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Comparable length at weaning in cetaceans

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ABSTRACT

Weaning represents the transition of mammalian life from maternal dependence to independence in both energetics and behavior. The length at weaning (*Lw*) is determined by the maternal investment during gestation and lactation. It affects calf survival and impacts on the long-term persistence of species, but the measurement is not readily obtainable for many cetaceans. A general linear model and residual correlation were used to explore the correlations between the published *Lw* and five other life history traits of cetaceans, including female asymptotic length (*Lx*), length at birth (*Lb*), lactation period (*LP*), gestation period (*GP*), and calving interval (*CI*). *Lx* was a significant confounding parameter on the other five traits. By eliminating the confounding *Lx*, ANCOVA revealed that baleen whales (Mysticeti) and toothed cetaceans (Odontoceti) had comparable *Lw*. By residual correlation, which factors the confounding *Lx*, *Lw* was significantly correlated with *Lb* but not with *GP*, *LP*, and *CI*. After *Lb* was further eliminated, convergent *Lw* in cetaceans could still be observed. Therefore, we proposed a generic expression $Lw = 1.239Lx^{0.877}$, which allows us to further estimate *Lw* of undocumented cetacean species.

Key words: life history, lactation, maternal investment, weaning.

Mammalian reproductive investment is marked by the following events: mating (courtship and estrous cycle), gestation, lactation, weaning, postweaning parental care, and maternal recovery (Gittleman and Thompson 1988). Among them, lactation takes up most energy expenditure (Yasui and Gaskin 1986, Lockyer 2007). For the calves, weaning represents the transition from maternal dependence to independence in energetics and behavior (Perrin and Reilly 1984, Noren and Edwards 2007). Before weaning, infants optimize their growth and develop skills so as to successfully meet the demands of an independent life (Arnould *et al*. 2003). The size and time

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at weaning significantly affect calf survival (McMahon *et al.* 2000, Hall *et al.* 2001) and long-term viability of species (Muelbert *et al.* 2003, McMahon *et al.* 2005). Large size at weaning will facilitate calf survival but will deplete maternal nutrition reserve, especially the thickness of blubber (Lockyer 1984, Yasui and Gaskin 1986, Oftedal 1997, Lockyer 2007), and thus potentially increases maternal mortality rate (Soderquist 1993, Neuhaus and Pelletier 2001). For mothers, weaning means that they no longer allocate their energy to the calves. Instead, the energy can be used to enhance their own survival (by recovering their energy reservoirs) or can be conserved for the next offspring (to increase the lifetime fitness) (Fouts *et al.* 2005). Therefore, the size at weaning may reflect a compromise between the maternal abilities to meet energetic requirements during lactation and the offspring's attainment of a threshold size for independence.

Two complementary patterns describe the energetics of reproduction, depending on whether the maternal nutrition supplies are built in advance of (capital breeders) or concurrent with (income breeders) reproduction (Jönsson 1997, Houston *et al.* 2007). The energetics of lactation in cetaceans has been described by Oftedal (1997), which shows that most baleen whales are capital breeders, whereas toothed cetaceans are income breeders. The differentiated cost of capital or income breeding tactics may affect the time and hence the size at weaning. How to estimate the size at weaning is an essential question in the discussion of cetacean reproductive investment.

Nonetheless, the length at weaning (*Lw*) in cetaceans is not readily measurable because of their strictly aquatic environments. The current methods used to measure *Lw* of cetaceans, including stomach contents analysis (Best *et al.* 1984, Perrin and Reilly 1984, Archer and Robertson 2004) and underwater behavioral records (Miles and Herzing 2003), cannot be applied to many cetacean species. The lethal nature of specimen collection for stomach contents analysis excludes rare and endangered species. Underwater behavioral observation is primarily restricted to those populations that are habituated with human activity and is limited by the highly sensitive nature of mother–calf pairs and low individual identification.

In view of potential difficulties, allometry in life history traits (LHT) (Trites and Pauly 1998) may provide an alternative method to extrapolate *Lw* of undocumented cetaceans. Maternal size (represented by female asymptotic length, *Lx*) is a decisive factor determining the reproductive investment (Lockyer 2007) and hence *Lw.* The length at birth (*Lb*) may also affect *Lw.* Calving interval (*CI*), including both gestation period (*GP*) and lactation period (*LP*), modulate the reproductive investment and may potentially correlate with *Lw.* As *Lw* reflects maternal reproductive investment and impacts on their long-term persistence, finding a reliable, accessible, and, most importantly, nonlethal method to measure *Lw* of cetaceans is one of the important steps toward understanding cetacean life histories. In this paper, we explore potential correlations that determine *Lw* of cetaceans. We then investigate the generic expressions of *Lw* and apply them to undocumented species. These data are essential to further study of the strategies of cetacean reproductive investments.

METHODS

Data Collection

Six LHT, including *Lx*, *Lb*, *Lw*, *GP*, *LP*, and *CI* that potentially correlate with reproductive investment, were collected from published literature. When the data were given as a range rather than as a fixed value, the midpoint of the range was taken. When more than one record was published for one species, we calculated the midpoint of each published value and took the average of these midpoints (as in Kovacs and Lavigne 1986, Allaine *et al.* 1987, Silva 1998, Trites and Pauly 1998, Schulz and Bowen 2004).

Data Processing and Statistical Analysis

All collected LHT were log-transformed for statistical analysis (Blueweiss *et al.* 1978, Allaine *et al.* 1987, Charnov 1991) as

$$Y = aLx^{b}, \quad \text{or} \quad \log a + b \log Lx, \tag{1}$$

where Y represented Lb, Lw, GP, LP, and CI. These allometries were explored by general linear model (GLM), whereas the differences in the allometries between baleen whales (Mysticeti) and toothed cetaceans (Odontoceti) were tested by ANCOVA.

Once the allometry of each LHT was determined, we calculated residuals (ε) of Lb, Lw, GP, LP, and LP by

$$\varepsilon = \log Y - (\log a + b \log Lx). \tag{2}$$

Pearson's correlation was used to explore the correlations between the residuals of Lw and those of the other four LHT (Lb, GP, LP, and CI). The significance of the correlations was tested by Bonferroni's probability. The generic expressions that describe Lw were determined by GLM, in which the differences between Mysticeti and Odontoceti were considered concurrently. Finally, we applied the generic expressions of Lw to other undocumented species.

RESULTS

Out of 87 species of cetaceans, records of 31 species' Lw were collected from published literature. Lx had a significant impact on Lb, Lw, GP, LP, and CI (Table 1). The difference in Lw was not significant between Mysticeti and Odontoceti (ANCOVA $F = 0.49$, $P = 0.49$), in contrast to the significant differences in Lb, GP, LP, and CI between Mysticeti and Odontoceti (Table 1). Therefore, the allometric coefficients of Lb, GP, LP, and CI were determined separately for the two suborders (Table 2).

Table 1. Effect of *Lx* and ANCOVA between suborders (Mysticeti *vs.* Odontoceti) on *Lb*, *Lw*, *GP*, *LP*, and *CI* in cetaceans by general linear model (*F*-matrix). The difference in *Lw*, after factoring out the confounding *Lx*, between Mycticeti and Odontoceti was not significant.

Effect	*Lw*	*Lb*	*GP*	*LP*	*CI*
Lx	395.9^{c}	875.01^{c}	30.0^{c}	7.7^{a}	12.93^{b}
Suborder	0.49	9.75^{b}	21.3^{c}	21.9^{c}	11.46^{a}

$^{a}P < 0.05$.
$^{b}P < 0.01$.
$^{c}P < 0.001$.

Table 2. Coefficients of allometry: $\log Y = \log a + b \log Lx$, where Y represents Lb, Lw, GP, LP and CI. The differences of allometries between two suborders Mysticeti and Odontoceti were considered.

	Suborder Mysticeti					Suborder Odontoceti			
	Lw	*Lb*	*GP*	*LP*	*CI*	*Lb*	*GP*	*LP*	*CI*
log *a*	0.09	0.096	1.003	0.082	0.443	−0.103	0.672	0.039	0.574
b	0.877	0.792	0.019	0.242	0.32	0.882	0.162	0.462	0.384
P of regression	< 0.001	< 0.001	0.75	0.312	0.122	< 0.001	< 0.001	0.02	< 0.01
r^2	0.976	0.877	0.011	0.101	0.222	0.918	0.409	0.168	0.279
n	31	12	12	12	12	59	46	32	35

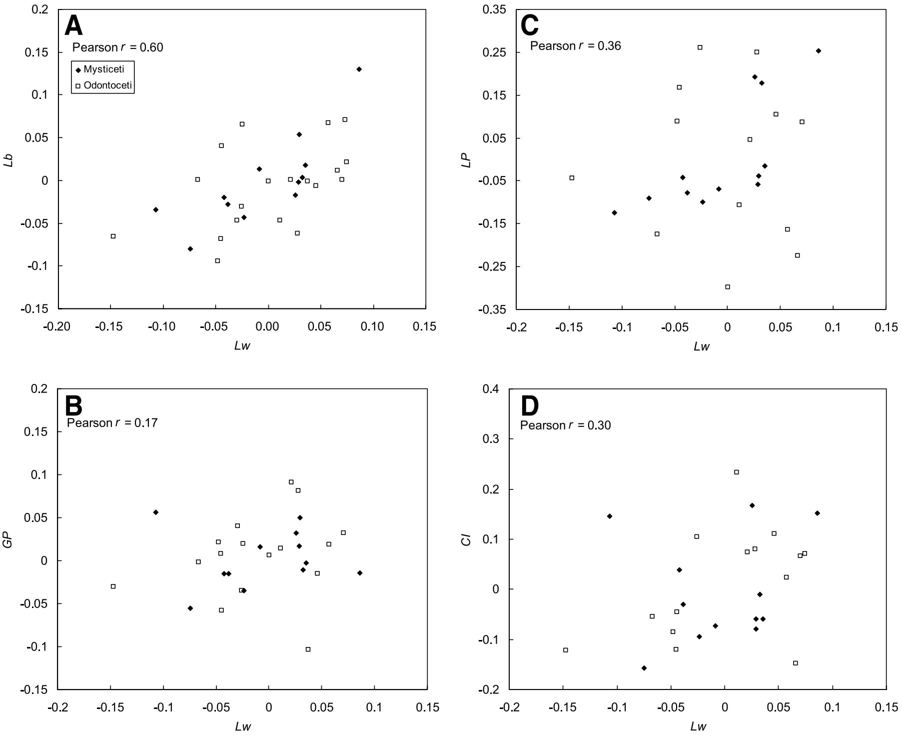

Figure 1. Residual correlations of *Lw* to (A) *Lb*, (B) *GP*, (C) *LP*, and (D) *CI* after factoring out confounding *Lx.* Only the correlation between *Lw* and *Lb* is significant (Bonferroni $P < 0.001$), whereas the rest are not.

We then calculated residuals of *Lb*, *Lw*, *GP*, *LP*, and *CI* by Equation (1) and explored the correlations between *Lw* and the remaining four LHT (*Lb*, *GP*, *LP*, and *CI*) (Fig. 1). *Lw* was significantly correlated with *Lb* (residual correlation, $r = 0.60$, Bonferroni $P < 0.001$) but not with *GP*, *LP*, and *CI* (residual correlation, $r = 0.17$, 0.36 and 0.30, respectively) (Fig. 1). When the two confounding variables, *Lx* and

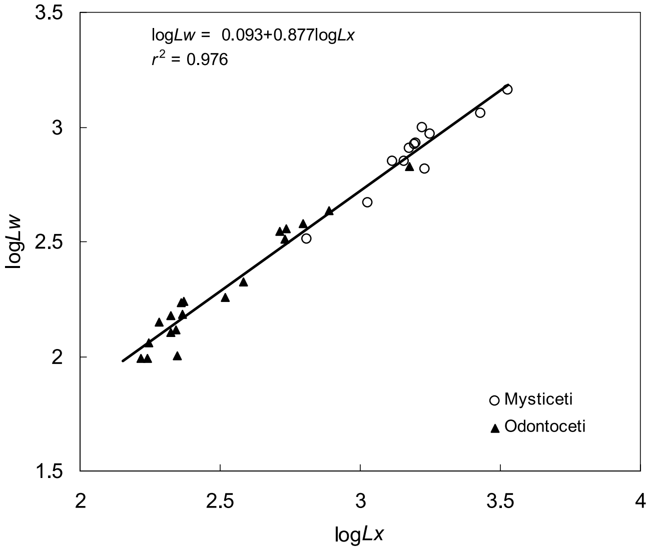

Figure 2. Linear least squares regression by general linear model between logLw and logLx in cetaceans.

Lb, were removed, both Mysticeti and Odontoceti had similar Lw (ANCOVA $F = 0.078$, $P = 0.782$). Therefore, we used one generic expression,

$$\log Lw = 0.93 + 0.877 \log Lx, \quad \text{or} \quad Lw = 1.239 Lx^{0.877} (r^2 = 0.976), \qquad (3)$$

to describe Lw (Fig. 2). The difference between the estimated Lw and the documented Lw was not significant (paired t-test $P = 0.399$). Estimates of Lw were then derived for all cetaceans by applying Equation (3) to Lx (Table 3).

DISCUSSION

Allometry of LHT offers conservation managers a practical tool to estimate LHT using available existing data. Of all cetacean species, the documented Lw of 31 species can be extended to 79 species by Equation (3), thus precluding the use of any lethal specimen collection. The comparable methods used in this study may also be used to estimate other LHT, such as length at sexual maturity or life span, which are essential for constructing effective conservation plans. Not only is allometry of LHT useful in extrapolating undocumented LHT but it also offers insight into how different factors, such as evolutionary divergence, reproductive investment, and behavioral systems, might affect the evolution of LHT (Costa *et al.* 1988, Riska 1989).

Analogous Lw *Suggestive of Convergent Maternal Investment*

Relative to maternal size, analogous size at weaning is not unique to the cetaceans but is universally observed in mammals, suggesting a balance between maternal abilities and energetic requirements (Konig and Markl 1987, Lee *et al.* 1991). Baleen

Table 3. Maximum body lengths (*Lx*, in cm) (from Ridgway and Harrison 1985, 1989, 1994, 1999; Perrin *et al.* 2002, Reeves *et al.* 2002), records, and estimations of *Lw* (in cm) for cetaceans.

Species	*Lx*	Observed *Lw*	Estimated *Lw*	Source of *Lw*
Balaenidae				
Eubalaena glacialis	1,780	850–1,100	878.3	Kraus and Hatch (2001), Kenny (2002)
E. australis	1,660	900–1,100	826.1	Kenny (2002)
Balaena mysticetus	1,702	600–800	844.4	Lockyer (1984), Rugh and Shelden (2002)
Neobalaenidae				
Caperea maginata	645	300–350	360.6	Kemper and Leppard (1999)
Eschrichtiidae				
Eschrichtius robustus	1,500	741–864.5	755.8	Perryman and Lynn (2002)
Balaenopteridae				
Megaptera novaeangliae	1,520–1,707	800–880	805.8	Lockyer (1984)
Balaenoptera acutorostrata	1,070	450–550	562.0	Lockyer (1984)
B. edeni	1,220–1,386	710	644.2	Lockyer (1984)
B. brydei	1,440.65	710	729.6	Lockyer (1984)
B. borealis	1,417–1,707	800–900	779.4	Lockyer (1984)
B. physalus	2,499–2,700	1,150	1, 265.6	Lockyer (1984)
B. musculus	3,358	1,280–1,600	1, 532.4	Lockyer (1984), Sears (2002)
Physteridae				
Physeter macrocephalus	1,494	670	753.2	Bannister *et al.* (1996)
Kogidae				
Kogia breviceps	380		226.7	
K. simus	270		168.0	
Ziphiidae				
Ziphius cavirostris	670		372.8	
Berardius arnuxii	1,000		529.7	
B. bairdii	1,110		580.4	
Tasmacetus shepherdi	660		367.9	
Hyperoodon ampullatus	870		468.8	
H. planifrons	780		426.0	
Mesoplodon hectori	440		257.8	
M. mirus	518	350	297.5	Bannister *et al.* (1996)
M. bidens	505		290.9	
M. grayi	430–560	360	318.5	Bannister *et al.* (1996)
M. peruvianus	372		222.5	
M. bowdoini	438		256.8	
M. carlhubbsi	523		300.0	
M. ginkgodens	490		283.3	

(Continued)

Table 3. (Continued)

Species	*Lx*	Observed *Lw*	Estimated *Lw*	Source of *Lw*
M. stejnegeri	525–544		305.8	
M. layardii	625	380	350.7	Bannister *et al.* (1996)
M. densirostris	471		273.7	
Indopacetus pacificus	750		411.6	
Iniidae				
Inia geoffrensis	199–228	100.1	141.2	Best and da Silva (1989)
Lipotidae				
Lipotes vexillifer	253		158.7	
Pontoporiidae				
Pontoporia blainvillei	174	90.5–104.5	114.3	Brownell (1984)
Platanistidae				
Platanista gangetica	252		158.1	
Monodontidae				
Monodon monoceros	379–420		247.5	
Delphinapterus leucas	474		275.2	
Delphinidae				
Sotalia guianensis	177.3–206	135.7–146.6	124.4	Rosas *et al.* (2003)
S. fluviatilis	149–179.8		108.7	
Steno bredanensis	255		159.8	
Tursiops truncatus	292–370	180	200.9	Bannister *et al.* (1996)
T. aduncus	238–252		155.2	
Stenella attenuata	215–227	122–154.3	139.8	Hohn and Hammond (1984), Archer and Robertson (2004)
S. frontalis	229	171.8	145.4	Herzing (1997)
S. longirostris	204–211		133.4	
S. clymene	190		123.4	
S. coeruleoalba	220–250	174	148.7	Baird *et al.* (1993)
Delphinus delphis	193–224	150	135.7	Bannister *et al.* (1996)
Lagenorhynchus albirostris	278		172.4	
L. acutus	250–283		166.1	
L. cruciger	183		119.4	
L. obliquidens	229–236		147.4	
L. obscurus	193–205		128.6	
L. australis	210		134.8	
Grampus griseus	366–400	212	228.3	Bannister *et al.* (1996)
Pepononcephala electra	256.8		160.7	
Feresa attenuata	243–259		157.6	
Pseudoorca crassidens	506		291.4	
Orcinus orca	670–853	430	421.8	Bannister *et al.* (1996)
Globicephala melaena	500–570	325.3	306.8	Bloch and Lockyer (1993)
G. macrorhychus	362–538		267.1	

(Continued)

Table 3. (Continued)

Species	*Lx*	Observed *Lw*	Estimated *Lw*	Source of *Lw*
Lagenodelphis hosei	260		162.5	
Lissodelphis borealis	210–310		162.5	
L. peronii	228		144.8	
Orcaella brevirostris	230–232	153	146.5	Stacey and Arnold (1999)
Sousa chinensis	235–244		151.3	
Cephalorhynchus commersonii	147–174		106.5	
C. eutropia	165		109.1	
C. heavisidii	168		110.8	
C. hectori	153		102.1	
Phocoenidae				
Phocoena phocoena	166–185	114.7	115.1	Lockyer *et al.* (2001)
P. sinus	134.9–150		95.9	
P. dioptrica	204		131.4	
P. spinipinnis	183–191		124.0	
Phocoenoides dalli	211	127.2	135.3	Jefferson (1988)
Neophocaena phocaenoides	165	96–100	109.1	Shirakihara *et al.* (1993)

whales and toothed cetaceans have quite different reproductive energetics. Such differences may be associated with their different allometric relationships in *Lb*, *GP*, *LP*, and *CI.* Nonetheless, cetaceans wean their calves at allometrically comparable *Lw*, suggesting convergent reproductive investment that determines the threshold size at independence.

Convergent *Lw* may suggest balanced reproductive allocation between gestation and lactation. Although the cost of lactation is much higher than that of gestation (Yasui and Gaskin 1986, Oftedal 1997), the importance of gestation cannot be neglected. Longer gestation periods usually result in larger size at birth, which raises neonatal viability (Kovacs and Lavigne 1986, 1992; Mellado *et al.* 2000). Yet, the length of gestation and size at birth are both morphologically and physiologically constrained, which may result in numerous pathological and even fatal entities (Abitbol 1993, Dombrowski *et al.* 1994, Wilson *et al.* 1999, Gude *et al.* 2004). The compromise between prenatal and postnatal investment may work to balance gestational stress and maternal depletion during lactation.

Socially Cohesive Cetaceans

Reproductive investment is highly associated with the behavioral system. Behavioral compensation by social learning and alloparental caring is an important strategy for minimizing the reproductive cost and developing the acquired skills (Gittleman and Thompson 1988, Hayssen 1993). In some terrestrial mammals, species having complex social organizations usually have small size at weaning to reduce the reproductive cost (Geffen *et al.* 1996). Some cetaceans, including sperm whale (*Physeter macrocephalus*), killer whale (*Orcinus orca*), false killer whale (*Pseudoorca crassidens*), and short-finned pilot whales (*Globicephala macrorhychus*), are considered eusocial cetaceans that have complex and lifetime-bound social organizations (Whitehead 1996, McAuliffe and Whitehead 2006, Foote 2008). Nonetheless, compared with other species, these species do not have smaller *Lw.*

Most cetaceans adopt a polygynous and promiscuous mating system such that males seldom engage in parental care. Reproductive investment must be independently provided by the mother. Nonetheless, reduced maternal investment is not observed in the eusocial cetaceans. The behavioral compensation resulting from social cohesion may therefore affect maternal investment in different ways, perhaps by raising neonatal survival rate (Russell *et al.* 2002, Field and Brace 2004), increasing maternal feeding success, and relieving energetic stress during gestation and lactation, which merits further exploration.

Factors Affecting Weaning Failure

Successful weaning is primarily dependent on maternal nutrition status achieved and maintained either in advance of or concurrent with lactation. The quality and availability of the potential preys determine to a large extent the maternal nutrition supplies (Konig and Markl 1987, Benoit-Bird 2004). Some potential factors, including global warming and unsustainable fisheries (Neira and Arancibia 2004, Richardson and Schoeman 2004, MacLeod *et al.* 2005), may alter the spatial distribution of primary and secondary production, concurrently reducing the resource availability, especially the high-quality prey. Most baleen whales, as they are capital breeders, may not reproduce until enough nutritional reserves have been achieved (Kraus and Hatch 2001, Reeves *et al.* 2001). On the other hand, many toothed cetaceans may wean their calves earlier than expected, which results in smaller *Lw.* The impact may be even worse on small-sized cetaceans because their lactation energetics depends on enhanced daily feeding success (Yasui and Gaskin 1986, Cheal and Gales 1991, Kastelein *et al.* 2002). Their feeding depends on prey that presumably is accessible diurnally (Benoit-Bird 2004). A shortage of potential food for 1–2 d may have a catastrophic effect on their lactation.

Another possible factor for weaning failure may have to do with anthropogenic separation caused by fisheries (Archer *et al.* 2006, Noren and Edwards 2007) or vessels in dolphin-watching tourism (Bejder *et al.* 2006). Both may lead to mortality of the calves. This threat may be independent of the problem of reduced food but could further contribute to weaning failure. Upon perceiving a potential threat, cetaceans move away from the disturbance immediately (Au and Perryman 1982). For the more sensitive nourishing mother–calf pairs, such retreat is more drastic, leaving the calves falling behind their mothers (Weihs 2004), and often causes long-term separation of the calf from the mother (Bejder *et al.* 2006, Noren and Edwards 2007). These separations potentially increase calf mortality. We therefore suggested that when forming conservation acts and establishing marine protected areas for cetaceans, considerations should be given to maintaining high-quality and low-impact waters to reduce the potential risk of weaning failure.

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