In all porpoises, the combined masses of blubber and total muscle account for 50–60% of total mass, but the
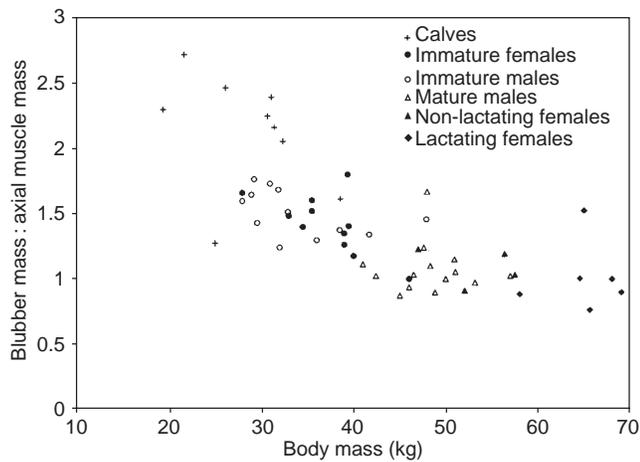
Fig. 2. The ratio of blubber mass to axial muscle mass plotted against total body mass for different reproductive classes of harbour porpoises *Phocoena phocoena*. Calves tend to possess two to three times more blubber mass than axial muscle mass. As harbour porpoises mature they reduce the mass of blubber relative to that of axial muscle mass.

Fig. 3. The mass of reproductive tissue (testes or mammaries) plotted against total body mass for harbour porpoises *Phocoena phocoena*. Female porpoises maintain *c*. 100 g of mammary tissue until they first become reproductive at which point mammary mass undergoes a step increase to > 500 g. Testicular mass increases continuously, reaching masses similar to that of mammary tissue in females.

relative proportions of these tissues change significantly during growth (Fig. 2). While total muscle grows positively allometrically, blubber displays strong negative allometry, and, thus, represents a smaller percentage of total body mass as the porpoise matures. This pattern of relative blubber to muscle mass was noted by Lockyer (1995*a*,*b*) for harbour porpoises in the waters surrounding the U.K.

The negatively allometric growth of blubber means that calves possess relatively more blubber than any other reproductive class investigated in this study. Porpoise calves allocate significantly more of their total body mass to blubber (37%), than all other porpoise reproductive classes (mean = 27%) (see Table 4). Lockyer (1995*a*,*b*) reported that neonatal porpoises, a reproductive class not available in this study, allocated 43% of their total body mass to blubber. The relatively large percentage of total body mass allocated to blubber by neonates and calves may contribute to pos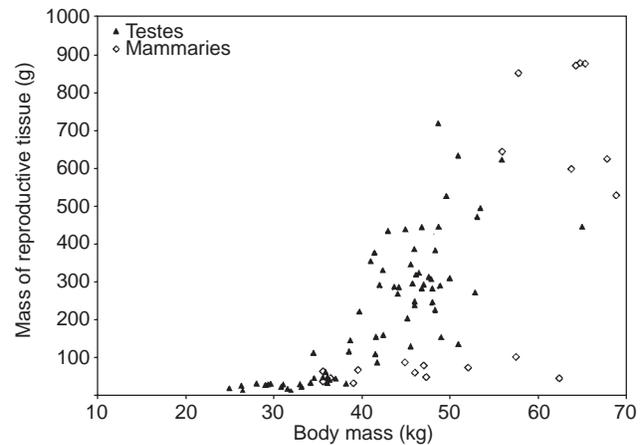itive buoyancy, short-term energy storage and increased thermal insulation during these vulnerable life history stages. Porpoise calves also have thicker blubber than any other reproductive class (Read, 1990*b*; Koopman, 1998). Increased insulation from blubber would function to decrease heat loss to the environment during the growth period when porpoises have a disadvantageously large surface area to volume ratio. This hypothesis, similar to that proposed by Lockyer (1995*a*,*b*), Koopman (1998) and Read (1990*b*), could be tested by measuring thermal conductance properties of blubber from different reproductive classes.

Miyazaki *et al.* (1981) offer the most reliable comparative data available for another small-bodied odontocete, the striped dolphin *Stenella coeruleoalba*. Striped dolphins, > 2 years old, allocate 14–19.2% (mean 17.3%) of their total body mass to blubber. Thus,

not only do porpoise calves possess significantly more blubber than adults, but adult porpoises possess relatively more blubber than striped dolphins (see also Worthy & Edwards, 1990).

The contribution of blubber to the adult total body mass of larger cetacean species varies: 23–24% for long-finned pilot whales *Globicephala melas* (Lockyer, 1993), 15% for minke whales *Balaenoptera acutorostrata*, 18–24% for fin whales *B. physalus*, 27% for blue whales *B. musculus*, 31–32% for sperm whales *Physeter macrocephalus*, and 43% for right whales *Balaena glacialis* (data reported in Lockyer, 1991). Thus, despite their small body size, adult harbour porpoises do not seem to allocate disproportionately more of their total body weight to blubber than do some larger cetacean species.

Musculoskeletal system

The musculoskeletal system, although continuously growing and changing, must function at all ages to provide those forces required for movement and support (Carrier, 1983). The force generating capacity of a muscle is a function of its physiological cross-sectional area. Thus, if a muscle grows at a rate proportional to total body mass$^{1.0}$, the relative force generating capacity of the muscle would decrease as the animal grows (Carrier, 1983; Stewart & German, 1999). In porpoises, as in rats (Stewart & German, 1999) and rabbits (Carrier, 1983), total muscle mass increases at a significantly higher rate than total body mass. Miyazaki *et al*. (1981) also report that growth of total muscle mass in striped dolphins is positively allometric. Muscle mass also grows at a higher rate than skeletal mass in porpoises, as it does in rats (Hurov *et al.*, 1988) and striped dolphins (Miyazaki *et al.*, 1981). This positive

allometric growth, at least in part, contributes to maintaining muscle strength as the animal grows (Hurov *et al.*, 1988; Stewart & German, 1999).

The dissection technique used in this study allows one to investigate the growth of individual muscle components. The axial and abdominal muscles, both considered locomotor muscles in cetaceans (Arkowitz & Rommel, 1985; Pabst *et al.*, 1998), increase in relative mass as porpoises grow. Dearolf *et al.* (2000) also noted that the axial muscles of bottlenose dolphins *Tursiops truncatus* increase as a percentage of total body mass during development, and attributed this growth to increased functional demands of swimming. Bryden (1969) noted a similar growth pattern for the spinal muscles of elephant seals, soon after the pups became aquatic, and likewise attributed the growth of these muscles to their specific role in powering swimming. This functional hypothesis is consonant with the developmental pattern of the axial and abdominal muscles seen in porpoises. The hypothesized relationship between locomotor muscle performance and growth could be tested explicitly by comparing those architectural features of muscle that control force generating capacity and excursion potential (e.g. Carrier, 1983; Pabst, 1993) across reproductive classes of porpoises.

Brain and viscera

Brain growth is the most negatively allometric of any body component investigated in this study, with a growth coefficient similar to that reported for striped dolphins (Miyazaki *et al.*, 1981) and elephant seals (Bryden, 1972). Negative allometry in brain growth is typical for mammals (Pagel & Harvey, 1990).

Unlike the brain, most other organs of harbour porpoises grow at isometric or positively allometric rates. Except for the heart and spleen, all organs (even those that grow isometrically) represent a larger percentage of the adult body mass than they do in calves. This pattern of high growth rates for viscera is different than that reported in rats, where visceral growth rates are strongly, negatively allometric (von Bertalanffy & Pirozynski, 1952; Stewart & German, 1999). Organ growth rates in *Stenella* spp. vary from 0.6 to 1.1, although whether these rates differ from isometry is not clear (Perrin & Roberts, 1972; Miyazaki *et al.*, 1981). Thus, although comparative samples are rare, the thoracic and abdominal viscera of harbour porpoises seem to grow at rates higher than those of other mammals.

Reproductive tissues

The reproductive tissues of female and male porpoises display the highest growth rates of any body component (Fig. 3). While the female reproductive tract achieves its final adult contribution to total body mass in mature, non-lactating females, it is not until lactation begins that the mammaries reach their adult morphology. The male reproductive tract and the pelvic bones, upon which it is anchored, grow at similarly high rates ($b = 2.5$–2.8). The pelvic bones provide the skeletal origin for the crura of the fibroelastic penis of cetaceans (Pabst *et al.*, 1998). The high growth rates of the pelvic bones suggests that although these elements no longer provide support for hind limbs, they play an important role for support of the external genitalia. The testes increase in mass over 17-fold, and grow at the highest rate of any tissue measured in porpoises ($b = 5.054$). The only other published ontogenetic allometry for testes of which we are aware, is for Sprague–Dawley rats, where $b = 0.881$ (Stewart & German, 1999). Thus, the testicular growth rate for harbour porpoises is extremely high.

Reproduction is highly seasonal in harbour porpoises from the Gulf of Maine/Bay of Fundy (Read, 1990*a*; Read & Hohn, 1995). Because porpoises used in this study were collected across multiple seasons, the mass of some reproductive tissues could reflect both growth and seasonal changes. For example, Neimanis *et al.* (2000) report that harbour porpoises in the Gulf of Maine/Bay of Fundy display peak testis mass in early July. For mature males in this sample, testis mass did decline from summer to autumn, although no such differences were observed for immature males. Thus, growth rates and body composition data for testes do not reflect a single reproductive condition in mature males. Likewise, there may be seasonal differences in milk production in lactating females. The small samples sizes of mature porpoises in this study did not allow for stratification by season.

Ontogenetic allometries that differ between female and male porpoises

While most body components grow similarly in females and males, the heart, liver, mesenteric lymph node, and intestines grow at significantly higher rates in females than in males. Contrarily, in males, the axial, abdominal and total muscle, and pelvic bones grow at higher rates than in females. These sexual dimorphic ontogenetic allometries seem to prepare each sex for their early maturation and annual reproductive schedule.

Female harbour porpoises grow at a faster rate and achieve larger sizes than males (reviewed by Read & Tolley, 1997). Read & Tolley (1997) hypothesized that these growth patterns facilitate early reproduction, and permit the birth of relatively large offspring. The accelerated growth rates of visceral body components observed in this study support these hypotheses, and further suggest that the female body is specialized for processing food for the energetically costly demands of lactation.

Once a female harbour porpoise reaches 3 years of age, she will enter an annual reproductive schedule; thus, she will be simultaneously pregnant and lactating for most of her life (Read, 1990*a*; Read & Hohn, 1995). Lactation, which represents the largest energetic cost of

reproduction for female mammals, must be fuelled by increased rates of food consumption in species without large fat reserves (e.g. Pond, 1998; Costa & Williams, 1999). Lactating female porpoises do not seem to rely upon energy stored in their blubber, as their blubber is not significantly thicker than that of non-lactating females (Koopman, 1998). Lactating porpoises from the Bay of Fundy, though, have significantly larger quantities of food in their stomachs than other reproductive classes of porpoises (Recchia & Read, 1989). The primary prey species of Bay of Fundy porpoises is the lipid-rich, Atlantic herring *Clupea harengus* (Recchia & Read, 1989).

The liver, intestines and mesenteric lymph nodes function in the digestion, absorption, transport and processing of foodstuffs, especially lipids (Pond, 1998). The liver, the largest gland in the body, controls carbohydrate, protein and lipid metabolism, and produces bile, which emulsifies digested lipids (e.g. Lehninger *et al.*, 1993). Most ingested, emulsified lipids are absorbed across the intestinal wall, travel through lymph channels to be filtered through the mesenteric lymph nodes, and are subsequently transported *via* the thoracic duct to the circulatory system (Bezuidenhout, 1993; Pond, 1998). This study demonstrates that these three organs display positive allometry in females *vs* isometry in males, and that mature, lactating females allocate a larger percentage of their total body mass to liver than do mature males.

Recchia & Read (1989), as noted above, observed that lactating females eat more herring than other porpoises. Because the intestine mass reported here includes the contents of this organ, it is possible that the observed pattern of positive allometry is simply the result of higher feeding rates in lactating females, rather than real differences in growth rates between the sexes. If the positive allometry was being driven by elevated feeding rates in lactating females alone, it seems likely that this reproductive class would have a significantly higher percentage of their total body weight allocated to these tissues. Interestingly, this pattern is not seen. Immature females, mature/non-lactating, and lactating females allocate a similar percentage of their body mass to liver, intestines, and mesenteric lymph node.

The female heart also grows at a significantly higher rate (isometry) than does that of the male (negative allometry), a pattern that can be interpreted within the context of the annual reproductive schedule of this species. Females experience annual increases in blood volume associated with pregnancy (Bell, 1987). Although the percentage increase in porpoises is unknown, the blood volume of pregnant humans may increase by 50%, and that of pregnant ewes by 7–25% (Bell, 1987). The relatively accelerated growth rate of the female heart may prepare it for the mechanical demands imposed by this continuous cycle of increased blood volume.

Harbour porpoises along the California coast are apparently on a 2-year reproductive cycle, where lactation and pregnancy are separated by a rest period (Hohn & Brownell, 1990). A comparison of growth rates of the female heart and abdominal viscera between the North Atlantic and California populations may offer insights into the functional hypotheses presented here.

While females display accelerated growth rates of selected viscera, males display significantly higher growth rates of some musculoskeletal elements. Total muscle and axial and abdominal locomotor muscles (which together account for 81–84% of total muscle) grow at higher rates in males than in females. Although the mating system of porpoises is unknown, their reverse sexual dimorphism in body size, their large testes (Read, 1990*a*) and the lack of evidence of intra-specific aggression (A. J. Read, pers. obs.) suggest that they are promiscuous breeders (Connor, Read & Wrangham, 2000). A male porpoise's reproductive success may, therefore, be dependent upon his ability to gain access to as many females as possible. Accelerated growth of locomotor muscles may prepare males for high rates, or extended bouts, of locomotor activity required to gain that access. This functional hypothesis could be directly tested by comparing the swimming activities of mature males to those of other reproductive classes. Interestingly, mtDNA genetic studies of British porpoises have demonstrated that males range further geographically than females (Walton, 1997).

The abdominal muscle group also includes the rectus abdominus and ischiocaudalis, both of which are anchored to the pelvic bones. The pelvic bones, which grow at a highly accelerated rate relative to those of females, function as the bony anchor for the tissues of the male reproductive tract, including the external genitalia. The male reproductive tract, pelvic bones, and caudal abdominal muscles probably form an integrated unit that functions in supporting copulatory behaviour.

As one of the smallest cetaceans, harbour porpoises face a myriad of challenges to life in a cold, conductive medium. Porpoises meet these challenges by investing heavily in tissues that allow them to stay warm and maintain an intensive reproductive schedule. In particular, female porpoises are well adapted to process a large quantity of lipid-rich prey and to provide their calves with the large volume of milk that is needed to deposit and maintain a thick blubber layer.

SUMMARY

The growth of harbour porpoises in the western North Atlantic is characterized by a relatively large investment in blubber as calves (37% of total body mass), which may contribute to positive buoyancy, short-term energy storage and increased thermal insulation during vulnerable life history stages. Growth rates of muscle, viscera and reproductive tissues are high, and the growth rate for testes is the highest reported for any mammal. Female porpoises display significantly accelerated growth of their heart, liver, intestines and mesenteric lymph node relative to males. These high rates of

growth are hypothesized to prepare the heart for the mechanical demands of annual increases in blood volume associated with pregnancy, and the abdominal viscera for accelerated rates of processing lipid-rich prey to fuel the energetic costs of lactation. Males display significantly accelerated growth of locomotor muscle, which may prepare them for the intensive swimming activity required to gain reproductive access to females. Overall, growth rates for many body components are high in porpoises, which seems to contribute to their early maturation.

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