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CORRELATIONS IN CETACEAN LIFE HISTORY TRAITS

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***ABSTRACT.* –** Life history traits (LHT), profiling the schedule of growth and reproduction of organisms, directly determine the reproductive fitness and long-term persistence of species. Understanding the characteristic LHT of species is a crucial step in making sound conservation policies. Nonetheless, the complete LHT of many cetaceans is not readily elucidated, primarily due to their strictly aquatic lifestyle, often gigantic body size and long lifespan. In this study, we collected and analyzed six LHT from published literature, including female asymptotic length (Lx), length at birth (Lb), length at sexual maturity (Lm), calving interval (CI), age at sexual maturity (Am) and lifespan (Ax) in order to explore their potential correlations with LHT which determine their maternal fitness. In a general linear model, strong allometric relationships were observed between Lx and the other five LHT and, with high R^2, it was possible to extrapolate the Lb, Lm and Ax of undocumented species directly from their Lx. Furthermore, general linear model analysis indicated that the Ax of cetaceans is not only related to their Lx, but also their Am (where $Ax = 0.962\ Lx^{0.435} Am^{0.463}$). When the confounding effect of Lx is factored out, the differences between baleen and toothed cetaceans are valid for Lb and CI but not for Lm, Am and Ax. Based on the significantly different reproductive energetics (capital or income breeder) and the potential ecological differences between baleen and toothed cetaceans, we interpreted the effect of intrinsic and extrinsic factors on LHT allometric regressions.

***KEY WORDS*. –** Allometry, cetacean, conservation, life history, lifespan.

INTRODUCTION

Cetaceans are top marine predators but many of them face grave challenges in their long-term survival due to massive and unmonitored fishery bycatches (Dans et al., 2003), depleting potential food resources because of overfishing (Neira & Arancibia, 2004), bioaccumulation of pollutants (Aguilar & Borrell, 1994; Ylitalo et al., 2001), naval sonar manoeuvres (Fernandez et al., 2005), malignant whale-watching tourism (Bejder et al., 2006) and, perhaps, the effects of global climate change (MacLeod et al., 2005). Some difficulties in making conservation policies arise from the lack of knowledge of cetacean life history traits (LHT) (Parra et al., 2004).

Life history traits directly determine evolutionary fitness (Blueweiss et al., 1978; Allaine et al., 1987; Charnov, 1991, 2001; Metcalf & Pavard, 2006) and affect the long-term persistence of a species (Jefferson, 2000; Ferguson & Higdon, 2006). The reproductive fitness, in terms of the expected daughters per female per lifetime (R_0), is determined by LHT,

$$R_0 = \frac{b \times S(\alpha)}{M} \quad \text{(Charnov, 1991)} \qquad [1],$$

where b is the birth rate of daughters per unit time, $S(\alpha)$ is the survival rate of daughters from birth to sexual maturity and M is the instantaneous mortality rate. The factor b is potentially affected by calving interval, and size and age at sexual maturity (Charnov, 1991). The factor $\frac{1}{M}$ determines the potential lifespan (Ax) and is affected by body size and age at sexual maturity (Charnov, 1991). includes the survival rate of different stages of growth. For cetaceans, the survival in the first year (s_0) is significantly lower than in the following years (Small & Demaster, 1995; Barlow & Clapham, 1997; Mann et al., 2000; Best et al., 2001; Clapham et al., 2003;

Table 1. Effect (F-value) of Lx on Lb, Lm, CI, Am and Ax in cetaceans by GLM and significant tests between suborders Mysticeti and Odontoceti.

Effect	Lb	Lm	CI	Am	Ax
Lx	875.01	1427.7	12.93	9.35	35.74
Suborder	9.75	3.34^{NS}	11.46	3.57^{NS}	0.053^{NS}

NS: not significant at $p > 0.05$

Table 2. Coefficient of allometry regression to Lx in cetaceans, logY = a + blogLx, where Y represents Lb, Lm, CI, Am and Ax. The effect of suborder on Lb and CI were considered but excluding Lm, Am and Ax.

	Lb		Lm	CI		Am	Ax
	Mysticeti	Odontoceti		Mysticeti	Odontoceti		
a	0.091	-0.163	0.057	0.443	0.574	0.531	0.271
b	0.798	0.912	0.948	0.319	0.375	0.138	0.492
R^2	0.880	0.932	0.985	0.220	0.279	0.087	0.683
p	< 0.001	< 0.001	< 0.001	0.124	0.001	0.034	< 0.001

Bradford et al., 2006). Some studies have shown that s_0 is strongly affected by the size at birth (Pontier et al., 1993; Beekman et al., 1999; Chambellant et al., 2003; McMahon & Hindell, 2003). In other words, the maternal size, the size at birth, the size and age at sexual maturity, the calving interval, and lifespan are the potential LHT that significantly affect reproductive fitness in cetaceans.

The best way of obtaining first-hand LHT is to follow the fate of individuals and record the size and age at different stages of growth. However, this approach is constrained by the long lifespan of these organisms. Meta-analysis of existing databases is another alternative (Barreto & Rosas, 2006). Nonetheless, constructing a detailed database usually requires massive specimen collection from lethal operations. In cetaceans, many data come from fishery activities (Archer & Robertsona, 2004), incident stranding events, or both (Barreto & Rosas, 2006), which generally excludes the rare and endangered species. Unlike terrestrial mammals, many cetaceans are too large to be manipulated directly, or too long-lived to be monitored for generations. In addition, their strictly aquatic lifestyle makes them almost inaccessible to most researchers. Finding reliable, easy-to-use and, most of all, non-lethal ways to estimate LHT in cetaceans requires immediate attention, especially when some species are in decline, endangered or at the verge of extinction.

The potential method to reliably extrapolate the LHT of undocumented species is to use the allometric relationships in LHT, expressed by:

$$Y = aX^b \rightarrow \log Y = \log a + b \log X \text{ (Blueweiss et al., 1978)} \quad [2]$$

where Y and X represent the correlated LHT, a is the allometric coefficient and b the allometric exponent (Blueweiss et al., 1978; Allaine et al., 1987; Stearns, 1992). However, directly using bi-variate regressions without accounting for potential confounding factors, especially body size, may lead to over-simplified results (Stearns, 1992). Therefore, eliminating potential confounding effects before regressions is necessary. In this study, we seek to clarify the interactions in cetaceans' LHT and propose reliable expressions. In these analyses, the variation between the two suborders of cetaceans, baleen whales (Mysticeti) and toothed whales (Odontoceti), is considered. We focus particularly on the estimation of Ax which is one of the most difficult LHT to access, requiring life-long tracking or a data from a huge number of dead, mature cetaceans.

MATERIALS AND METHODS

Data collection. – We collected six LHT, i.e. female asymptotic length (Lx), length at birth (Lb), length at sexual maturity (Lm), age at sexual maturity (Am), calving interval (CI) and life span (Ax), based on data sourced from scientific journals, scientific reports and biological books published by scientific societies. When data were provided as a range rather than a fixed value, the midpoint of the range was taken. When there was more than one record published for a species, we calculated the midpoint of each published value and took the average of these midpoints in our operation (Kovacs & Lavign, 1986; Allaine et al., 1987; Pontier et al.,1993; Silva, 1998; Trites & Pauly, 1998; Read, 2001; Schulz & Bowen 2004).

Statistical analysis. – The correlations in LHT were first explored by the allometric relationship (expression [2]):

$$\log Y = \log a + b \log X,$$

where X was Lx and Y represented Lb, Lm, CI, AM and Ax. All LHT data were log-transformed and analysed by general linear model (GLM). The effect of suborders Mysticeti and Odontoceti on the allometries was also analysed by GLM. The applicability was set at $R^2 \geq 0.50$ (Blueweiss et al., 1978).

Table 3. Correlation of residuals in life history traits after removing the confounding Lx.

	Lb	Lm	CI	Am
Lm	0.502	–	–	
CI	-0.099	-0.106	–	–
Am	-0.142	-0.007	0.632	–
Ax	-0.074	-0.149	0.509	0.572

Table 4. The determination of Ax by stepwise GLM. The effect of CI was not significant and therefore removed, which yielded the generalized expression: logAx = -0.017 + 0.435 logLx + 0.463 logAm or $Ax = 0.962\ Lx^{0.435}\ Am^{0.463}$, $R^2=0.782$.

Effect	F	p	Coefficeint
Constant	–	–	–0.017
Lx	91.032	< 0.001	0.435
Am	8.828	0.005	0.463
CI	2.343	0.135	–

To further explore the interactions in LHT while avoiding the confounding effect of Lx, the correlation of residuals was analysed (Stearns, 1992). The residuals of each LHT (ε), except for Lx, was calculated by the following equation:

$$\varepsilon = \log Y - (\log a + b \times \log Lx) \quad \text{(Stearns, 1992)} \qquad [3],$$

where Y represents Lb, Lm, Am, CI and Ax. Finally, Pearson correlation coefficients were calculated with significance ($p < 0.05$) determined by Bonferroni tests.

RESULTS

The GLM results indicate that Lx had significant effect on Lb, Lm, CI, Am and Ax in cetaceans (Table 1). However, the effect of suborder affected homogeneity significantly for both Lb and CI, but not for Lm, Am and Ax (Table 1). Therefore, the allometric regressions on Lb and CI were tested separately for different suborders, while Lm, Am and Ax were explored for cetaceans as a group. For Am and CI, their R^2 values were too low ($R^2 = 0.086$ and 0.279, respectively) (Table 2) to extrapolate to other undocumented species. Therefore, four general expressions were left to estimate Lb (within two cetaceans groups), Lm and Ax of cetaceans:

$$\log Lb = 0.091 + 0.0796 \log Lx \ (Lb = 1.234\ Lx^{0.796}) \text{ for baleen whales} \qquad [4],$$

$$\log Lb = -0.163 + 0.932 \log Lx \ (Lb = 0.687\ Lx^{0.932}) \text{ for toothed whales} \qquad [5],$$

$$\log Lm = 0.057 + 0.948 \log Lx \ (Lm = 1.140\ Lx^{0.948}) \qquad [6],$$

and

$$\log Ax = 0.271 + 0.492 \log Lx \ (Ax = 1.865\ Lx^{0.492}) \qquad [7].$$

The residuals of Lb, Lm, CI, Am and Ax and their correlations were calculated (Table 3). Lb and Lm were significantly correlated with each other ($r = 0.50$, Bonferroni $p = 0.001$), but neither of them were correlated with CI, Am and Ax. We therefore conclude that size at birth and at sexual maturity do not have a direct effect on life span, calving interval, and age at sexual maturity in cetaceans. Furthermore, both CI ($r = 0.509$, Bonferroni $p = 0.001$) and Am ($r = 0.572$, Bonferroni $p < 0.001$) were significantly correlated with Ax. Nonetheless, they were also significantly correlated with each other ($r = 0.632$, Bonferroni $p < 0.001$) and this required further exploration.

By stepwise GLM, either forward or backward, the effect of CI on Ax was not significant (Table 4). That is, the seeming correlation between CI and Ax indeed comes from the confounding Am. Consequently, we presented another general proxy expression of Ax determination with a higher R^2,

$$Ax = 0.962\ Lx^{0.435}\ Am^{0.463},\ R^2 = 0.782 \qquad [8].$$

DISCUSSION

Ax of 45 species has so far been documented. By expressions [7] and [8], we expand current knowledge about cetaceans' lifespan to 79 species of 14 families (Fig. 1). In general, baleen whales and the sperm whale (*Physeter macrocephalus*) live longer, from 40 years for the pygmy right whale (*Caperea maginata*) to more than 100 years for the bowhead whale (*Balaena mysticetus*), than medium or small cetaceans, that live from 14 years for the harbour porpoise (*Phocoena phocoena*) to approximately 60 years for pilot whales (*Globicephala macrorhychus* and *G. melaena*).

Cetaceans are phylogenetically divided into two suborders, Mysticeti for baleen whales and Odontoceti for toothed cetaceans. Baleen whales are quite different from toothed cetaceans in morphology, anatomy, body size, feeding niches, reproductive energetics and mating systems (Oftedal, 1997; Boness et al., 2002). Any potential variations in life histories between baleen and toothed cetaceans may therefore result from the differences in these traits. However, this study shows that when the confounding Lx is factored out, variations in five LHT (Lb, Lm, Am, CI and Ax) do not always associate with the phylogenetic difference, only Lb and CI are significantly different between baleen and toothed whales but Lm, Am and Ax are not.

Factors potentially affecting length at birth (Lb) and calving interval (CI)

Size at birth is determined by maternal investment during gestation (Kovacs & Lavigne, 1986, 1992; Pontier et al., 1993; Boltnev & York, 2001; Read, 2001; Gorman & Nager, 2004). Prenatal investment depends on the type and availability of the food resources (Leon & De Nobrega, 2000; Georges & Guinet, 2001). Baleen whales primarily feed on plankton while toothed whales feed on fishes, cephalopods and other marine mammals. For toothed whales, their feeding may be primarily limited by time and efficiency rather than seasonality of available prey (Benoit-Bird, 2004). In contrast, the seasonality of prey availability is critical for baleen whales. The patterns of foraging during gestation are quite different between baleen and toothed whales. Baleen whales reduce their feeding success and nourish their offspring using their somatic reservoirs (Lockyer, 1984; Oftedal, 1997) while toothed cetaceans concurrently feed themselves during gestation (Yasui & Gaskin, 1986; Cheal & Gales, 1991; Kastelein et al., 1993, Kastelein et al., 2002), corresponding to two forms of reproductive energetics: “capital” and “income” breeders (Stearns, 1992; Jonsson, 1997; Bonnet et al., 1998). Capital breeders such as baleen whales acquire and store energy in advance of the reproduction. Conversely, income breeders such as toothed cetaceans elevate their feeding levels concurrently with the breeding to meet the cost of reproduction. The different slopes of allometries in Lb between baleen and toothed cetaceans may potentially come from a combination of their different reproductive energetics and their different diets.

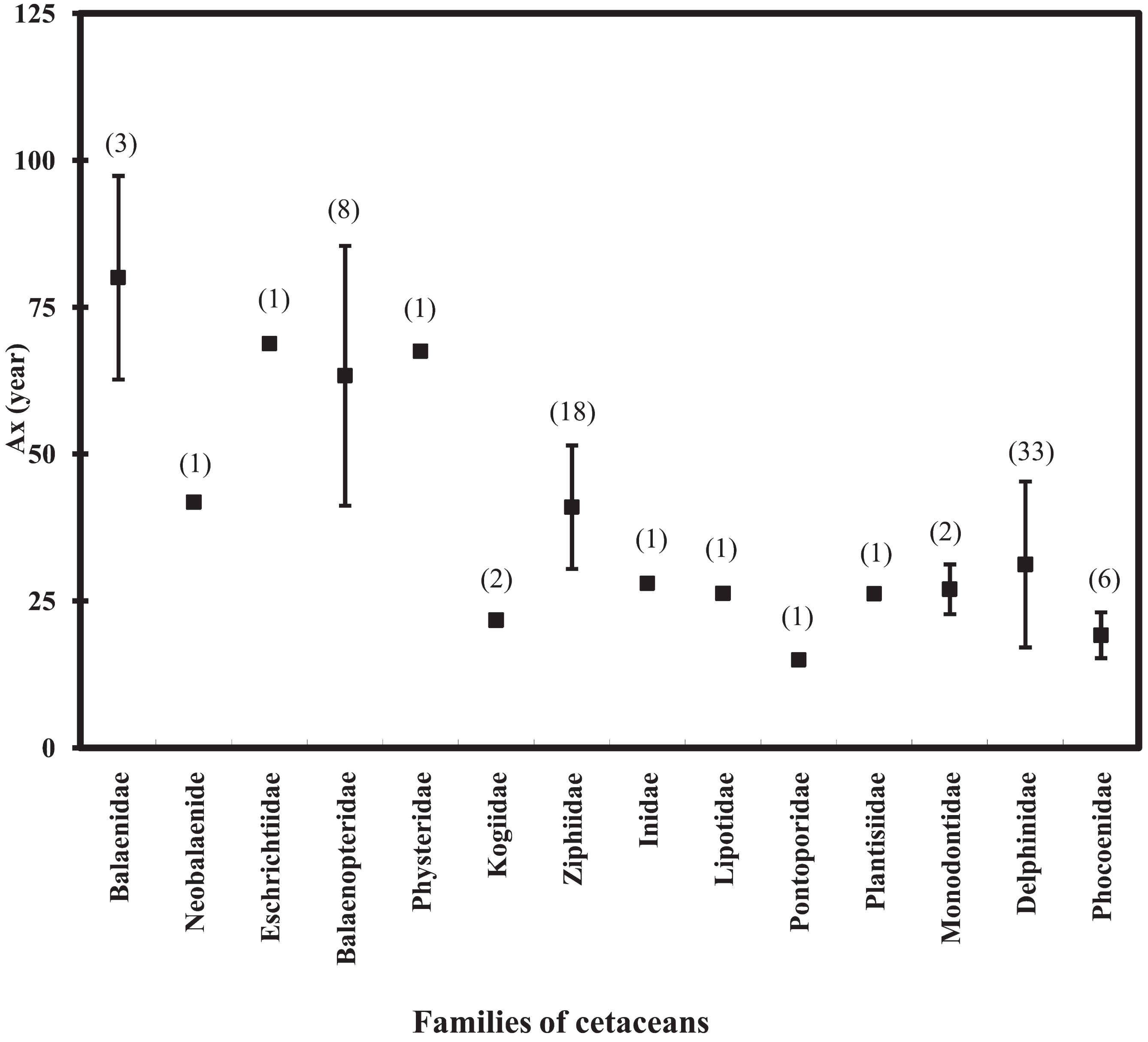

Fig. 1. Mean and range (± SD) of longevity (Ax*)* in cetaceans. Numbers above each family represent number of available species.

For capital breeders, availability and seasonality of potential food may have important effects on CI (Stearns, 1992; Jonsson, 1997). In baleen whales, Reeves et al. (2001) reported an inverse relationship between CI and marine productivities, however, body size had little effect on CI, consistent with our own findings. On the other hand, organisms in resource-rich and predictable environments usually use income strategies, coupled with long CI to reduce their daily energy expenditure (Johnsson, 1997; Dufour & Sauther, 2002). Organisms with large body size generally have longer CI (Blueweiss et al., 1978; Stearns, 1983), potentially due to longer growth time, longer period of maternal dependence, and skewing to K-strategy end of life histories (Allaine et al., 1987). The social parental care system, especially when the alloparent helper in a cooperative system is included (Geffen et al., 1996), sometimes results in extra-long CI. In toothed whales, such as the killer whale (*Orcinus orca*) and the sperm whale (*Physter macrocephalus*), have complex maternal social linkages and very long CI (Best et al., 1984; Perrin & Reilly, 1984; Whitehead, 1996; Whitehead et al., 2004; Foote 2008). Nonetheless, high sociability is not necessarily associated with large body size. For example, the beaked whales—toothed whales comparable in size to killer whales—do not have high sociability (Gowans et al., 2001) and seldom have long CI. Furthermore, many small-sized mammals also feature alloparental-care reproductive systems, further complicating and reducing the correlation of CI to body size. Therefore, the statistically significant correlation between CI and body size in toothed cetaceans may be the joint result of body size, reproductive energetics and sociability.

Factors adjusting lifespan (Ax)

The potential Ax is determined by both intrinsic and extrinsic mortality. The asymptotic size is one of the most direct and decisive parameters, either in theoretical approaches (Charnov, 1991) or in empirical approaches (as this study). Life history theory predicts low mortality will result in long Ax and large body size (Charnov, 1991; Stearns 1992). However, the evolution of body size is also shaped by phylogeny, resource availability and environmental conditions (Brown et al., 1993; Diniz-Filho & Veira, 1998; Symonds & Elgar, 2002; Savage et al., 2004; West et al., 2004). When the effect from phylogeny is factored out, organisms that live in resource-rich and environment-stable patches are usually large and have a long lifespan.

The age at sexual maturity is another important parameter in determining Ax (Charnov, 1991; Stearns, 1992). When organisms attain sexual maturity and start to reproduce, their mortality increases and Ax shortens due to aging after conception. Though organisms with large size generally have low mortality, long lifespan and, perhaps, high reproductive fitness, it is usually accompanied with late sexual maturity (George et al., 1999). When environment stability is low or the resource distribution and availability is stochastic, life histories of early sexual maturity, small body size, high mortality and short Ax should increase the probability of successful reproduction.

The Ax is not only affected and constrained by intrinsic parameters but is also determined by extrinsic mortality. For cetaceans, extrinsic mortality comes from fishery bycatches, ship collisions (Kraus, 1990) and mother-calf separation (Noren & Edwards, 2007), for example. The fluctuation and availability of potential food also has profound effects on extrinsic mortality. For toothed cetaceans, the availability of their potential prey, rather than their feeding efficiency, will have a decisive effect on the daily energetic maintenance (Benoit-Bird, 2004). Even a shortage of food for one to two days can have catastrophic effects on their lives. On the other hand, for baleen whales, characterized by their huge body size and non-continuous feeding, short-term fluctuation and availability of food seemingly has less effect on mortality because of huge body size and associated fat reservoirs. However, the distribution and amount of their potential prey, primarily plankton, is largely dependent on the primary productivity of ocean systems. Large-scale environment changes, such as those predicted with global climate change, will alter the distribution and seasonality of their potential food (Neira & Arancibia, 2004; Richardson & Schoeman, 2004; MacLeod et al., 2005), potentially affecting their mortality and the consequent Ax.

In some situations, extrinsic mortality may also affect the intrinsic parameters and further reduce Ax. When a stock or species is over-exploited, compensation effects result in early maturation, shortening Am, reducing asymptotic size and finally shortening Ax (Lockyer, 1984; Kasuya, 1991; Chivers & Demaster, 1994; Kasuya, 1999). For example, the Am declined from 10 to 6 years in the fin whale (*Balaenoptera physalus*), 11.4 to 7 years in the sei whale (*B. borealis*) and 14 to 6 years in the minke whale (*B. acutorostrata*) (Lockyer, 1984). Unfortunately, the extent to how over-exploitation affects the asymptotic size or the Ax which in cetaceans is unknown. In future studies examining life histories and stock persistence of cetaceans, the net effect from extrinsic mortality, especially from anthropogenic mortality, on Lx and Am should be monitored because they both are fundamental to cetacean lifespan.

Empirical CI and AM are required

Over-extrapolating the observed regressions, especially those which are statistically significant but with low R^2 (< 0.50), such as CI and Am of the cetaceans in this study, should be viewed with caution (Blueweiss et al., 1978). That is, only through direct measurements, either non-lethal or lethal, can identify CI and Am of the remaining undocumented species. This work requires immediate attention because many of these species are rare and/or endangered. Long-term fishery activities should be continuously monitored, not only for evaluating if the annual removal exceeds the PBR (potential biological removal) (Wade, 1998), but also because it provides first hand data on CI and Am with minimal lethal specimen collection. This work should given highest priority in future studies, not only to better cetacean LHT but also to ensure the long-term existence of these ocean giants.

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