

ARTICLE

Marine Mammal Science



Allocation and use of body energy reservoirs in striped dolphins and Blainville's beaked whales: Snowball effect in negative energetic balance

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Funding information

H2020 Marie Skłodowska-Curie Actions (Y. Bernaldo de Quirós), Grant/Award Numbers: H2020-MSCA-IF-GF-2019, "ArterialAging" #89227; Office of Naval

Abstract

Climate change, overfishing, and other anthropogenic activities can negatively impact the energetic balance and body condition of cetaceans. Still, cetaceans must meet their energetic demands for survival, which are more expensive to maintain in the marine environment. The resilience of cetaceans to negative energy balance periods is unknown. We analyzed where striped dolphins, a medium-sized dolphin with shallow-intermediate diving habits, and Blainville's beaked

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Research Global, Grant/Award Number: N00014-13-1-0773; Ministry of Science, Innovation and Universities, Spanish Government, Grant/Award Number: PGC2018-101226-B-I00; Margarita Salas Postdoctoral Call-2021 (M.Arregui), Ministry of Science, Innovation and Universities, Spanish Government; Canary Islands Government has helped fund the Canary Islands stranding network

whales, a larger odontocete with an extreme diving profile, store their energy reserves and how they use that energy. We performed dissections of body mass compartments of fresh dead adults of similar total body lengths but different body masses, determined the lipid and protein content of blubber and muscle, and calculated oxygen stores and the aerobic dive limit. Proteins in muscle were the largest source of energy stores for both species, followed by lipids in the blubber and muscle. Both species catabolized blubber and muscle simultaneously when losing body mass to avoid impairing other important functions. When these functions are impaired, a cascade of increased field metabolic rate and decreased energy intake may occur, decreasing their resilience to environmental challenges and making them more susceptible to diseases, ultimately resulting in death by starvation.

KEYWORDS

adaptations, bioenergetics, body condition, catabolism, climate change, conservation, emaciation, resilience, response

1 | INTRODUCTION

Concern about the ocean's health is increasing due to climate change and the impact of human activities (Halpern et al., 2015; Schuldt et al., 2016; Slenning, 2010; van Weelden et al., 2021). Cetaceans are important sentinels of the ocean's health since they have long life spans, thus experiencing an accumulation of impacts throughout their life. Also, many species feed at a high trophic level, which makes them susceptible to any change in the trophic chain (Aguirre & Tabor, 2004; Moore, 2008; Reddy et al., 2001). Climate change (Cunningham et al., 2021; Gallagher et al., 2022; von Biela et al., 2019) and overfishing (FAO, 2012), among other anthropogenic disturbances, can negatively impact the energy balance of cetaceans by reducing prey abundance and energy density. However, the resilience of cetaceans to the shortage of prey availability remains unknown. Cetaceans, as mammals, must continue to meet their energetic demands for thermoregulation, reproduction, and growth while diving to forage (McHuron et al., 2022). Their body energy reserves diminish, potentially resulting in poor body condition if the balance between energy intake and energy expenditure is negatively altered (Castrillon & Bengtson Nash, 2020). Body condition has a direct impact on the animal's survival as well as the rates of reproduction and calf survival (i.e., animals with greater energy reserves [good body condition] show higher rates of reproduction and survival) (Hodges et al., 1999; Lockyer, 1986; Millar & Hickling, 1990; Milner et al., 2003). Thus, suboptimal body condition can adversely impact the conservation of a given population.

Lipids are the most efficient source for energy production, containing two times more energy (per gram) than proteins (Brody, 1968). Lipids can be stored as discrete fat pads within the body cavity (visceral or mesenteric fat), subcutaneously, hypodermis (it is called "blubber" in marine mammals), and as intracellular droplets within tissues (Secor & Carey, 2016). Blubber has historically been considered the most critical site for the storage of energy reserves in marine mammals (Pond, 1978). Energy reserves are also stored in the cetacean's skeletal muscle (onward referred to as muscle) (Lockyer, 1987; Víkingsson, 1995), similar to other terrestrial mammals'

(Barboza & Parker, 2008; Boismenu et al., 1992). However, there is very little research on how starvation affects blubber (Dunkin et al., 2005; Dunkin et al., 2010) or muscle (Stegall et al., 1999). There is even less research on how a reduction in blubber or muscle energy stores would reduce the other functions of those tissues—for example, insulation, buoyancy, locomotion, and oxygen storage (Dunkin et al., 2005; Dunkin et al., 2010; Farmer et al., 2018; Rosen et al., 2007). If any of these functions are altered, there could be increased metabolic demands, resulting in a positive feedback loop of increased tissue catabolism to account for increased energy demands, compromising the health and survival of the animal (Rosen et al., 2007).

Studies of changes in body composition and preferential tissue usage during starvation in marine mammals have focused primarily on pinnipeds and baleen whales (Castellini & Rea, 1992). Baleen whales and some pinnipeds are capital breeders such that they store energy during the feeding season and later utilize it for reproduction and restorative processes (e.g., molting and wound healing), which often occur when the animal is fasting (Lockyer, 1986; Lockyer, 1987; Slip et al., 1992). Thus, their body condition varies with reproductive class and migratory stage (Irvine et al., 2017). Fewer studies have focused on the changes in body condition in toothed whales, which, unlike baleen whales, are income breeders with relatively constant body conditions assuming sufficient prey consumption (Derous et al., 2020; Irvine et al., 2017).

Income breeders (most dolphins) must feed continuously throughout the year to maintain their body condition. Thus, they require more stable or predictable environments, making them less resilient to starvation and more susceptible to acute environmental disturbances than capital breeders (Farmer et al., 2018; Irvine et al., 2017; Kastelein et al., 2019). Kastelein et al. (2019) found that harbor porpoises (*Phocoena phocoena*, Linnaeus, 1758) lose 4% of their body mass after 24 h of fasting and that blubber mass decreased. An increase in free fatty acids and other lipid metabolites together with a reduction in amino acids and creatinine was measured in the plasma of common bottlenose dolphins (*Tursiops truncatus*, Montagu, 1821) after a similar period of fasting, suggesting the utilization of lipids and preservation of proteins (Houser et al., 2021). The existing literature suggests that there might be interspecies differences in strategies regarding the anatomical location of the energy reservoirs, following ecophysiological constraints, but the evidence is scarce. For example, blubber seems to be the largest energetic reservoir for striped dolphins (*Stenella coeruleoalba*, Meyen, 1833), a shallow diving species (Gómez-Campos et al., 2011), whereas muscle has been reported to be the greatest energy reservoir for deep-diving long-finned pilot whales (*Globicephala melas*, Traill, 1809) (Lockyer, 1993).

Since little is known about the use of energy stores in cetaceans that are income breeders, and since these species might be more susceptible to environmental disturbances, the aims of this study were as follows: to compare the body composition (i.e., where the animals store their energy reserves) of two income-breeding cetaceans that have very different foraging and diving habits, to determine how their body composition changes with body condition (i.e., how they use these reserves during negative energy balance), and to provide a framework regarding how these changes in body condition may affect the other important functions of these tissues and their energetic consequences. For this study, we have selected the striped dolphin, a medium-sized dolphin of shallow-intermediate diving habits, and the Blainville's beaked whale (*Mesoplodon densirostris*, Blainville, 1817), a larger-sized odontocete with an extreme diving profile. To study how these species use their energy reserves, we compared specimens of similar total body length (TBL) but with very different total body masses (TBMs) and used animals in good body condition as a reference for the optimal quantity of energy reserves.

2 | MATERIAL AND METHODS

2.1 | Animals

Dissections of body mass compartments were conducted on seven striped dolphins and one Blainville's beaked whale stranded in the Canary Islands, Spain (Table 1). To assess body condition, the seven striped dolphins were

TABLE 1 Biological and body composition data of the seven striped dolphins, one Blainville's beaked whale stranded in the Canaries (CET 824), and two more Blainville's beaked whales obtained from the literature ^(a): PEM1519/70 (Ross, 1984) and WAM593 (Pabst et al., 2016).

Species	Identification code	Life history category	Sex	TBL (cm)	TBM (kg)	Integument (kg) (TBM %)	Muscle (kg) (TBM %)	Bones (kg) (TBM %)	Visceral organs (kg) (TBM %)	Cause of stranding and/or death
Striped dolphin	CET 748	SA	M	195	74	11.4 (15.3)	34.1 (46.0)	9.1 (12.2)	7.7 (10.4)	Stress response syndrome
	CET 750	A	F	214	87	10.3 (11.7)	43.0 (49.0)	11.2 (12.8)	14.2 (16.1)	Infectious pancreatitis and hepatitis
	CET 787	A	M	211	75	11.3 (15.0)	38.2 (51.0)	9.4 (12.5)	9.8 (13.0)	Multiorgan parasitosis
	CET 802	A	M	215	92	14.4 (15.6)	41.8 (45.5)	11.2 (12.1)	12.4 (13.5)	Infectious encephalitis
	CET 837	A	M	188	70	10.5 (15.0)	29.4 (41.8)	6.9 (9.7)	9.7 (13.7)	By-catch
	CET 1034	A	F	200	74	7.9 (10.7)	37.3 (50.4)	7.6 (10.3)	12.0 (16.3)	Stress response syndrome
	CET 1063	A	M	203	111	14.2 (13.0)	56.8 (52.0)	9.3 (8.5)	13.1 (12.0)	Stress response syndrome, infectious pneumonia
Mean ± SD				204 ± 10	83 ± 15	11.4 ± 2 (13.7 ± 2)	40.1 ± 9 (50.0 ± 4)	9.2 ± 2 (11.2 ± 2)	11.3 ± 2 (13.6 ± 2)	
Blainville's BW	WAM 593 ^a	A	F	423	940	182.36 (19.4)	455.9 (48.5)	84.6 (9.0%)	45.12 (4.8)	
	PEM 1519/70 ^a	A	M	456	1034	218.1 (21.1)	495.0 (47.9)	93.0 ^b (9.0)	49.61 ^b (4.8)	
	CET 824	A	F	454	820	136.31 (16.6)	278.2 (33.9)	70.2 (8.6)	44.36 (5.4)	Cerebral nasitremitiasis

Note: Compartment size for bones and visceral organs was not reported for PEM1519/70. Given the similarities in relative compartment size for integument and muscle with WAM593, the relative compartment size of bones and visceral organs was assumed to be the same as in WAM593 ^(b). Abbreviations: A, adult; BW, beaked whale; F, female; M, male; SA, subadult.

evaluated along with data from 39 other striped dolphins stranded in the Canary Islands, Spain. Similarly, the body condition of Blainville's beaked whales was examined in comparison with 11 more Blainville's, whose data were obtained from stranded individuals in the Canary Islands, from the literature (Pabst et al., 2016; Ross, 1984) and from archives (Smithsonian National Museum of Natural History Collection). For lipid and protein content in blubber and muscle, and for muscle myoglobin concentration, we analyzed samples of two additional Blainville's beaked whales from our tissue bank (CET852; i301/14). All data and samples were collected from dead, individually stranded cetaceans (Geraci & Lounsbury, 2005). Only animals in fresh condition (code 2) or with incipient autolysis signs (early code 3: mild changes in coloration and the presence of gas in the intestines, but with no relevant changes in coloration or texture in other organs) were included (Ijsseldijk et al., 2019). Dissections of body mass compartments were performed either within 24 hr of notice of the stranding (CET748, CET750, and CET824) or following immediate storage at -4°C . For thawing, dolphins were submerged in water at 4°C . No experiments were performed on live animals. Permission for the handling of stranded cetaceans was granted by the Spanish Ministry of Environment.

Only adults and subadults were included in this study to avoid ontogeny-related changes in body composition. Pregnant females were not included in the study. We define adults as sexually mature specimens and subadults as specimens that have reached the length of sexual maturity for that species but possess immature gonads: 190 cm males and 184 cm females for striped dolphins, as well as 376 cm males and 384 cm females for Blainville's beaked whales. For striped dolphins, these length thresholds were established based on sexually mature dolphins (i.e., determined histologically) stranded in the Canary Islands, Spain. For Blainville's beaked whale, lengths were established according to existing literature (Allen et al., 2011; Best & Folkens, 2007; Ross, 1984) and by measuring stranded animals in the Canary Islands.

2.2 | Body condition

The body condition of 46 striped dolphins stranded in the Canary Islands was assessed through linear regression analyses of their TBM, TBL, TBM/TBL, TBM/TBL^2 (Quetelet's index), and TBM/TBL^3 (Fulton's index) (Peig & Green, 2010). These analyses were used to determine the best body condition index independent of TBL. Further statistical analyses were only carried out with the best body condition index. Sexual dimorphism (males, $n = 28$; females, $n = 17$) of the best body condition index was explored using two independent samples Mann–Whitney U test.

The body condition of 12 Blainville's beaked whales was similarly explored. Sexual dimorphism for TBL has not been described for this species (MacLeod, 2006) and was not further explored given our low sample size (males, $n = 8$; females, $n = 4$).

2.3 | Volume and whole-body density calculations

Volume was rendered from computed tomography (CT) images, when possible, for a subset of animals stranded on the island of Gran Canaria, Canary Islands, where access to a CT scan was available. We performed two scans: apex rostrum until vertebrae 53 and vertebrae 53 to the end of the fluke. Three-dimensional images were obtained from the DICOM files with the software Horos 2.0.2. and converted into multiple polygons using Cinema 4D r23, from which volume was calculated using Powershape 2020. The total volume of those animals for which we only had the first scan up to vertebrae 53 was calculated by adding the volume from vertebrae 53 to the end of the fluke of another dolphin of matched length. This calculation was based on the assumption that blubber from caudal tailstock is less metabolically labile than the trunk blubber with no changes in integument density with body condition (Castrillon & Bengtson Nash, 2020; Dunkin et al., 2010; Gómez-Campos et al., 2011; Koopman et al., 1996; Pabst et al., 1999). Whole-body density was calculated as $\text{TBM} / \text{total body volume}$.

2.4 | Dissections of body mass compartments

Body carcasses, excluding cranial soft tissues, were dissected into discrete anatomical components (integument, muscle, organs, and bones) following McLellan et al.'s (2002) mass dissection protocol and weighed separately. Organs were opened and cleaned of fluids as much as possible. Whole body blood volume was not measured separately. The relative contribution of each body compartment to body composition was calculated as (compartment mass/carcass TBM \times 100), as described by Grand (1977).

At necropsies, blubber samples were taken at approximately 5 cm anterior to the dorsal fin and 5 cm ventral to the dorsal ridge on the left side, integrating the entire tissue depth. Also, muscle samples were collected from the middle of the *longissimus dorsi*. Samples were stored at -80°C for future lipid, protein, and myoglobin analyses.

2.5 | Body composition versus body condition

The body composition of all animals was analyzed and compared, but to better understand how body composition changes with body condition, we compared animals of the same species with similar TBL but different TBM. Given the similarities in TBL, we assumed that the TBM and body compartment size (weight) would have been the same if both animals had similar body conditions. Thus, the TBM and body compartment size of the animal with a higher TBM was considered as the ideal TBM and compartment size for that particular TBL. The difference between the ideal weight and the actual weight of the animal with a lower TBM was interpreted as mass loss for that animal.

Given the difficulty in accessing and studying fresh Blainville's beaked whale specimens, the results from our study were complemented with previously published data (Pabst et al., 2016; Ross, 1984). The body composition data from one of these Blainville's beaked whales (WAM593) were directly comparable with ours since the same dissection methods and body compartment definitions were used. In contrast, the other Blainville's beaked whale (PEM1519/70) was weighed in pieces and corrected for 10% loss of body fluids during dissection (Ross, 1984) (Table 1).

2.6 | Blubber and muscle lipid and protein content

Blubber and muscle lipid and protein content were assessed in the seven striped dolphins and the one Blainville's beaked whale. Given the scarce data in the literature for lipid or protein content in Blainville's beaked whales, we analyzed samples of two additional Blainville's beaked whales from our tissue bank (CET852; i301/14). Unfortunately, we did not have the TBM of these animals, only body condition estimates based on external appearance. Hence, these whales were only included in this section and for myoglobin determination to provide additional data for Blainville's beaked whales.

Three samples per animal of 0.5 g of blubber, located approximately 5 cm anterior to the dorsal fin and 5 cm ventral to the dorsal ridge on the left side integrating the entire tissue depth, and 0.5 g of middle *longissimus dorsi* were analyzed for lipid content. Samples were diluted in 16 ml chloroform/methanol (2:1), homogenized (IKA Ultra-Turrax T18), and left on ice for 1 hr. Then, 4 ml of 0.88% KCl was added, mixed, and incubated on ice for 10 min. Samples were centrifuged at 8,000 g for 15 min at 4°C (Eppendorf, Centrifuge 5804 R). Afterward, the chloroform-lipid phase (lower phase) was transferred to a preweighed tube, evaporated to remove the solvent under a stream of N_2 , and weighed to calculate lipid percentage. The mean lipid content for the three replicates was calculated and plotted against the body condition index determined to be the best metric independent of TBL. The relation between lipid content and body condition was examined using simple linear regression. Lipid extracts were stored at -80°C until sample preparation for NMR experiments (detailed below).

To determine protein content, blubber (~ 1 g) and muscle samples (~ 0.5 g) were analyzed following Kjeldahl (1883). Blubber samples were first digested in 25 ml of 98% sulfuric acid at 400°C for 75 min in the presence

of 10 g catalyst (9.34 g SO_4K_2 + 0.56 g SO_4Cu + 0.09 g Se), resulting in a solution of ammonium sulfate. Muscle samples were first digested in 20 ml of 98% sulfuric acid at 400°C for 60 min in the presence of 10 g catalyst (9.8 g SO_4K_2 + 0.2 g SO_4Cu). Then, ammonium sulfate was distilled, and ammonia was retained in 0.5 M boric acid. Finally, the amount of ammonium ion concentration was calculated by titration using HCl 0.1 N.

The total lipid and protein content in the blubber and the muscle were calculated by multiplying the lipid and protein percentage by the integument or muscle mass. Linear regression studies were used to analyze the total lipid and protein content against the best body condition index for stripped dolphins. Lipid and protein loss or usage with body condition was calculated by subtracting the total lipid and protein content of animals in poorer body conditions from animals in better body conditions of similar TBL. Blubber and muscle lipid and protein content were not reported for PEM1519/70 or WAM593. To calculate total lipid and protein values in blubber and muscle, we used the lipid percentage in blubber reported by McClelland et al. (2012) in a robust Blainville's beaked whale and the highest value from our analyzed whales for all calculations as our best estimate. We multiplied the lipid and protein percentage by PEM1519/70's blubber and muscle mass. Finally, lipids and proteins were converted into kilocalories, as previously described (Brody, 1968), to estimate energy expenditure from each tissue compartment.

2.7 | Blubber and muscle lipid composition by NMR

Lipid extracts were analyzed by NMR following standard procedures (Tugnoli et al., 2003). The peak assignment was confirmed with information from databases and literature (Scano et al., 2005; Wishart et al., 2018). Signals were quantified automatically with an integration template in Mestre Nova 12 and normalized to total intensity. Normalized integration values were used in the multivariate analysis with SIMCA 16 (Umetrics).

To assess changes in the blubber and muscle lipid composition of striped dolphins, animals were divided into two groups following a Quetelet's index above or below the median (19.8 kg/m^2). For principal component analyses, tables were unit-variant-scaled, and partial least squares regression was validated with permutation and cross-validation (Li et al., 2016). For univariate analysis, multiple Mann-Whiney tests were used, and the q -value (p -value adjusted for a 5% false discovery rate) was considered to establish statistical significance. In the case of the Blainville's beaked whale, the animals were compared based on their external evaluation of body condition. However, no statistical tests were conducted, given the small sample size.

2.8 | O_2 stores

Total body O_2 stores were calculated as the sum of the lung, blood, and muscle O_2 stores. For the lung, we assumed that each animal dove on total lung capacity (TLC) and that the fraction of O_2 available was 15% of the TLC. The estimated TLC (TLCest) for the dolphin was estimated by the equation developed for small- to medium-sized cetaceans (TBM in kilograms) (Fahlman et al., 2011; Kooyman, 1973):

$$\text{TLCest (L)} = 0.135 \times \text{TBM}^{0.92}.$$

For beaked whales, we assumed that TLCest was similar to the value reported for the northern bottlenose whale (*Hyperoodon ampullatus*) of 25 ml kg^{-1} (Miller et al., 2016; Scholander, 1940).

For blood O_2 stores, we assumed that the blood volume for the striped dolphin was equal to the common bottlenose dolphin of 7.4% of TBM (Ridgway & Johnston, 1966), while for the Blainville's beaked whale, it was estimated as the reported blood volume for the sperm whale (*Physeter macrocephalus*, Linnaeus, 1758) of 20% of TBM (Sleet et al., 1981). The hemoglobin concentration ($[\text{Hb}]$, g dl^{-1}) was assumed to be equal to the bottlenose dolphin (14 g dl^{-1}) (Ridgway & Johnston, 1966) and sperm whale (22.9 g dl^{-1}) (Sleet et al., 1981) for the striped dolphin

and beaked whale, respectively. The total volume was divided into arterial (33%) and venous (67%) blood with arterial being fully saturated and venous at 75% saturation.

For muscle O_2 stores, we used the measured muscle mass for each individual animal and multiplied it by the measured myoglobin concentration (g myoglobin 100 g^{-1} muscle) at the middle of the *longissimus dorsi* following Arregui et al. (2021). For PEM1519/70 or WAM593, we used the same measured Mb of our Blainville's beaked whale (CET824) and multiplied it by the muscle mass reported for those whales.

2.9 | Resting metabolic rate calculation and calculated aerobic dive limit (cADL)

Oxygen consumption ($\dot{V}O_2$) in $L\ O_2\ \text{min}^{-1}$ at rest or resting metabolic rate (RMR), as well as mass-specific metabolic rate (sRMR or $s\dot{V}O_2$) in $ml\ O_2\ \text{min}^{-1}\ \text{kg}^{-1}$ for striped dolphins, was estimated using the equations developed from wild bottlenose dolphins inactive in water (Fahlman et al., 2018).

$$\log_{10}[\dot{V}O_2] = -1.28 + 0.43 \cdot \log_{10}[\text{TBM}]$$

$$\log_{10}[s\dot{V}O_2] = \frac{\log_{10}[\dot{V}O_2]}{\text{TBM} \cdot 1000} = \frac{-1.28 + 0.43 \cdot \log_{10}[\text{TBM}]}{\text{TBM} \cdot 1000}$$

For Blainville's beaked whales, RMR and sRMR were calculated as described for an allometric regression of terrestrial mammals by Kleiber (1975):

$$\text{RMR} = \dot{V}O_2 = 0.0093 \cdot \text{TBM}^{0.75}$$

$$\text{sRMR} = s\dot{V}O_2 = \frac{0.0093 \cdot \text{TBM}^{0.75}}{\text{TBM} \cdot 1000}$$

Finally, cADL is the ratio of usable O_2 stores ($ml\ O_2\ \text{kg}^{-1}$) and the rate at which these stores are used, that is, the diving metabolic rate (Butler, 2006). Given that the diving metabolic rate is challenging to measure, the resting metabolic rate ($ml\ O_2\ \text{kg}^{-1}\ \text{min}^{-1}$) was used instead (Burns et al., 2005).

2.10 | Statistics

Simple linear regression was applied using the least square method. Significance was set at $\alpha = 0.05$ and assessed via IBM SPSS 24 and GraphPad Prism 9.4.0. Post hoc computing achieved power for the main outcomes (total lipids in blubber and muscle, and total protein in muscle) was calculated using Free Statistics Calculators 4.0.

3 | RESULTS

3.1 | Body condition and sexual dimorphism

No striped dolphins included in this study were considered emaciated upon external evaluation of the carcass. There was a positive linear relation between TBM and TBM/TBL against TBL and a negative linear relation between Fulton's index (TBM/TBL^3) and TBL (Figure 1). In contrast, the Quetelet's index (TBM/TBL^2) was unrelated to TBL

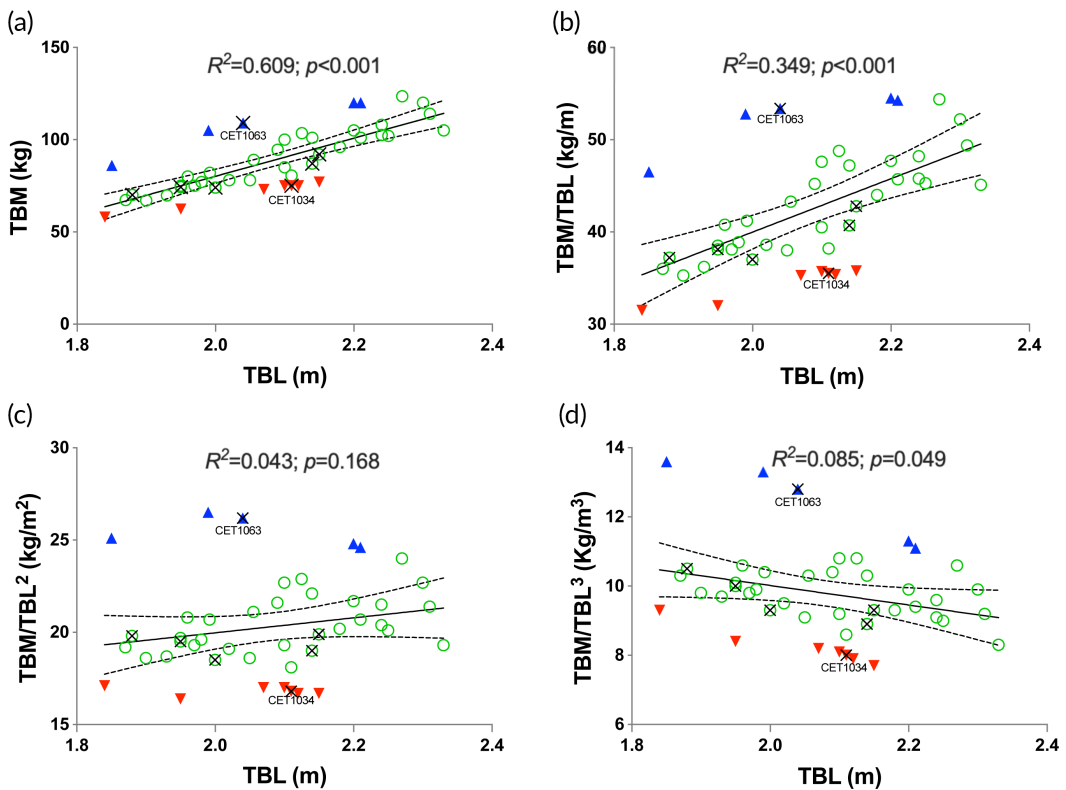


FIGURE 1 Evaluation of body condition index in striped dolphins. The figure shows TBM (a), TBM/TBL (b), TBM/TBL² (c), and TBM/TBL³ (d) against TBL with a confidence interval of 95% of 46 striped dolphins. Dolphins in good body condition (Quetelet's index of ≥ 24.6) are shown in blue triangles, in moderate body condition (Quetelet's index between 17.1 and 24.5) are shown in green open circles, and in poor body condition (Quetelet's index < 17.1) are shown with inverted red triangles. Dolphins with dissections of body mass compartments are additionally marked with black crosses.

($R^2 = .043$; $F = 1.970$; $p = .168$) (Figure 1). Thus, the Quetelet's index was the best body condition index to represent body condition independent of TBL.

The population subset studied for body condition determination ($n = 46$) had a Quetelet's index with a mesokurtic distribution ($G2 = 0.065$) but with a slight positive asymmetry ($G1 = 0.688$) (Figure 2a). To demonstrate which animals were in poorer or better body conditions, we first calculated percentiles 10 (17.0 kg/m²) and 90 (24.7 kg/m²). We then compared these values with the frequency of real values observed by the stem-and-leaf plot (Figure 2b). On the lower end, seven values were ≤ 17.1 kg/m², a close value to 17.0 kg/m² (10th percentile); on the higher end, five values were ≥ 24.6 kg/m². These dolphins were considered as animals in poor or good body condition, respectively. The remaining dolphins falling between these two categories were classified as animals in “moderate body condition.” However, the asymmetry study shows that many had moderate-to-poor body condition (Figure 2). The three categories were well separated in the Quetelet's index against the TBL plot (Figure 1c).

Of the striped dolphins in which we performed dissections of body mass compartments (shown in black crosses in Figure 1), one dolphin (CET1064) clearly had a better body condition than the rest of the animals presenting a Quetelet's index of 26 kg/m², and one dolphin presented a poor body condition (CET787). The remaining five dolphins were in moderate-to-poor body condition—the Quetelet's index of 20 kg/m² or lower.

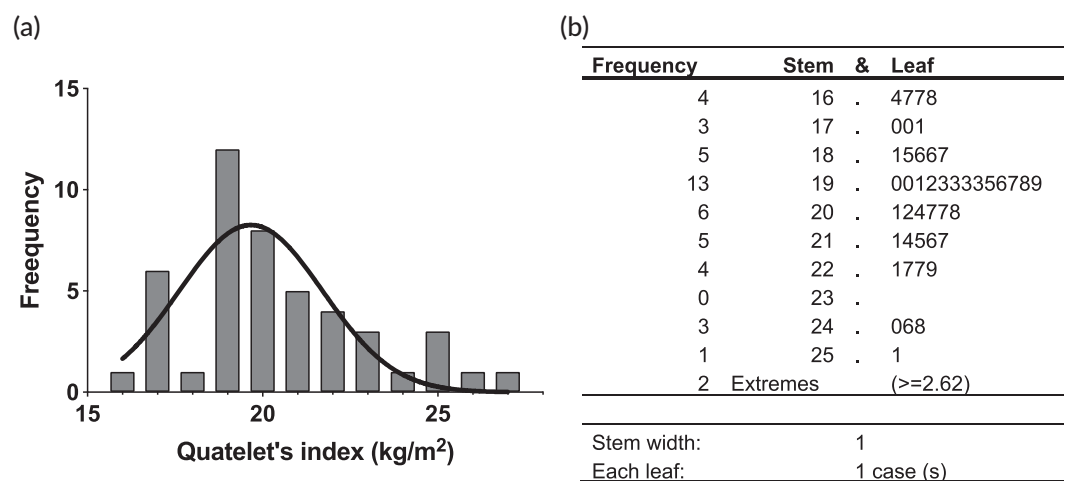


FIGURE 2 Histogram of the Quetelet's index for 46 striped dolphins stranded in the Canary Islands (a), as well as steam and leaf plot (b).

The median and interquartile ranges for male striped dolphins were 20.2 (19.0; 22.4) kg/m² and 19.2 (18.5; 20.6) kg/m² for females. There was no sexual dimorphism for the Quetelet's index ($n = 46$, $Z = -1.604$, $p = .109$) in the subpopulation of striped dolphins; thus, no further differentiation between males and females was pursued.

The Blainville's beaked whale from our study stranded in the Canary Islands (CET 824) had very poor body condition upon external evaluation of the carcass. Many of the animals recovered from the literature were described as “skinny,” similar to our specimen. In contrast, PEM1519/70 and WAM593 were described as in good body condition. Regarding body condition index, the same trends as for striped dolphins were identified: TBM and TBM/TBL index tended to increase with TBL, while Fulton's index decreased with TBL (Figure 3). However, only TBM was statistically related to TBL (Figure 3a). The one index that did not show a trend with TBL was the Quetelet's index ($R^2 = .002$; $F = .230$; $p = .881$) (Figure 3c). Thus, the Quetelet's index was also considered the best body condition index for Blainville's beaked whales.

3.2 | Body composition, volume, and whole-body density

The relative contribution of each compartment to TBM was very similar among the seven striped dolphins, suggesting that body composition varied little with TBM among adult and subadult striped dolphins: $13.7 \pm 2.0\%$ integument, $50 \pm 3.7\%$ muscle, $11.2 \pm 1.6\%$ bones, and $13.6 \pm 2.1\%$ organs (Table 1). The integument, muscle, and organ compartments had higher coefficients of determination with TBM than the Quetelet's index, while the skeleton compartment had a better regression with TBL. The muscle compartment was the only one that was statistically associated ($p = .041$) with body condition (Quetelet's index) and explained over 50% of the variation in body condition ($R^2 = .599$) (Table 2).

We next sought to determine how body composition changes relative to body condition. To accomplish this, we compared the animal that was in better body condition within the specimens studied for body composition, “CET1063,” with the closest dolphin in length, “CET1034,” which showed a moderate-to-poor body condition. These two striped dolphins were similar in length ($\Delta 3$ cm) but with a 37 kg difference in weight (Figure 1a). The relative contribution of each compartment to TBM varied little with body condition: Integument and muscle decreased their contribution to TBM by 2.3% and 1.6%. In comparison, bone and organs increased their contribution to TBM by 1.8% and 4.3%, respectively (Table 1). However, CET1034 had 37 kg less of TBM, of which at least

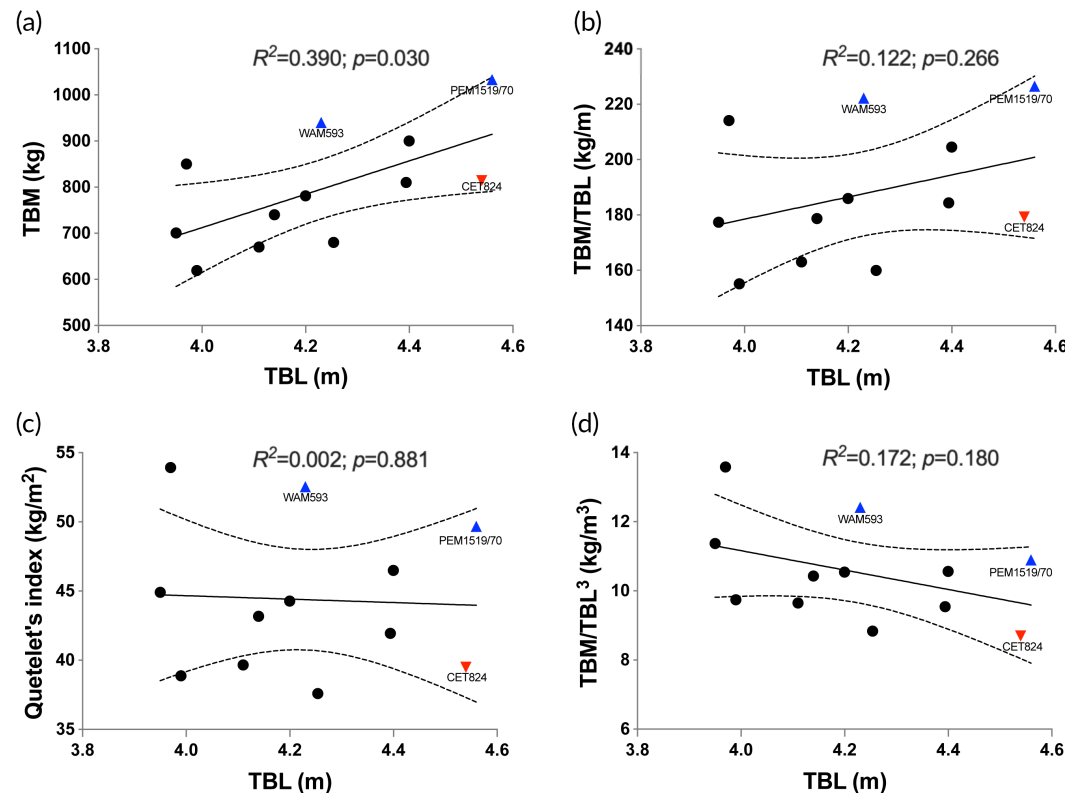


FIGURE 3 Evaluation of body condition index in Blainville's beaked whales: TBM (a), TBM/TBL (b), TBM/TBL² (c), and TBM/TBL³ (d) against TBL with a confidence interval of 95% of 12 Blainville's beaked whales. In (b), PEM1519/70 and WAM593 were in good body condition and are shown in blue triangles, while CET 824 is shown as a red triangle since it was in very poor condition. The rest of Blainville's beaked whales, whose body condition remained unclear, are shown as black dots.

6.3 kg was of integument mass, 19.5 kg of muscle mass, and 1.7 kg of skeleton mass compared with those of CET1063. CET1034 had 44% less integument mass, 34% less muscle mass, and 18% less skeleton mass (Table 3).

These changes in body mass translated into changes in body volume and whole-body density; CET1034 had a volume of 65.6 dm³ and a whole-body density of 1128.4 kg/m³, while CET1063 had a volume of 97.7 dm³ and a whole-body density of 1,136.4 kg m⁻³ (Table 3). Thus, CET1034 was 32.9% smaller in volume (approx. one-third smaller; hence, CET1034 had two-thirds the volume of CET1063). Assuming surface area remained similar, the surface-to-volume ratio for heat loss (following the equations below) was increased by 50%:

1. Dolphin in good body condition : Surface – to – volume ratio for heat loss = $\frac{S}{V}$
2. Dolphin in poor body condition : $\frac{S}{\frac{2}{3}V}$
3. Dolphin in poor body condition : $\frac{3}{2}$ Surface to volume ratio for heat loss = $\frac{S}{\frac{2}{3}V}$

In Blainville's beaked whales, the relative contribution of each compartment to TBM was similar for PEM1519/70 (Ross, 1984) and WAM593 (Pabst et al., 1999): 21.1%–19.4% integument and 48.5%–47.9% muscle

TABLE 2 Summary statistics for the best linear regression fit of body index, in addition to the Quetelet's index, for each body compartment of striped dolphins against TBL.

Compartment	Body index	R^2	F	p-value
Integument	TBM	.526	5.570	.065
	TBM/TBL ²	.323	7.460	.041
Muscle	TBM	.921	57.960	<.001
	TBM/TBL ²	.599	7.460	.041
Skeleton	TBL	.772	19.960	.009
	TBM/TBL ²	.000	.000	.987
Organs	TBM	.431	3.795	.109
	TBM/TBL ²	.155	.917	.382

(Table 1). The relative size of the bone and organ compartments was not reported for PEM1519/70. However, given the similarities with WAM593 for integument and muscle, we assumed that the bone and organ compartments were the same size as WAM593: 9.0% bones and 4.8% organs (Table 1). Our animal, CET824, was in poor body condition, and the contribution of the integument and muscle compartments was lower than that of PEM1519/70 and WAM593, with a relative contribution to TBM of 16.6% integument, 33.9% muscle, 8.6% bones, and 5.4% organs (Table 1).

To better understand how body composition changes with body condition in Blainville's beaked whales, we compared CET824 with PEM1519/70: two female adult Blainville's beaked whales with very similar lengths (4.54 and 4.56 m) but with an almost 220 kg weight difference (814 and 1,033 kg) (Figure 3a; Table 3). CET824 had 213.5 kg less TBM, of which 81.7 kg was integument mass, 216.8 kg was muscle mass, 22.8 kg was skeletal mass, and 5.3 kg was visceral organ mass. CET824 had 38% less integument mass, 44% less muscle mass, 25% less skeletal mass, and 11% less visceral organ mass (Table 3). For logistical reasons, the body volume and whole-body density changes could not be calculated for Blainville's beaked whales.

3.3 | Blubber and muscle lipid content

Blubber lipid content (% g wet weight) for striped dolphins ranged between 25% and 65% g wet weight, and it was higher with body condition, although this was not statistically significant (Figure 4a). The association was stronger when considering the total lipid (kg) stored in the integument ($R^2 = .910$, $p = .003$, power = .999; Figure 4b). CET1034 had lower blubber lipid content and blubber mass than CET1063. Thus, CET1034 had 5.20 kg less lipids, suggesting that she used 49,086 kilocalories from blubber (56% of kilocalories stored as lipids in the blubber) (Table 3).

Muscle lipid content for striped dolphins ranged between 1.04% and 1.33% g wet weight. Although lipid content tended to be higher with body condition, this was not statistically significant ($R^2 = .376$, $p = .196$; Figure 4c); however, the total amount of lipids stored in the muscle was significant ($R^2 = .840$, $p = .010$; power = 0.985; Figure 4d). CET1034 also had lower muscle lipid content and muscle mass than CET1063. It had 0.28 kg less lipids, which is 2,677 kcal obtained from its muscle (37% kcal stored as lipids in the muscle) (Table 3).

Blubber lipid content for the three Blainville's beaked whales from our tissue bank varied between 63% and 79% g wet weight on the three whales examined in this study, with CET824 presenting the lowest value. None of these whales were in good body condition. In contrast, PEM1519/70 was in good body condition. Hence, we assumed that its lipid content should be close to the highest value found in the literature for a Blainville's beaked

TABLE 3 Calculations of changes in mass compartment, energy storage, O₂ storage, sRMR, and cADL with body condition for the striped dolphin CET 1034 and the Blainville's beaked whale CET 824 compared to animals in good body condition (CET 1063 and PEM1519/70 respectively).

Striped dolphins	CET 1034	CET 1063	Difference	% Loss
TBM (kg)	74	111	−37	−33
Body volume (dm ³)	65.6	97.7	−32	−33
Whole-body density (kg/m ³)	1,128.4	1,136.4	−8	−0.7
Integument mass (kg)	7.9	14.2	−6.3	−44
Lipid content in blubber (%)	52.63	65.80	−13.2	−20
Energy from lipids stored in blubber (kcal)	39,217	88,303	−49,086	−56
Muscle mass (kg)	37.3	56.8	−19.5	−34
Lipid content in muscle (%)	1.27	1.33	−0.06	−4.51
Energy from lipids stored in muscle (kcal)	4,477	7,154	−2,677	−37
Protein content in muscle (%)	94.1	98.2	−4.1	−4.2
Energy from proteins stored in muscle (kcal)	198,332	315,798	−117,466	−37
Skeleton mass (kg)	7.6	9.3	−1.7	−18
Organ mass (kg)	12.0	13.1	−1.1	−8.4
O ₂ muscle (L)	3.80	5.85	−2.05	−35
O ₂ Lung (L)	1.1	1.5	−0.4	−31
O ₂ blood (L)	0.9	1.3	−0.4	−31
RMR (L O ₂ min ^{−1})	330	400	−70	−17.5
sRMR (ml O ₂ kg ^{−1} min ^{−1})	3.39	3.06	0.33	10.8
cADL (min)	21.8	24.4	−2.6	−10.7
Blainville's beaked whales	CET 824	PEM1519/70	Difference	% Loss
TBM (kg)	820	1,034	−214	−21
Integument mass (kg)	136.3	218.1	−81.8	−38
Lipid content in blubber (%)	63.3	81.8*	−18.5	−23
Energy from lipids stored in blubber (kcal)	815,386	1,685,610	−870,224	−52
Muscle mass (kg)	278.2	495.0	−216.8	−44
Lipid content in muscle (%)	1.13	1.13	0.0	0.0
Energy from lipids stored in muscle (kcal)	29,710	52,861	−23,151	−44
Protein content in muscle (%)	91.9	98.8	−6.9	−7.0
Energy from proteins stored in muscle (kcal)	1,444,616	2,763,315	−1,318,699	−48
Skeleton mass (kg)	70.2	93.0	−22.8	−25
Organ mass (kg)	44.4	49.6	−5.2	−11
O ₂ muscle (L)	44.7	79.5	−34.8	−43.8
O ₂ Lung (L)	3.1	3.9	−0.8	−20.5
O ₂ blood (L)	41.6	52.8	−11.2	−21.2
RMR (L O ₂ min ^{−1})	1.5	1.8	−0.3	−16
sRMR (ml O ₂ kg ^{−1} min ^{−1})	1.9	1.8	0.1	5.6
cADL (min)	59	75.3	−16.3	−21.6

Note: Asterisks denotes data from McClelland et al. (2012).

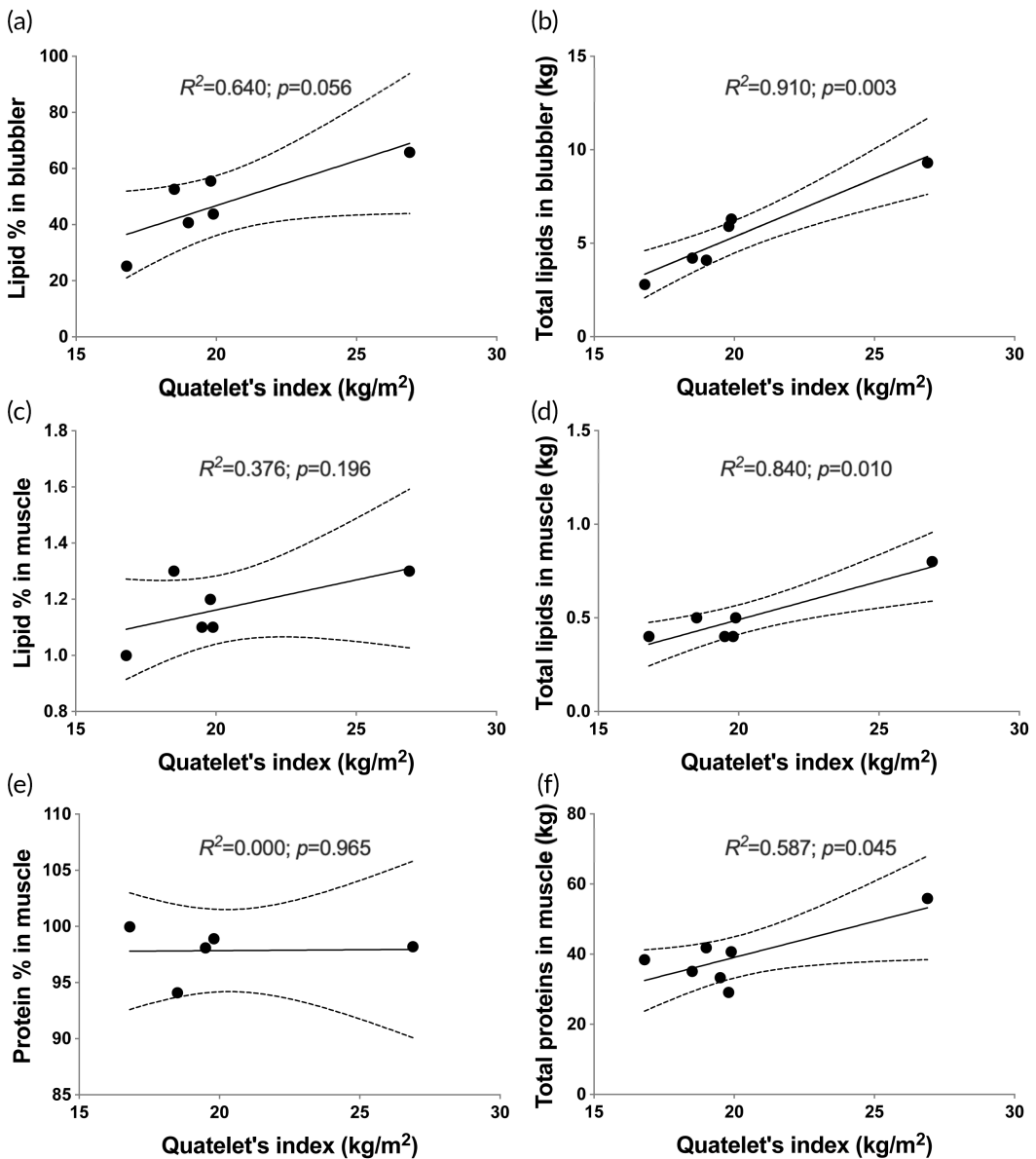


FIGURE 4 (a) Blubber and (c) muscle lipid content (% g wet weight), total lipid content in (b) blubber and (d) muscle, as well as (e) protein (%) and (f) total protein in muscle against body condition (TBM/TBL²) in the striped dolphins studied with a 95% CI.

whale (81.8% g wet weight) (McClelland et al., 2012). CET824 had 278 kg of lipids less in its blubber, 870,224 kcal (52% kilocalories stored as lipids in the blubber), than PEM1519/70 (Table 3).

Muscle lipid content for Blainville's beaked whales varied between 0.60% and 1.13% g wet weight on the three whales examined. CET824 did not present the lowest value as expected, suggesting interindividual variability. Although there was not an apparent decrease in muscle lipid content, there was a decrease in the total amount of lipids stored in the muscle since the muscle mass decreased. CET 824 had 1.3 kg less lipids in its muscle or 23,151 less kcal (44% kcal stored as lipids in the muscle) (Table 3).

3.4 | Blubber and muscle lipid composition

Principal component analysis showed a species-specific lipid composition for blubber and muscle, as shown in the score plot (Figure 5a). The loading plot (Figure 5b) depicts the different lipid classes that were identified (over 25) and how they are distributed in the different tissues. In striped dolphins, the blubber presented higher levels of unsaturated lipids and triacylglycerols (TAG), while the muscle presented greater cholesterol. In Blainville's beaked whales, the blubber stood out as containing higher fatty alcohols of wax esters (WE), while the muscle presented more linear lipids.

Body condition affected the number of stored lipids and their composition. There was a good partial least square regression between the Quetelet's index and lipid type in the blubber (Figure 5c) and muscle (Figure 5d) of striped dolphins. This regression analysis was not performed for Blainville's beaked whale due to the small sample size. In the case of blubber, the overall lipidic profile changed with body condition, although these changes were not explained by individual lipid types. For muscle, however, specific lipid types were shown to change with body condition (Figure 6a,b). For instance, the lipid composition of striped dolphins in moderate-to-poor body conditions was characterized by higher levels of cholesterol and polyunsaturated fatty acids (PUFA). In contrast, moderate-to-good body condition dolphins had higher triacylglycerols, fatty acids, linear lipid chains, and lipid acyl groups (Figure 6a,b). Also, Blainville's beaked whales showed similar tendencies in TAGs, PUFAs, and cholesterol proportions with body conditions (Figure 6c). Blainville's beaked whales also presented a higher relative concentration of phospholipids and a lower relative concentration of fatty alcohols in animals with poor body condition (Figure 6c).

3.5 | Blubber and muscle protein content

Neither protein content (i.e., protein %) nor total proteins (protein % \times blubber mass) in blubber varied with body condition in striped dolphins ($p = .105$ and $p = .814$). Protein content in blubber varied between 27% and 45%. Protein content (i.e., %) in muscle was also unrelated to body condition ($R^2 = .000$, $p = .965$; Figure 4e) with mean values of $97.8 \pm 2\%$. For this reason, a protein percentage of 97.8 was attributed to two samples whose protein content could not be analyzed in order to increase the sample size for calculations of total protein in muscle. Total proteins in muscle (protein % \times muscle mass) were significantly related to body condition ($R^2 = .587$, $p = .045$, power = .715; Figure 4d). CET1034 lost 20.6 kg of proteins from its muscle, corresponding to 117,466 kilocalories compared with CET1063 (37% kilocalories stored as muscle proteins) (Table 3).

In Blainville's beaked whales, blubber protein content varied between 12.6% and 18.6% g wet weight. Muscle protein content ranged between 91.9 and 98.8 g wet weight. CET824 presented the lowest protein values in blubber and muscle of the three Blainville's studied from our tissue bank. Muscle protein content was not reported for PEM1519/70 or WAM593; thus, we assumed that PEM1519/70 would have at least the same or more protein content as the whale with the highest protein content of our samples. CET824 lost 233.3 kg of proteins from its muscle, 1,318,699 kcal, compared with PEM1519/70 (48% kcal stored as proteins in the muscle) (Table 3).

3.6 | O₂ storage, RMR, and cADL

The striped dolphin CET1034 had 31%–35% less O₂ stores from each of the three tissue compartments (muscle, lungs, and blood) than CET1063. At the same time, its sRMR was 10.8% higher than CET1063, resulting in a 10.7% cADL decrease (Table 3). The Blainville's beaked whale CET824 had 43.8% less O₂ stores in muscle, 20.5% less in the lungs, and 21.2% less in the blood compartments than PEM1519/70; however, its increase in sRMR (5.6%) was smaller than in the striped dolphin even though its body condition was worse. Still, this whale showed a reduction of 21.6% from its ideal cADL (Table 3).

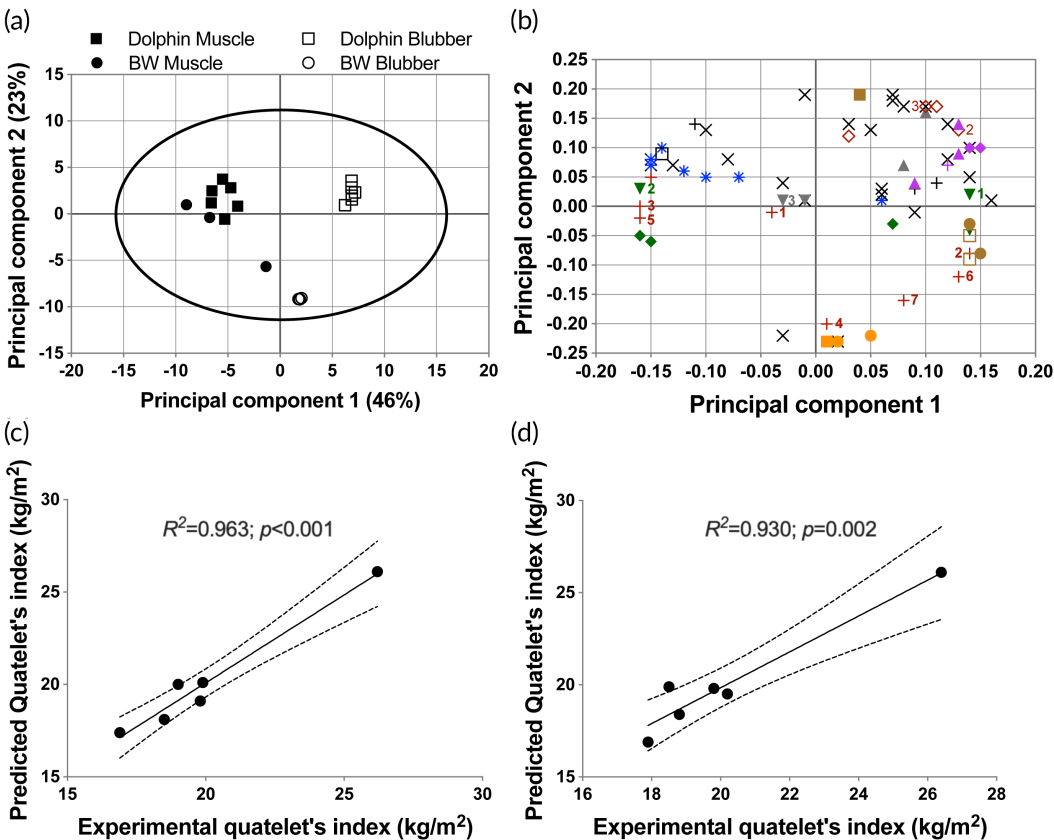


FIGURE 5 Multivariate analysis of the lipid composition of the muscle and blubber compartment in the striped dolphins and Blainville's beaked whales: (a) Principal component analysis score plot, $R^2X(\text{cum}) = 0.69$, $Q^2(\text{cum}) = 0.63$, 2 component model, univariate scaling. The variability explained by each of the principal components is indicated next to the axes. BW, beaked whale. (b) Principal component analysis loading plot. Black, isolipids (open square = Isovaleryl WE; plus = Isobranched lipids) and unknown (cross); blue star, cholesterol; brown, unsaturated lipids (open square, monounsaturated fatty acid; closed square, PUFA; dot, unsaturated lipids); violet, TAG (diamond, glycerol backbone in TAG; plus, isovaleric acid in TAG; triangle, sn-1;3 isovaleryl TAG; inverted triangle, sn-2 TAG; circle, fatty alcohols in waxes; square, Fatty alcohols in WE); red, all lipids together; gray, linear lipids (inverted triangle, linear lipids; diamond, linear fatty acids 2 except n-3); gray, n-3 acyl groups (triangle, n-3 acyl groups; inverted triangle, linear lipids acyl group). Different lipid subtypes within a specific lipid category are differentiated with numbers. (c) Partial least squared regression *observed* versus *predicted* plot of the blubber lipid composition versus the Quetelet's index of striped dolphins with a confidence interval of 95%. $R^2Y(\text{cum}) = 0.97$, $Q^2(\text{cum}) = 0.69$, 2 component model, univariate scaling. (d) Partial least squared regression *observed* versus *predicted* plot of the muscle lipid composition versus the Quetelet's index of striped dolphins with a 95% CI. $R^2Y(\text{cum}) = 0.96$, $Q^2(\text{cum}) = 0.62$, 2 component model, univariate scaling.

4 | DISCUSSION

Our comprehensive analysis of body mass and composition of selected striped dolphins and Blainville's beaked whales revealed a significant effect of body condition on different body compartments, which can compromise the function of these tissues and ultimately compromise the survival of these animals. The Quetelet's index was the best body index to assess body condition in striped dolphins and Blainville's beaked whales. Blainville's had larger integument mass, while striped dolphins had larger viscera and bone mass. Muscle mass and total lipids in the

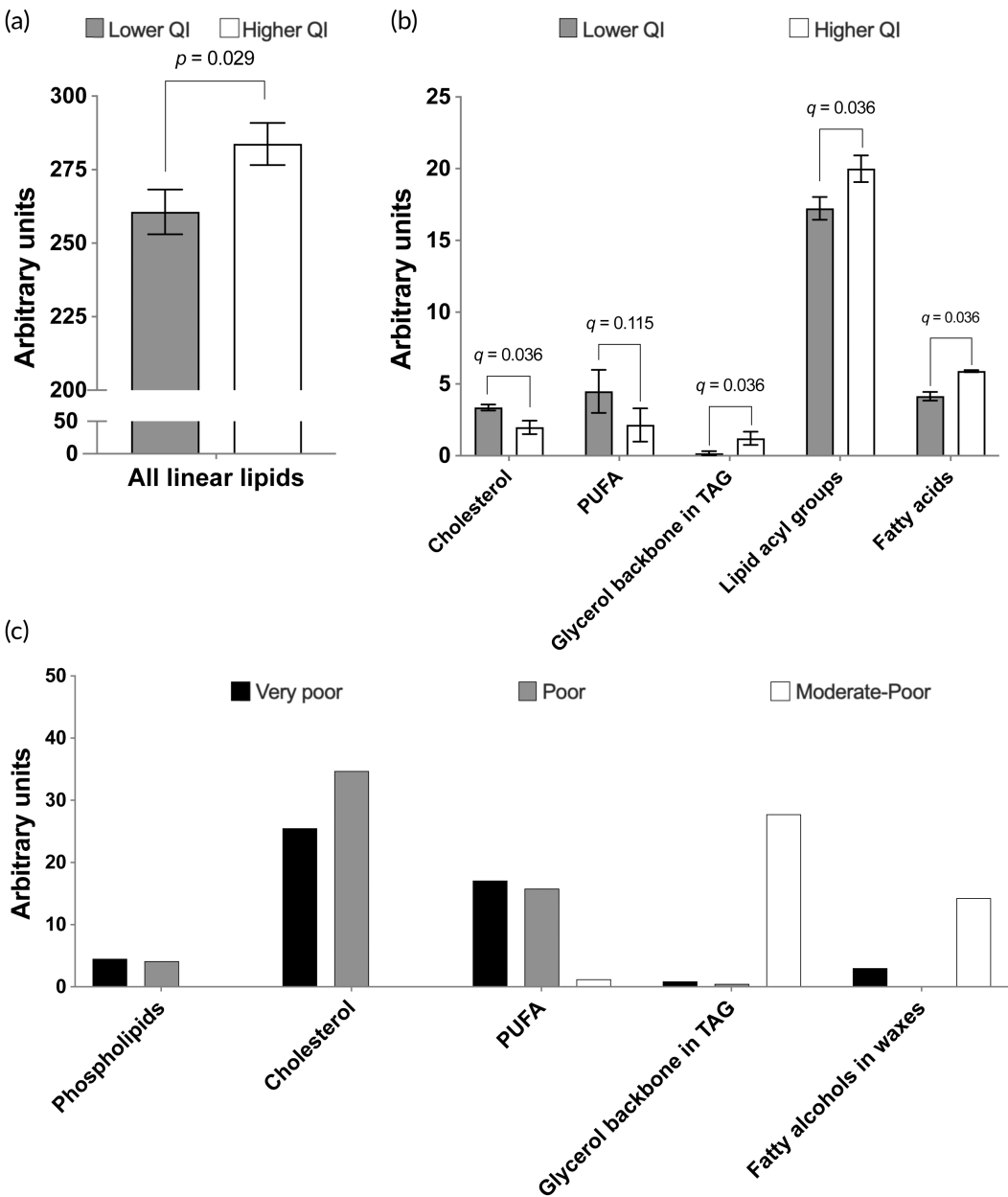


FIGURE 6 Lipid composition changes in muscle with body condition of (a) and (b) striped dolphin, as well as (c) Blainville's beaked whale.

blubber and muscle were significantly associated with body condition. The largest energy store in both species was in the form of proteins in the muscle, followed by lipids in the blubber and muscle. Both species likely used these energy stores when losing body mass. However, striped dolphins appeared to preferentially use the energy stored in the blubber compared with Blainville's beaked whales, which catabolized their muscle.

Marine mammals have more challenges than terrestrial mammals when losing body mass because of the physical properties of water compared with those of air (higher thermal conductivity and density) and the paradox of breathing atmospheric air but feeding underwater. The reduction in body mass due to the loss of blubber and muscle

directly impacts their metabolism and ecophysiology, increasing their energy expenditure for maintenance and locomotion and reducing the time available for feeding (cADL), ultimately reducing energy intake. This results in a positive feedback loop of energy balance and body mass (loss of blubber and muscle mass), which can have lethal consequences.

4.1 | Body condition and body composition

We used the body composition technique to describe each body compartment as a percentage of total body mass (Grand, 1977), providing quantitative data on the distribution of body mass. The body composition technique has been used with allometric scaling to investigate how the animal changes its investment in the different body compartments according to ontogeny and reproduction status in a few marine mammal species, focusing exclusively on animals in “good” body condition, that is, robust animals (Bryden, 1969; Lockyer, 1995; Mallette et al., 2016; McLellan et al., 2002; Miyazaki et al., 1981; Perrin & Roberts, 1972). Only a few studies have investigated how these energy reserves (body compartments) are used as the animal loses body mass. However, they have focused exclusively on the blubber compartment (Dunkin et al., 2005; Dunkin et al., 2010; Montie et al., 2008; Struntz et al., 2004; van der Hoop et al., 2017). To our knowledge, this is the first study quantifying energy use from the different body compartments as the animals lose weight.

A single tissue sample was used for both blubber and muscle studies. The sample locations were selected based on previous research, which determined that trunk blubber is the optimal site for detecting changes in lipid content (Koopman et al., 1996; Pabst et al., 1999), while the mid-belly of the longissimus muscle is the most suitable site for estimating total myoglobin and O₂ storages (Arregui et al., 2021).

This study was based on stranded cetaceans, a biased population subsample with several limitations. Individually stranded cetaceans are frequently sick and often present chronic diseases that affect their body condition (Arbelo et al., 2013; Díaz-Delgado et al., 2018; Kershaw et al., 2017). As such, they are not representative of the body condition of the population in the wild. Some animals from our study only presented those signs associated with a live stranding (stress response syndrome); others were bycaught or presented infectious and parasitic diseases (Table 1). The Quetelet's index was the best body index indicator in agreement with Kershaw et al. (2017). The Quetelet's index presented positive asymmetry distribution in our subsample of stranded striped dolphins. If we had more animals in good body condition, the distribution would shift to the right, and some of the animals we assigned in this study as “moderate” would likely fall under the poor body condition category.

Cancer, infections, diabetes, and organ failure, among other conditions, enhance muscle catabolism in humans (Sartori et al., 2021). Some of the animals from the present study presented different pathologies, which might affect the rate of and preferential energy use of the muscle. Yet, other dolphins (e.g., CET1034) presented no relevant pathologies and were in poor body condition, suggesting they were starving for some unknown reason. Overall, there was a good positive regression for muscle mass and the Quetelet's index regardless of the cause of death. Moreover, the comparison between two specific animals of the same length but different body mass provides an approximation/example for understanding the physiological consequences of losing body mass in broad terms, rather than exact values, and should be interpreted with caution.

The difficulties in accessing carcasses in fresh preservation status of adults of the same species with different body conditions precluded us from having a larger sample size. This is logistically more challenging when referring to any beaked whale species, including Blainville's beaked whales. For this reason, we have complemented this study with data from the literature and tissues from our tissue bank (as available), given how scarce and valuable these data are. Regardless of these pitfalls, we were able to describe differences in body composition between the two species studied and to assess, for the first time, how striped dolphins and Blainville's beaked whales use their energy stores when losing TBM by comparing animals of the same species, same life history category, same-sex in the Blainville's beaked whale (no sexual dimorphism in the Quetelet's index for striped dolphins), similar TBL, but very different TBM. Hence, animals in good body condition were used as a reference for animals in poor body condition of similar TBL.

The distribution of body mass depends in large part on the ecophysiology of the species: Deep divers have relatively smaller brain and viscera mass percentages but larger integument, bone, and muscle mass percentages than shallow divers (Pabst et al., 2016). The striped dolphin is a social, active, and energetic pelagic small delphinid common in warm temperate to tropical waters (10–26°C) around the world (Archer II, 2018). It feeds primarily on benthopelagic cephalopods and fish (Miyazaki et al., 1973; Ringelstein et al., 2006; Spitz et al., 2006). Diving depths for this species have been inferred from its prey habitat. Hence, depths of 200 to 700 m deep have been proposed, although the stomach content analyses suggest that they prey early at night when the prey migrate closer to the surface (Archer II, 2018). Blainville's beaked whales are 4–5 m long and live in small populations with high site fidelity in tropical to temperate waters worldwide (Baird, 2019; Pitman, 2009). They are extreme divers such that they dive on average to depths greater than 800 m and for durations longer than 45 min (Arranz et al., 2011; Baird, 2019; Baird et al., 2006; Tyack et al., 2006).

Striped dolphins and Blainville's beaked whales had, in proportion, similar muscle mass, but the striped dolphin had larger bone and visceral organ compartments. In contrast, Blainville's beaked whales had a larger integument (blubber) compartment. The body composition data of the only striped dolphin studied in good body condition were highly similar to that reported for striped dolphins of the Pacific coast of Japan but with a relatively lower integument mass (Miyazaki et al., 1981). This might be explained by the difference in water temperatures in Japan versus the Canary Islands. Changes in blubber morphology and lipid content have been described for bottlenose dolphins inhabiting different geographic locations and exposed to different water temperatures (Montie et al., 2008). Our striped dolphins in moderate and poor body conditions presented even lower blubber and muscle masses than the striped dolphins of Japan (Miyazaki et al., 1981). To our knowledge, there are no published data on the body composition of striped dolphins or Blainville's beaked whales in moderate or poor body conditions, highlighting the importance and novelty of these data.

4.2 | Blubber mass loss and its consequences on function

Total lipids in blubber were more strongly related to body condition than blubber mass or lipid content alone and may be used as indicators of body condition. Both the striped dolphin (CET1034) and the Blainville's beaked whale (CET824) had significantly less blubber mass (44% and 38%, respectively), and their blubber was composed of lower lipid content than animals in good body condition (20% and 23%). Importantly, the striped dolphin (CET1034) was in moderate-to-poor body condition but not emaciated to the extent of the Blainville's beaked whale. Hence, the striped dolphin could have still catabolized more lipids and tissues if it lived longer. Previous studies focused on blubber lipid content or thickness alone but did not calculate total lipids (Dunkin et al., 2005; Dunkin et al., 2010; Struntz et al., 2004). Still, these authors reported a decrease of up to 48% in lipid content in the blubber of emaciated adult bottlenose dolphins compared with that of robust animals (Dunkin et al., 2005; Struntz et al., 2004). Aside from energy storage, the blubber of whales and dolphins also contributes to body core insulation, positive buoyancy, streamlining, and regulating the metabolism and immune responses (Bagge et al., 2012; Dunkin et al., 2010; Kershaw et al., 2018; Kipps et al., 2002; McLellan et al., 2002; Pabst et al., 1999). These other functions may be compromised if this body compartment is significantly reduced.

Emaciation negatively affects thermoregulation by decreasing blubber insulation in dolphins and porpoises (Dunkin et al., 2005). The blubber's insulation capacity depends on its quantity (mass) and quality (lipid content and composition) (Dunkin et al., 2005; Worthy & Edwards, 1990). CET1034 and CET824 experienced a decrease in both blubber quantity and quality. We did not identify changes in specific lipid groups with body condition, but overall lipid content decreased. Even though we did not analyze the thermal properties of the blubber, we can infer from the decrease in blubber quantity and quality of CET1034 and CET824 that their blubber insulation was profoundly impacted as described for emaciated bottlenose dolphins (Dunkin et al., 2005), increasing the rate of heat loss.

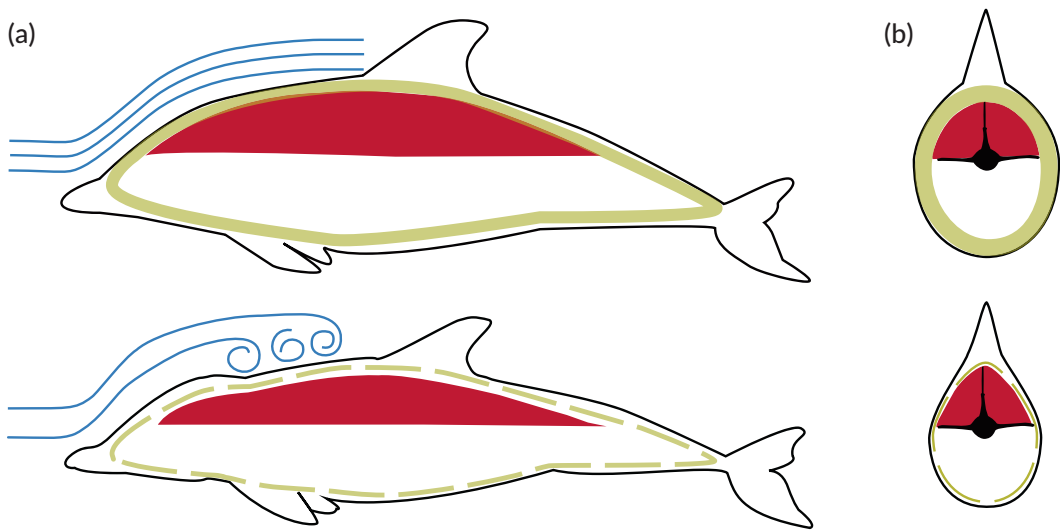


FIGURE 7 Schematic illustration representing changes in the silhouette and blubber (yellow) and epaxial muscle (red) compartments in dolphins as a result of a decrease in TBM. (a) Longitudinal axes; (b) transversal section at the dorsal fin level. Volume is decreased while the surface is maintained, increasing the surface-to-volume ratio for heat loss. At the same time, the quantity and quality of blubber (thick continuous line vs thin discontinuous line) is decreased, decreasing blubber insulation, and further increasing heat loss. Changes in the silhouette from a hydrodynamic shape to a shape with more edges will change the laminar flow and increase the surface contact, increasing the drag.

When an animal loses body mass, it maintains its length but reduces its volume. As a result, the surface-to-volume ratio for heat exchange is increased (Figure 7). The striped dolphin CET1034 had a volume 32.9% smaller than CET1063 even though it was only 3 cm shorter in TBL, suggesting that its surface-to-volume ratio was increased by 50%. Emaciated dolphins and whales may increase their metabolic rate to compensate for the increase in heat loss following the surface hypothesis (Rubner, 1883) as described for fasting king penguins (*Aptenodytes patagonicus*) (Fahman et al., 2006). Based on our calculations, CET1034 and CET824 increased their sRMR by 10% and 6%, respectively. However, these allometric equations only account for changes in the surface-to-volume ratio and do not consider changes in the quality of insulation. Hence, our results are likely underestimating the increase in sRMR. Future studies on metabolic function in animals in poor body conditions that undergo rehabilitation and regain body mass will help calculate changes in sRMR due to changes in surface-to-volume ratio and blubber insulation.

Previous reports suggest that a decrease in blubber mass will result in negative buoyancy and an increase in energetic costs for locomotion and foraging (Dunkin et al., 2010). Changes in buoyancy have been associated with changes in swimming and gliding patterns (Skrovan et al., 1999). Dunkin et al. (2010) showed that the integument of emaciated adult bottlenose dolphins was denser than seawater and 12 times more negatively buoyant than robust adults. The more robust striped dolphin had higher lipid content than CET1034 and presumably a lower blubber density, in agreement with Dunkin et al. (2010). However, when we calculated whole-body density, the dolphins in moderate-to-poor body condition and those in good body condition presented similar whole-body densities. Interestingly, the animal in worse body condition (CET1034) was slightly less dense than the dolphin in better condition. This might be explained by the fact that CET1034 not only had less blubber but also less muscle, which is denser than fat. Also, CET1034 was in moderate-to-poor body condition but was not emaciated, unlike the animals studied by Dunkin et al. (2010). Our results highlight the importance of studying whole-body density versus blubber density alone, given that other factors, such as muscle, contribute significantly to body density and buoyancy. Further studies of body density in emaciated dolphins are needed to confirm whether changes in body mass do indeed affect whole-body density, buoyancy, and, ultimately, the energetic cost of locomotion.

The blubber of beaked whales has traditionally been considered inert (Pabst et al., 2016) as it is composed almost exclusively of wax ester (Koopman, 2006), a lipid that most mammals cannot metabolize (Pond, 1998), and with low blood perfusion (McClelland et al., 2012). Wax esters have higher energy density (Koopman, 2018) and thermal quality (Bagge et al., 2012; Singleton et al., 2017) than triacylglycerols. Our results confirmed that the blubber of Blainville's beaked whales was mainly composed of wax esters. However, CET824 had less blubber mass and blubber lipid content compared with the more robust Blainville's beaked whale, challenging this dogma. Although the Blainville's beaked whale CET824 was in worse body condition than the striped dolphin CET1034, it catabolized less of its blubber. This might be explained by the differences in the ecophysiology of both species. While both species inhabit temperate waters, Blainville's beaked whales forage at depths >800 m (Arranz et al., 2011; Baird, 2019; Baird et al., 2006; Tyack et al., 2006) where the water temperature is only 5°C (Joyce et al., 2016). Hence, insulation in Blainville's beaked whale may be important for proper thermoregulation.

4.3 | Muscle mass loss and its consequences on function

Muscle mass and total lipids in muscle were associated with body condition in striped dolphins. The muscle lipid composition was also altered by body condition in striped dolphins and Blainville's beaked whales. Rapidly mobilized lipids (triacylglycerol) decreased with body condition loss. In contrast, structural lipids (cholesterol, phospholipids, and polyunsaturated fatty acids) relatively increased as they became more abundant as a proportion of total lipids. This increment in structural lipids may also be explained due to an increase in the membrane versus cytosol ratio owing to the reduction in muscle cell volume, similar to adipocyte shrinkage in emaciated animals (Koopman et al., 2002; Struntz et al., 2004). In the muscle of beaked whales, lipids were stored not only in the form of triacylglycerols but also partially as wax esters, as has already been described in other deep-diving species, like the sperm whale (Lockyer, 1991). Interestingly, the proportion of these wax esters is also reduced in animals with lower body conditions, suggesting a potential metabolization of these less mobile lipids. The Blainville's beaked whale (CET824) made greater use of the lipids stored in its muscle than the striped dolphin CET1034.

The striped dolphin CET1034 and the Blainville's beaked whale CET824 presented 34% and 44% less muscle mass, respectively, than the reference specimens in good body condition (Table 3). Both species obtained the most energy from muscle proteins. The physiological cross-sectional area of the muscle has long been related to muscle force-generating capacity. It has been used to calculate the swimming force produced by various cetacean species, including some beaked whale species (Arthur et al., 2015), although this association has recently been challenged (Barry et al., 2015; Jones et al., 2008; Rospars & Meyer-Vernet, 2016). Reduced muscle force-generating capacity will imply higher locomotory efforts to swim the same distance, hence a higher energetic cost. Also, smaller muscle fibers (as those expected in animals in poor body conditions) will have a larger surface-to-volume ratio, requiring higher energy demands to maintain the Na/K-ATPase pump, which represents 40%–50% of the muscle resting metabolic rate in a wide range of species, including mammals (Jimenez et al., 2011). If muscle mass is reduced, the cross-sectional area of the muscle and muscle fiber size is also likely reduced. Future studies on muscle fiber size of animals in poor body condition compared with that of animals in good body condition will help to assess this increase in muscle metabolic cost. Presumably, the swimming velocity would be slower because of the reduced muscle force-generating capacity, which might negatively impact the prey's success rate and energy intake (Figure 8).

The muscle was the largest oxygen storage site in these species. The striped dolphin CET1034 and the Blainville's beaked whale CET824 presented 35% and 44% less oxygen stored in their muscle than their counterparts in good body condition (Table 3). As a result, their cADL was 10.7% and 21.6% less, respectively, meaning that they have 10.7% and 21.6% less time for foraging, which might result in a further reduction in energy intake (Figure 8). Given the large size of the muscle compartment in these species, one could hypothesize that they might use the muscle preferentially not to compromise the other functions of blubber. However, a reduced

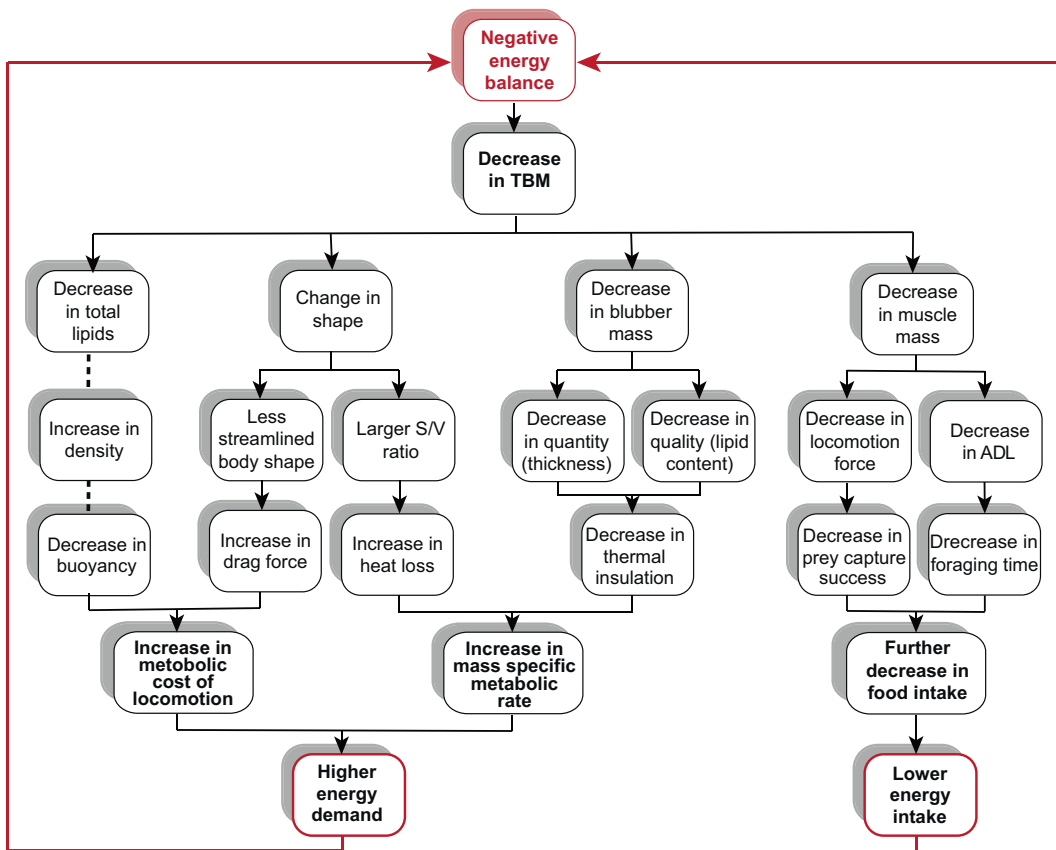


FIGURE 8 Schematic of the positive feedback loop between negative energy balance, loss of body mass, increased energetic demands, and lower energy intake.

cADL will make them more vulnerable to shifts in prey abundance and distribution similar to inexperienced foragers (Acosta et al., 1999; Costa et al., 2001).

4.4 | Implications of detrimental body condition: a positive feedback loop

We have discussed not only how the resting metabolic rate could have increased via an increase in the surface-to-volume ratio following the surface hypothesis, but also that this was likely underestimated as it did not account for the reduction in insulation. Additionally, the reduction in the cross-sectional area of the muscle would likely increase the metabolic cost of locomotion. Finally, the reduction in blubber and muscle mass may also result in reduced streamlining (Figure 7), further increasing the metabolic cost of locomotion. Globally, this would represent an increase in field metabolic rate; however, with oxygen stores reduced, time for foraging would also be reduced, decreasing energy intake (Figure 8). In theory, this results in an even greater negative energy balance requiring further catabolism of energy stores resulting in a positive feedback loop (Figures 8 and 9), which can have detrimental effects on an animal's health, for example, dehydration (Castellini & Rea, 1992). By-products of lipid catabolism can have neurotoxic and immunotoxic effects (Mazzariol et al., 2011), lower immunity, and higher susceptibility to infectious and parasitic diseases (Katona & Katona-Apte, 2008). These diseases, whether together or in isolation, may further accelerate the positive feedback loop. If the energy balance is not balanced before reaching the

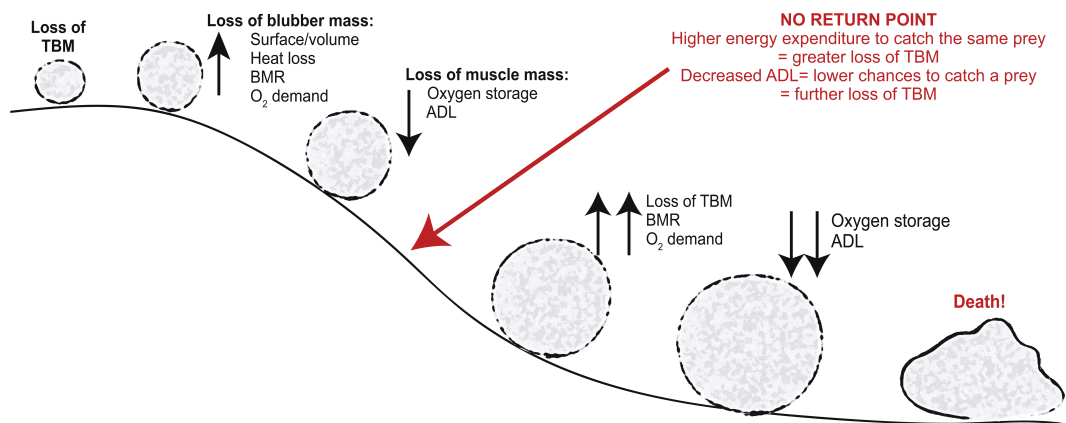


FIGURE 9 Snowball effect diagram. When the animal loses body mass, it loses blubber mass, which results in an increase in surface-to-volume ratio, heat loss, and RMR. Hence, energy expenditure and thus oxygen demand are increased. However, the animal also loses muscle mass, meaning decreased oxygen stores resulting in a decreased ADL. The loss of blubber mass and muscle mass together results in higher energy expenditure to catch the same prey, while having less time to catch it. This will cause a lower energy intake causing further loss of TBM, resulting in a snowball effect with fatal consequences. There is a point beyond which the animal will not be able to stop and reverse this snowball effect. This is the “no-return point.”

no-return point, the animal will likely die from disease or starvation (Figure 9). In such a debilitated state, reproduction failure is also expected as described for other marine mammal species (Hodges et al., 1999; Lockyer, 1986; Millar & Hickling, 1990; Milner et al., 2003). Therefore, the no-return point is key for delimiting the impact of disturbances on the survival of an individual and is, therefore, essential for mitigation measures and conservation strategies. The no-return point will likely vary within species but also within individuals of the same species, since health conditions such as diseases may accelerate the snowball effect.

Future studies on field metabolic rate in animals in poor body condition that undergo rehabilitation and regain body mass will help to calculate changes in field metabolism more accurately due to changes in body condition and help determine the no-return point. Additionally, further studies on body composition changes with body condition are necessary to understand energy allocation and utilization, as this may vary according to the ecophysiology of the species. Also, understanding how these changes might affect brain thermoregulation and function could be critical for these species (Manger et al., 2021).

In summary, we demonstrated that the Quetelet's index is a good indicator of body condition and that muscle proteins are the largest energy stores for the striped dolphin and the Blainville's beaked whale, challenging the dogma of blubber being the largest energy reservoir. Catabolism of both blubber and muscle might be strategic, not to impair the other functions of either of these body compartments. When impaired, it results in a positive feedback loop of increased metabolic field and lowered energy intake, decreasing their adaptability to environmental changes or disturbances, making them more susceptible to infectious diseases, and ultimately resulting in death. A shortage in prey availability, due to climate change, overfishing, or other activities, can initiate a downward spiral earlier in income-breeder cetaceans than in terrestrial mammals of similar size, given the higher energetic demands of living in water and the paradox of breathing atmospheric air but feeding underwater. There is an urgent need for future studies on how changes in the ocean are affecting body condition, reproduction, and the survival of marine mammal species.

AUTHOR CONTRIBUTIONS

Yara Bernaldo de Quirós: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; supervision; validation; visualization; writing – original draft; writing – review

and editing. **Marina Arregui**: Data curation; formal analysis; investigation; methodology; validation; visualization; writing – original draft; writing – review and editing. **Manuel Arbelo**: Data curation; investigation; resources; supervision; writing – review and editing. **Ayoze Castro-Alonso**: Investigation; writing – review and editing. **Nakita Câmara**: Investigation; writing – review and editing. **Zachary S. Clayton**: Writing – review and editing. **Francesco M. A. Consoli**: Investigation; writing – review and editing. **Andreas Fahlman**: Funding acquisition; investigation; methodology; supervision; writing – original draft; writing – review and editing. **Martina Palomino-Schätzlein**: Data curation; formal analysis; investigation; methodology; visualization; writing – original draft; writing – review and editing. **Raquel Puig-Lozano**: Investigation; writing – review and editing. **Miguel A. Rivero**: Investigation; writing – review and editing. **Eva Sierra**: Investigation; writing – review and editing. **Cristian M. Suárez-Santana**: Investigation; writing – review and editing. **Marisa Tejedor**: Investigation; writing – review and editing. **Antonio Fernández**: Data curation; funding acquisition; investigation; project administration; resources; supervision; writing – review and editing.

ACKNOWLEDGMENTS

The authors thank Dr. Ann Pabst and William McLellan for consulting on mass dissections, Michael Moore and Misty Niemeyer for support at the beginning of this project, Miguel Fernandez for consulting on CT scan volume calculations, and Sagrario Miranda Otín for assistance with illustrations.

FUNDING INFORMATION

This study was supported by the US Office of Naval Research N00014-13-1-0773 and the Spanish National Project PGC2018-101226-B-I00. The Canary Islands Government has helped fund the Canary Islands stranding network. Dr. Bernaldo de Quirós is supported by the European Commission (H2020-MSCA-IF-GF-2019: “Arterial Aging” #89227), and Dr. Arregui is supported by the Spanish Ministry of Science (Margarita Salas 2021). Open access publishing was facilitated by the University of Las Palmas de Gran Canaria, as part of the Wiley–University of Las Palmas de Gran Canaria agreement via the Conference of Rectors of Spanish Universities (CRUE).

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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How to cite this article: Bernaldo de Quirós, Y., Arregui, M., Arbelo, M., Castro-Alonso, A., Câmara, N., Clayton, Z. S., Consoli, F. M. A., Fahlman, A., Palomino-Schätzlein, M., Puig-Lozano, R., Rivero, M. A., Sierra, E., Suárez-Santana, C. M., Tejedor, M., & Fernández, A. (2024). Allocation and use of body energy reservoirs in striped dolphins and Blainville's beaked whales: Snowball effect in negative energetic balance. *Marine Mammal Science*, e13200. <https://doi.org/10.1111/mms.13200>