

## Swimming speed estimation of extinct marine reptiles: energetic approach revisited

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**Abstract.**—Cruising speeds of Mesozoic marine reptiles have been estimated in the past by using a mathematical model of energetic equilibrium during steady swimming. This method suffered from a significant tendency to overestimate speeds of extant cetaceans for no clear reason, which raised questions about the validity of the approach itself. The present study identifies the factors that caused this shortcoming and proposes corrections and some additional modifications. These include the use of more accurate body shape models, updated metabolic rate models, and optimal rather than critical swimming speeds. The amended method successfully approximates published optimal speeds of several extant marine vertebrates, including cetaceans, showing that the basic framework of the energetic approach is valid. With this confirmation, the method was applied to Mesozoic marine reptiles, by assuming three different metabolic rate categories known in extant swimming vertebrates (i.e., average ectothermic, raised ectothermic, and marine endothermic levels). The results support previous inferences about the relative cruising capabilities of Mesozoic marine reptiles (i.e., ichthyosaurs > plesiosaurs > mosasaurs). *Stenopterygius*, a thunniform ichthyosaur, was probably capable of cruising at a speed at least comparable to those reported for some extant thunniform teleosts with similar diets (~1 m/second).

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### Introduction

Swimming capabilities of aquatic vertebrates reflect their behavior, physiology, locomotory biomechanics, and other aspects of their biology. Therefore, estimating swimming speeds of extinct marine vertebrates is an important step toward understanding the biology and evolution of these animals. Characteristic swimming speeds, such as the critical speed (the maximum speed that can be sustained) and optimal speed (the speed at which the energy required to move the body for a unit length is minimal), are not easily obtained even for extant vertebrates, and for this reason, some may question the feasibility of estimating swimming speeds in animals that are long extinct. However, physical constraints in the aquatic environment are very stringent, especially for large vertebrates whose Reynolds numbers during locomotion are large (i.e., high  $10^5$  to low  $10^7$ ). Fluid dynamics constrains the feasible swimming speed of a vertebrate, according to its body shape, size, and physiology. Thus, by identifying these constraints, it should be possible to delimit the range of the typical swimming

speed of a given vertebrate from its morphological and physiological features. If the ranges of speed thus obtained were too broad to make useful predictions about their behaviors, the hypothesis of stringent constraints would be rejected. It would then be possible to state with confidence for the first time that speed estimation of extinct aquatic vertebrates is not feasible. If the ranges were sufficiently narrow, however, they would enable useful predictions about the behavior and other biological aspects of these swimming vertebrates.

There are at least three ways to limit the possible ranges of typical swimming speeds for aquatic vertebrates. The first one takes an energetic perspective and uses a simple equation stating that the amount of energy spent for locomotion at a constant speed equals the amount of work done to overcome drag (e.g., Massare 1988). This method is applicable to a wide range of body shapes, and is the focus of the present contribution. The second approach uses the hydrodynamic properties of propulsive organs, such as caudal flukes (e.g., Bose and Lien 1989). It requires the three-dimensional shape and several mechanical

properties of the propulsive organ to be known and therefore is difficult to apply to extinct animals. The third approach is to use the observed scaling effects of caudal fin kinematics, which will be described elsewhere.

In 1988, Judy Massare published the first speed estimates for Mesozoic marine reptiles, which she later emended in 1994. Her methods were based on a model of energetics in swimming vertebrates, which allowed calculation of swimming speeds from metabolic rates and certain physiological and hydrodynamic constants. Although her breakthrough study was reasonably well supported theoretically, it overestimated the swimming speeds of extant cetaceans by a factor of 1.4 to 8.3 (Massare 1988). She suggested that such errors were probably caused by drag coefficients, which she thought were most likely underestimated in her study (Massare 1988); she used equations for rigid bodies to estimate drag coefficients, whereas it is generally accepted that actively swimming vertebrates experience more drag than when passively dragged at the same speed. However, the differences between drag coefficients used by Massare (1988) and those estimated for several cetaceans (Fish 1998) are too small to account for the large differences between estimated and measured speeds.

This paper provides support to Massare's (1988, 1994) theoretical framework by establishing that the reasons for the original overestimation were mostly calculation errors. It is much easier today to detect these errors thanks to technological advancements in personal computing. I will then propose some modifications that will strengthen the method, and test the revised method with data for extant swimming vertebrates. Finally, I will apply the method to some Mesozoic marine reptiles.

### Reexamination of Previous Studies

At the core of Massare's (1988, 1994) method lies a single equation that states that the amount of energy used to sustain a given speed equals that required to overcome the drag at that speed:

$$\varepsilon_p \varepsilon_A M_{Lcrit} = 0.5 \rho S C_d U_{crit}^3 \quad (1)$$

where  $\varepsilon_p$  is the propulsive efficiency of a given swimming mode,  $\varepsilon_A$  is the aerobic efficiency of muscle,  $\rho$  is the density of seawater, and  $M_{Lcrit}$ ,  $S$ ,  $C_d$ , and  $U_{crit}$  are the critical metabolic cost of locomotion (maximum metabolic rate sustainable for a given duration), surface area, wetted-area drag coefficient, and critical speed (or the maximum speed sustainable for a given duration) of an animal. To calculate  $U_{crit}$  from this equation, it is necessary to have reasonable estimates of  $S$ ,  $C_d$ ,  $\varepsilon_p$ ,  $\varepsilon_A$ , and  $M_{Lcrit}$ . Therefore, if the theoretical framework of Massare (1988) were to be defended despite the large error margin of the outcome, errors should be found in her estimates of these variables.

*Numerical Errors.*—The critical metabolic rate is the most difficult of the five to estimate. Massare (1988) referred to Bakker (1975) for regression equations that relate body mass to metabolic rates, and two errors were introduced at this stage. Bakker gave equations in the form of

$$M_{crit} = aW^{-0.25} \text{ (cal/gh)}$$

where  $W$  and  $M_{crit}$  are the weight and total maximum sustained metabolic rate of an animal, whereas  $a$  is a constant specific to a given taxon. Massare (1988) converted the unit to w/kg, but a simple arithmetic error was made in this unit conversion. The conversion factor is not  $4.184 \times 1000/3600 = 1.16$  as Massare (1988) calculated, but should be  $4.184 \times 1000^{0.75}/3600 = 0.207$ . This led to the overestimate of metabolic rates by a factor of 5.60.

The second error is the omission of basal metabolic rates ( $M_B$ ). Not all of  $M_{crit}$  is available for locomotion, but  $M_B$  should be subtracted from the total metabolic rate to obtain the part used for locomotion:

$$M_{Lcrit} = M_{crit} - M_B \quad (2)$$

In lizards,  $M_B$  is about a fifth of the average  $M_{crit}$  (Bakker 1975: Table 21.1), so the omission of  $M_B$  led to the overestimation of  $M_{Lcrit}$  by a factor of 1.25, and about 1.1 for mammals. When these errors were combined,  $M_{Lcrit}$  was overestimated by a factor of 7.00, which translates to a factor of 1.91 ( $= 7^{0.3333}$ ) for  $U_{crit}$  overestimation (about 1.81 for mammals).

TABLE 1. Corrected estimates of critical swimming speeds ( $U_{crit}$ ) for whales compared with the swimming speeds listed by Massare (1988) and Fish (1998). Even corrected values seem to overestimate observed swimming speeds. Note, however, that observed speeds do not necessarily represent critical or optimal speeds (see text). The speeds given by Fish (1998) based on aquarium cetaceans were added for comparison to show the variability of observed speeds. The speeds given by Massare (1988) were collected from the literature.

Species	Length (m)	Observed speed (m/s)		Estimated $U_{crit}$ (m/s)	
		Massare	Fish	Massare	Corrected
<i>Delphinus delphis</i>	2.5	2.0–3.0		7.1	3.9
<i>Tursiops truncatus</i>	3.5	2.0–3.0	1.2–6.0	7.4	4.0
<i>Delphinapterus leucas</i>	6.5	3.1	1.5–3.8	7.7	4.2
<i>Orcinus orca</i>	8	2.8–3.6	2.0–7.9	7.4	4.0
<i>Eschrichtius robustus</i>	13	1.0–1.5		8.2	4.5
<i>Physeter catodon</i>	14	5.2		8.3	4.5
<i>Balaena mysticetus</i>	15	1.0		8.3	4.5
<i>Megaptera novaeangliae</i>	16	1.1–2.6		8.2	4.5
<i>Balaenoptera physalus</i>	21	5.2–6.2		8.4	4.6
<i>Balaenoptera musculus</i>	25	5.2–6.2		8.5	4.6

The volume and surface area of an extinct animal are also difficult to estimate. Massare's (1988) solution was to simplify the task by assuming that prolate spheroids could approximate the shape of marine reptiles. This, as she admitted, leads to overestimates of both surface area and weight. I applied the same method to four species of cetaceans examined by Fish (1998) and obtained overestimation factors of 1.41 and 1.07 for body mass and surface area, respectively. However, as evident from equation (1), these errors compensate for each other, and consequently, the combined overestimation of  $U_{crit}$  from these two factors is only 1.06.

As a result of the combined effect of the errors stated above,  $U_{crit}$  values calculated by Massare (1988) were overestimated by a factor of 2.02 ( $= 1.91 \times 1.06$ ) on average for reptiles, and 1.82 for mammals. Thus, by dividing the published speeds (Massare 1988: Table 1 and appendix) by these factors, it is possible to obtain corrected estimates given her model (Table 1). Such estimates for cetaceans are much closer to the observed speeds listed by Massare (1988), suggesting that the majority of the differences between estimated and measured speeds are attributable to the simple errors described above (Table 1). This is partly because observed speeds do not necessarily represent critical speeds: the animals can conserve energy by swimming at a speed lower than the critical speed. For example, Marsac and Cayré (1998) reported a median speed of 0.90 m/s

for a yellowfin tuna (fork length 0.58 m; from the tip of the snout to the fork of the caudal fin), which is slightly less than the optimal speed (1.0 m/second) for an individual 10% smaller (fork length 0.51 m; Dewar and Graham 1994a). Critical speeds are usually expected to be higher than optimal speeds and therefore it is difficult to test estimated critical speeds with observed speeds.

*Other Points.*—Although much of the original discrepancy can be removed by applying the correction factors described above, some problems remain. First, speeds are still overestimated for many extant cetaceans (Table 1). Second, the estimated speeds do not scale with body size as much as expected. For example, all ichthyosaurs examined by Massare (1988;  $n = 65$ ), ranging in body length from 0.47 to 11.35 m, have average estimated speeds between 1.08 and 1.29 m/second (after correction). Cetaceans ranging from 2.5 to 25 m in body length have estimated speeds between 3.9 and 4.6 m/second (after correction). Although critical swimming speed does show negative allometry with body length in fishes (e.g., Webb and Keyes 1982; Webb and Kosteki 1984), the allometric slopes from Massare's (1988) estimated speed are obviously too small. Third, Massare (1988: Figs. 5, 6) found that animals with narrower bodies had lower critical speeds, but higher fineness ratios, found in narrower bodies, are known to reduce drag coefficients (Vogel 1994). These

three points suggest that a modification of the model is necessary.

There is another and more fundamental problem, which is specific to the application of the method to marine reptiles. The maximum sustained metabolic rates for reptiles, given by Bakker (1975: Table 21.1), is achieved at a high body temperature of about 38°C. However, only endotherms, and some intermediate ectotherms such as tunas and leatherback turtles, can maintain raised body temperature in water, which contradicts the use of metabolic rates derived from average ectothermic reptiles. Also, even large obligatory swimmers, such as minke whales, do not sustain such a high core temperature (Folkow and Blix 1992). Therefore, the application of the maximum aerobic metabolic rates listed by Bakker (1975) would lead to a large overestimation of swimming speeds for aquatic reptiles.

### Proposed Modifications

Many of the problems pointed out in the previous section can be resolved by the following five modifications: (1) use of optimal swimming speed instead of critical speed; (2) improvement of the data on metabolic rate, such as consideration of "intermediate physiology" found in leatherback turtles and tunas; (3) use of a correction factor to compensate for errors in the estimated values of constants, such as  $\varepsilon_p$ ,  $\varepsilon_A$ , and  $C_d$ ; (4) use of an equation for drag coefficient that incorporates the scaling effect with the Reynolds number; and (5) use of improved estimates for body mass and surface area. Detailed explanations of the five follow.

*Optimal versus Critical Speeds.*—As explained earlier with equation (2), estimation of critical swimming speeds requires a priori knowledge of the difference between the basal and critical metabolic rates (the latter refers to the maximum rate that can be sustained). This is disadvantageous for two reasons. First, subtracting an estimated value from another necessarily lowers the confidence level of the outcome. Second, the critical metabolic rates of extinct marine reptiles are difficult to estimate: it would be necessary to know their thermal strategy, as well as aerobic and anaerobic scopes.

A solution to these problems is found in the use of optimal swimming speed ( $U_{opt}$ , the speed at which the total cost of transport is minimal) instead of  $U_{crit}$ . Without adding any assumptions to the model,  $U_{opt}$  can be calculated without knowledge of the critical metabolic rate. A more general form of equation (1) is given as

$$\varepsilon_p \varepsilon_A M_L = 0.5 \rho S C_d U^3 \quad (1')$$

where  $M_L$  is the metabolic cost of locomotion at speed  $U$  (Hind and Gurney 1997). The total metabolic rate ( $M$ ) can be expressed as the sum of three components, viz., the basal metabolic rate ( $M_B$ ), the metabolic cost of thermoregulation through extra heat generation ( $M_T$ ), and the metabolic cost of locomotion (Hind and Gurney 1997):

$$M = M_B + M_T + M_L \quad (3)$$

The total cost of transport ( $COT_{TOT}$ ) is defined as the metabolic energy generated while transporting the body over a unit distance (Williams 1999). Therefore, at speed  $U$ ,

$$COT_{TOT} = M/U \quad (4)$$

From equations (1'), (3) and (4):

$$COT_{TOT} = (M_B + M_T)/U + 0.5 \rho S C_d U^2 / \varepsilon_p \varepsilon_A \quad (5)$$

$M_T$  is a function of  $U$  and is known to decrease with increasing  $U$ , as excess heat generation from locomotion surpasses the heat loss from the body surface (Hind and Gurney 1997).  $M_T$  can be considered approximately zero for the true ectotherms, which, by definition, are not supposed to thermoregulate metabolically. For other swimming vertebrates (those with homeothermy or modest thermoregulatory ability),  $M_T$  can also be considered zero at the optimal swimming speed, except in low water temperatures. Hind and Gurney (1997: Fig. 4) found that  $M_T$  became approximately zero before the optimal speed was reached in a sea lion, and the same seems to be true for other taxa at a water temperature of 20°C, judging from their Figures 3 and 6.  $COT_{TOT}$  is minimal at the optimal speed, which means that the first derivative of  $COT_{TOT}$ , as given in equation (5), equals zero at  $U_{opt}$ . With these conditions,

the following equation can be derived from equation (5):

$$U_{opt} = (\varepsilon_p \varepsilon_A M_B / 0.5 \rho S C_d)^{0.3333} \quad (6)$$

It may appear counterintuitive that the optimal speed may be defined as a function of the basal metabolic rate, not the exercise metabolic rate. However, equation (6) does incorporate exercise metabolic rates, as is obvious from its derivation.  $M_B$  is the intercept when plotting  $M$  against  $U$ , and therefore appears in (6).

**Correction Factor.**—Hind and Gurney (1997) introduced a single correction factor that enables a higher fit of theoretical equations to actual data. With the addition of this factor,  $\lambda$ , equation (6) is modified to:

$$U_{opt} = (\varepsilon_p \varepsilon_A M_B / 0.5 \rho \lambda S C_d)^{0.3333} \quad (6')$$

Hind and Gurney (1997) interpreted  $\lambda$  as the ratio between active and passive drag coefficients. However,  $\lambda$  actually functions as a correction factor for all elements of the equation, especially those with less well established values (e.g.,  $C_d / \varepsilon_p \varepsilon_A$ ), and not just for  $C_d$  alone. The value of  $\lambda$  was calculated to be about 0.20 in minke whales, 0.39 in sea lions, and 0.80 in seals (Hind and Gurney 1997: Table 3). However, these values assumed very low  $\varepsilon_A$  values obtained from the following equation:

$$\varepsilon_A = 0.0679 + 0.441(U/5)^3 - 0.422(U/5)^6$$

where  $U$  is in meters per second. When using the  $\varepsilon_A$  value of 0.17,  $\lambda$  should be calibrated accordingly. At the optimal speeds given by Hind and Gurney (1997), the average values of recalculated  $\lambda$  are about 0.20, 0.82, and 1.6 for minke whales, sea lions, and seals, respectively.

Hind and Gurney (1997) suggested that  $\lambda$  was probably a constant specific to swimming modes. This, however, is not well established at present. Therefore, I first assume that their suggestion is correct. If this assumption leads to large errors when the method is applied to extant vertebrates whose optimal speeds are known, then the assumption is probably wrong and should be abandoned. If it does not, however, then  $\lambda$  is probably a variable with very narrow value range, or possibly a constant. Theoretical justification of  $\lambda$  will be discussed later.

**Metabolic Rates.**—The metabolic rates for mammals and reptiles listed by Bakker (1975) assume a constant allometric slope of 0.75 between body mass and metabolic rates. This slope is widely accepted theoretically (Schmidt-Nielsen 1997). However, for the purpose of this study, which is to obtain a reasonable approximation of basal metabolic rates based on body mass with ranges, the slope itself is not as important as the actual data distribution. Therefore, I used 95% prediction bands from the actual plot as the model of metabolic rates.

I collected published basal metabolic rates for mammals (Heusner 1990; Hind and Gurney 1997), reptiles (Bennett and Dawson 1976; Paladino et al. 1990; Lutcavage et al. 1992), and tunas (Dewar and Graham 1994a). A double logarithmic plot of the data is given in Figure 1A, with 95% prediction bands for mammals and reptiles (except leatherback turtles). If one more point of, say, a mammal were to be added to the plot, it would fall within the prediction bands for mammals with a probability of 95%. These bands are significantly wider than the confidence bands of the same probability.

The majority of mammalian data are not associated with the record of ambient temperature (Heusner 1990) and therefore were not used for the speed calculation that follows; the mammalian prediction band is depicted for general comparison only. The other data were mostly taken at the ambient temperature of about 18–22°C, but up to 27°C in the case of leatherback turtles. Although a more precise temperature control is desirable, I assume that the ambient temperature was similar among the data points, at about 20°C. Another possible problem is that the data for reptiles had been taken on land, whereas the basal metabolic rates of a single animal may differ between the terrestrial and aquatic environments. In the absence of the more appropriate data, I assume that such differences are sufficiently small not to result in large errors in estimated speeds. This assumption may not be met for the average reptiles, which cannot maintain their optimal exercise body temperature in water. If so, the speed estimates using

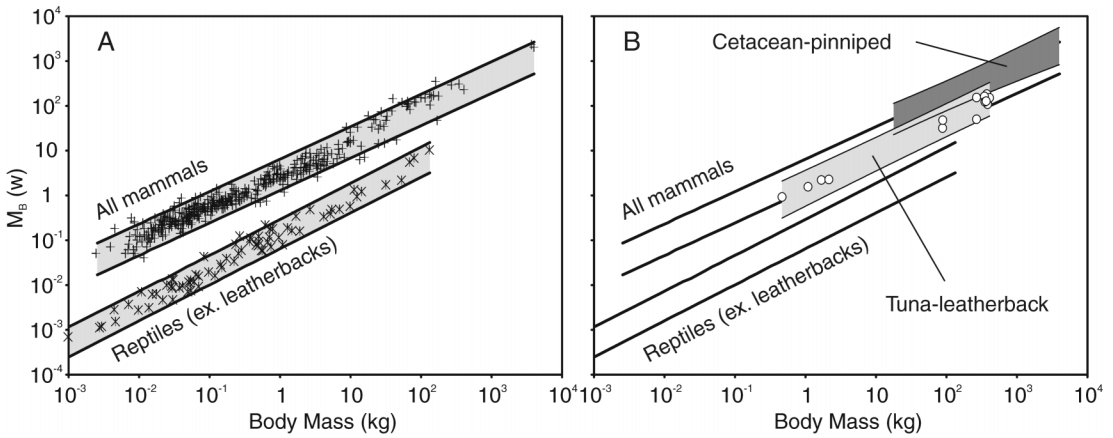


FIGURE 1. Metabolic rates of extant amniotes and tunas. A, Basal metabolic rates of mammals ( $n = 399$ ) and reptiles except leatherback turtles ( $n = 74$ ), with 95% prediction bands (light gray). Equations for regression are given in the text as equations (7) and (8), respectively. B, 95% prediction bands for tunas and leatherback turtles (light gray,  $n = 16$ ) and cetaceans and pinnipeds (dark gray,  $n = 8$ ), overlap upon those for mammals and reptiles (except leatherbacks) as given in A. Equations are given in the text as equations (9) and (10), respectively. Data were obtained for mammals from Heusner (1991) and Hind and Gurney (1997), for reptiles from Bennett and Dawson (1976), for tunas from Dewar and Graham (1994a), and for leatherback turtles from Paladino et al. (1990) and Lutcavage et al. (1992).

average reptilian metabolic rate should be considered as overestimates.

As widely known, the 95% prediction bands for mammals and reptiles (except leatherbacks) do not overlap (Fig. 1A). The equations of the prediction bands for reptiles (except leatherbacks) are

$$M_B = 0.140 W^{0.802} \times 10^{\pm PI}$$

$$PI = 0.430$$

$$\times \{1.01 + 1.04 \times 10^{-2} [\log(W) + 0.585]^2\}^{0.5},$$
(7)

whereas those for mammals are

$$M_B = 2.93 W^{0.723} \times 10^{\pm PI}$$

$$PI = 0.459$$

$$\times \{1.00 + 1.94 \times 10^{-3} [\log(W) + 0.500]^2\}^{0.5},$$
(8)

where  $PI$  refers to prediction intervals.

The clear distinction between the endothermic and ectothermic distributions disappears when adding leatherback turtles and tunas. These animals, which have raised basal metabolic rates above those of average ectotherms, overlap the lower range of mammals (Fig. 1B). Their thermal strategies may not be

exactly the same, but they seem to form a single distribution. The equations for these animals are

$$M_B = 1.36 W^{0.760} \times 10^{\pm PI}$$

$$PI = 0.358$$

$$\times \{1.06 + 5.60 \times 10^{-2} [\log(W) - 1.85]^2\}^{0.5}.$$
(9)

Cetaceans and pinnipeds have higher basal metabolic rates than average mammals. The prediction bands for these marine mammals are given as:

$$M_B = 6.45 W^{0.694} \times 10^{\pm PI}$$

$$PI = 0.319$$

$$\times \{1.09 + 2.26 \times 10^{-1} [\log(W) - 1.95]^2\}^{0.5}.$$
(10)

It should be noted that equation (10) is not based on all marine mammals, but only on cetaceans and pinnipeds. For example, the basal metabolic rates of sirenians, which are low for mammals, are comparable to those of leatherback turtles.

*Drag Coefficients.*—Massare (1988, 1994) estimated drag coefficients by using an equation given by Hoerner (1965):

TABLE 2. Present estimates of optimal swimming speed ( $U_{opt}$ ) compared with published  $U_{opt}$  values that are independent of the present methodology.

Species	Length (m)	Published $U_{opt}$ (m/s)	Present $U_{opt}$ (m/s)	References
<i>Thunnus albacares</i>	0.51	1.0	1.2 (0.89–1.6)	Dewar and Graham 1994a
<i>Phoca vitulina</i>	1.1	0.84†	1.0 (0.79–1.4)	Hind and Gurney 1997
	1.36	1.05†	1.1 (0.81–1.4)	Hind and Gurney 1997
<i>Zalophus californicus</i>	1.3*	1.38–1.70	1.5 (1.1–1.9)	Hind and Gurney 1997
<i>Halichoerus grypus</i>	1.47	0.86†	1.1 (0.83–1.4)	Hind and Gurney 1997
	2.16	0.86†	1.1 (0.87–1.5)	Hind and Gurney 1997
<i>Tursiops truncatus</i>	2.5‡	2.1, 2.5	2.5 (1.9–3.3)	Williams et al. 1993
				Yazdi et al. 1999
<i>Balaenoptera acutorostrata</i>	7.25	3.25, 3.49	3.0 (2.2–3.9)	Folkow and Blix 1992
				Hind and Gurney 1997

\* Based on two individuals of body lengths 1.23 and 1.31 m.

† Based on published graphs of Hind and Gurney (1997).

‡ Present estimate based on 2.51 m individual named Toad (Fish 1993), and published  $U_{opt}$  values based on individuals ranging from 2.3 to 2.5 m in fork length.

$$C_d = Cf[1 + 1.5(W/L)^{1.5} + 7(W/L)^3] \quad (11)$$

where  $Cf$ ,  $W$ , and  $L$  are the skin friction component of the drag, depth, and length of the body, respectively. The equation, however, is for rigid bodies, so some errors are expected when using it for oscillating animals. Also, it does not fully incorporate the scaling of  $C_d$  with the Reynolds number (Vogel 1994). This is partly because Massare (1988, 1994) used a constant  $Cf$  value of 0.004 for all marine reptiles, whereas  $Cf$  should scale with Reynolds number. One way to incorporate this scaling effect is to use the following equation to approximate  $Cf$  values:

$$Cf = 0.072Re^{-0.2} \quad (12)$$

This equation is widely used to estimate the wetted-area drag coefficient of a flat plate in turbulent flow (Vogel 1994). It is also known that the wetted-area drag coefficients of marine mammals can be approximated by this equation (Vogel 1994).

**Body Mass and Surface Area.**—As pointed out earlier, the model of a prolate spheroid largely overestimates the body mass of animals, and possibly their surface area. Also, it fails to account for taxonomic differences in general body shape, which should have large implications for hydrodynamic properties during locomotion (e.g., long-necked elasmosaurs and fusiform ichthyosaurs clearly have different surface area/body mass ratios, even when their fineness ratios are equal). I therefore used a computer program, PaleoMass (Motani

2001) to calculate body mass and surface area from orthogonal views.

### Test Using Extant Marine Vertebrates

The present method was tested on six species of extant marine vertebrates whose optimal swimming speeds have been determined through physiological studies (Table 2). Oxygen consumption rates at varying speeds were measured in these studies, and from these rates, the speeds that minimize the amount of oxygen consumption for a unit length of body movement (i.e.,  $U_{opt}$ ) were found. These  $U_{opt}$  values, of course, are within the observed speed ranges for the species examined.

Three major swimming styles have been proposed for Mesozoic marine reptiles: thunniform swimming for parvipelvic ichthyosaurs (e.g., McGowan 1983, 1991, 1992), subaqueous flight for plesiosaurs (e.g., Godfrey 1984; Robinson 1975), and inefficient axial swimming for mosasaurs and basal ichthyosaurs (e.g., Massare 1988, 1994, 1997). The swimming modes of the six species used in this test encompass all three major types of swimming styles, i.e., cetaceans for thunniform swimming, otariids for subaqueous flight, and seals for inefficient axial swimming. The differences among the three types are reflected in the correction factor  $\lambda$ . Thus, the most efficient of the three (thunniform swimming) has the smallest  $\lambda$  value of 0.20, and the most inefficient (inefficient axial swimming) has the largest (1.9). Hind and

TABLE 3. Optimal swimming speeds of Mesozoic marine reptiles at 20°C estimated by the present method. Institutional abbreviations: BSPM, Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich; GPIT, Geologisch-Paläontologisches Institut Tübingen; MHH, Museum Hauff, Holzmaden; PMU, Paleontologiska Museet, Uppsala Universitet, SMNS, Staatliches Museum für Naturkunde, Stuttgart.

Genus	Specimen/Reference	L* (m)	W (kg)	Reptile $M_B$ $U_{opt}$ (m/s)	Leatherback- Tuna $M_B$ $U_{opt}$ (m/s)	Cetacean- Pinniped $M_B$ $U_{opt}$ (m/s)
<i>Stenopterygius</i>	SMNS 16811	2.40	163–168	0.78 (0.54–1.1)	1.6 (1.2–2.2)	2.5 (1.9–3.3)
	PMU R158	1.18	17.1–17.5	0.67 (0.46–1.0)	1.4 (1.1–2.0)	2.4 (1.8–3.1)
	Munich2	1.14	17.3–17.7	0.66 (0.46–1.0)	1.4 (1.1–1.9)	2.3 (1.8–3.1)
	TUB Re1297/1	1.10	13.3–13.7	0.68 (0.47–1.0)	1.5 (1.1–2.0)	2.4 (1.8–3.2)
	TUB Q07	1.05	11.7–12.1	0.65 (0.45–0.94)	1.4 (1.0–1.9)	2.3 (1.8–3.1)
	SMNS 56631	1.01	11.1–11.4	0.65 (0.45–0.93)	1.4 (1.0–1.9)	2.3 (1.8–3.1)
	Hauff9	0.966	9.10–9.34	0.64 (0.45–0.92)	1.4 (1.0–1.9)	2.3 (1.7–3.0)
	PMU R435	0.636	2.46–2.52	0.60 (0.42–0.85)	1.3 (1.0–1.8)	2.3 (1.7–3.0)
	SMNS 54818	0.597	2.26–2.32	0.58 (0.41–0.83)	1.3 (0.94–1.8)	2.2 (1.7–2.9)
	SMNS Small	0.454	0.900–0.924	0.55 (0.38–0.78)	1.2 (0.89–1.7)	2.2 (1.6–2.9)
<i>Platecarpus</i>	Williston 1910	4.00	246–253	0.38 (0.26–0.55)	0.78 (0.58–1.1)	1.2 (0.91–1.6)
<i>Plesiosaurus</i>	Hauff and Hauff 1981	2.94	172–177	0.49 (0.34–0.71)	1.0 (0.75–1.4)	1.6 (1.2–2.1)
	Brown 1981	4.00	737–756	0.51 (0.35–0.7)	1.0 (0.76–1.4)	1.6 (1.2–2.0)
<i>Cryptocleidus</i>	Brown 1981	4.00	737–756	0.51 (0.35–0.7)	1.0 (0.76–1.4)	1.6 (1.2–2.0)
<i>Rhomaesaurus</i> †	Hauff and Hauff 1981	3.34	482–494	0.48 (0.33–0.69)	1.0 (0.72–1.3)	1.5 (1.1–2.0)

\* Fork length (length between the tip of the snout and median recess of the caudal fin) for *Stenopterygius* and total length for the others.

† Based on ventral view only.

Gurney (1997) treated seals as if they were undulatory swimmers, but Fish et al. (1988) showed that such was not true. Therefore, the use of seals as models for mosasaurs cannot be fully justified. Seal swimming most likely involves less internal recoil (Webb 1992) than mosasaur swimming, given the higher vertebral count and more elongated body profile in the latter. Therefore, if any error were to be introduced by using seals as the model for mosasaurs, it should work toward overestimation of the swimming speed. This will not affect the discussion of relative swimming speed among marine reptiles, as discussed later.

For the present estimates, equations (6'), (11), and (12) were simultaneously solved, together with equation (10) for marine mammals, and with equation (9) for a tuna. The constants  $\varepsilon_p$ ,  $\varepsilon_A$ , and  $\rho$  were assumed to be 0.85, 0.17, and 1024 (kg/m<sup>3</sup>), respectively (Hind and Gurney 1997). The values of body length, mass, and surface area were adopted from the literature for each species (Table 2), except the surface area of *Thunnus albacares*, for which no data were given. The surface area of this species was calculated using PaleoMass (Motani 2001), on the basis of the dorsal view depicted by Dewar and Graham (1994b) and the lateral view by Collette and Nauen (1983).

Superelliptical body cross-sections ( $k = 2.5$ ) were assumed (Motani 2001), resulting in the value of 0.14 m<sup>2</sup>.

The comparison between published optimal swimming speeds and the present estimates is given in Table 2. The present estimates are generally very close to the published values, but there seems to be a trend to overestimation in smaller animals (about 1 m or less in body length) and underestimation in larger ones (about 7 m). Nevertheless, the published values are never outside the prediction range of the present method.

### Application to Mesozoic Marine Reptiles

Given the reasonably high predictive value of the present method in estimating the optimal swimming speeds of extant marine vertebrates, it is probably safe to apply it to extinct forms. The largest problem would be to make correct assumptions of basal metabolic rates for these extinct animals, whose physiology is unknown. I therefore provide in Table 3 and Figure 2 estimates based on three different assumptions, derived from three of the four categories of basal metabolic rates known among extant vertebrates: the average reptilian metabolism, the raised metabolism seen in tunas and leatherback turtles, and the high



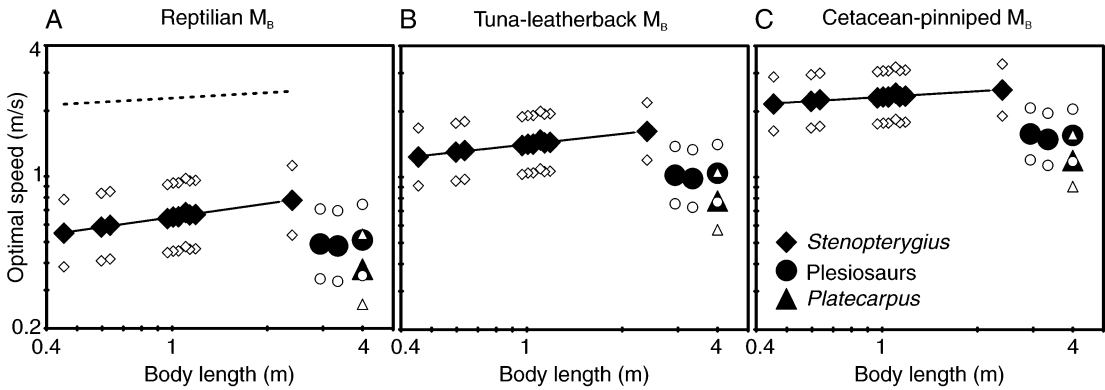


FIGURE 2. Scaling of estimated optimal swimming speed for Mesozoic marine reptiles with body length. Three graphs represent different assumptions of basal metabolic rates, i.e., ones based on the average of reptiles except leatherback turtles (A), tuna and leatherbacks (B), and cetaceans and pinnipeds (C). See also Table 3. Large black marks represent the estimates based on the least-square regression equations relating basal metabolic rates to body mass, whereas white and smaller marks represent those based on 95% prediction limits of the regression equations. Dotted line in A represents a least-square regression line for *Stenopterygius*, based on Massare’s (1988) calculation using average reptilian metabolic rates.

metabolism of cetaceans and pinnipeds (Fig. 1). The average mammalian metabolism was omitted because it entirely overlaps the last two in the size range examined (Fig. 1B), and because the ambient temperatures are not reported. Also, most mammals in the size range belong to the cetacean-pinniped level of basal metabolic rates (Fig. 1A) except one species, a sirenian. Other assumptions were kept identical to the ones made for extant marine vertebrates. Body length, mass, and surface area were calculated using PaleoMass, based on photographs of the specimens (Motani 2001).

Table 4 summarizes the calculated values of  $C_d$  at likely  $U_{opt}$ .

The estimated optimal swimming speeds show negative allometry with body size in *Stenopterygius* (Fig. 2). The allometric slope becomes smaller with increasing basal metabolic rates: the allometric slopes are 0.207, 0.160, and 0.0870 for reptilian, tuna-leatherback, and cetacean-pinniped basal metabolic levels, respectively. Massare’s (1988) original estimates gave a very small slope of 0.0830 using a reptilian metabolic model (Fig. 2A: dotted line), probably because of overestimated speed.

TABLE 4. Estimated optimal swimming speed ( $U_{opt}$ ), drag coefficient ( $C_d$ ), and correction factor ( $\lambda$ ) for Mesozoic marine reptiles.

Genus	Specimen/Reference	$U_{opt}$ (m/s)	$C_d$	$\lambda$	
<i>Stenopterygius</i>	SMNS 16811	1.6	4.0E-03	0.20	
	PMU R158	1.4	4.7E-03	0.20	
	Munich2	1.4	5.0E-03	0.20	
	TUB Re1297/1	1.5	4.7E-03	0.20	
	TUB Q07	1.4	4.9E-03	0.20	
	SMNS 56631	1.4	5.0E-03	0.20	
	Hauff9	1.4	4.9E-03	0.20	
	PMU R435	1.3	5.3E-03	0.20	
	SMNS 54818	1.3	5.6E-03	0.20	
	SMNS Small	1.2	5.7E-03	0.20	
	<i>Platecarpus</i>	Williston 1910	0.38	4.4E-03	1.9
	<i>Plesiosaurus</i>	Hauff and Hauff 1981	0.49	4.8E-03	0.82
<i>Cryptocleidus</i>	Brown 1981	0.51	4.7E-03	0.82	
<i>Rhomaleosaurus*</i>	Hauff and Hauff 1981	0.48	5.0E-03	0.82	

\* Based on ventral view only.

## Discussion

The method outlined in this study is far from perfect: it makes many simplifying assumptions that should increase the error level of the outcome. Nevertheless, the method is capable of estimating optimal speeds with ranges that are reasonably narrow, as demonstrated by the test using extant vertebrates (Table 2). This new finding supports the hypothesis stated earlier: physical constraints on large cruising vertebrates are sufficiently stringent to allow useful estimations of their typical cruising speed. It is probably pessimistic to deny any possibility of making useful speed estimates for Mesozoic marine reptiles.

The swimming speeds estimated for extinct animals in this study are not testable using the present method itself. However, it is possible to test them with another set of estimates, derived from logically different frameworks. If the two sets of estimates closely approximate each other, then they can corroborate each other. One such set can be obtained by analyzing the scaling of the kinematic variables of propulsive organs. This method will be described elsewhere.

Of the three assumed metabolic models, the average reptilian metabolism is probably not very feasible for many Mesozoic marine reptiles, whose large body sizes probably allowed them to maintain body temperature at least to some degree. Also, obligate aquatic reptiles are not capable of basking on land by definition, and the high heat conductance of water (Hind and Gurney 1997) limits the efficiency of submerged basking behavior. Marine iguanas (*Amblyrhynchus cristatus*), for example, have to maintain their body temperatures by basking on land to keep their biochemistry functional (Dawson et al. 1977). Therefore, it is unlikely that obligate aquatic reptiles, such as the parvipelvian ichthyosaur *Stenopterygius*, could have survived with the low metabolic rates of average extant reptiles. With basal metabolic rates higher than the average ectothermic level, *Stenopterygius* would have been capable of cruising at least at 1 m/s, which is approximately the average cruising speed of some extant cruising teleosts, such as the Pacific blue marlin (Block et al. 1992) and

yellowfin tunas (Block et al. 1997; Marsac and Cayré 1998). It is noteworthy that *Stenopterygius* had a similar diet to these teleosts (Keller 1976; Collette and Nauen 1983; Nakamura 1985).

The calculated  $U_{opt}$  values, although inconclusive because of the uncertainty in the assumed metabolic rates, have interesting implications to relative swimming capabilities among Mesozoic marine reptiles. If *Stenopterygius* did have basal metabolic rates comparable to those of leatherback turtles, the genus would have been faster than plesiosaurs or mosasaurs of the same body length, even if the latter had cetacean-pinniped basal metabolic rates. Basal ichthyosaurs most likely used undulatory swimming (Motani et al. 1996), as did mosasaurs in the present study. The evolutionary transition from undulatory to thunniform swimming, as in *Stenopterygius* and other parvipelvian ichthyosaurs (sensu Motani 1999), must have increased the distance that can be covered by cruising. This is unsurprising given that the latter swimming mode involves less internal recoil, which seems to be important in saving energy (Webb 1992).

Massare's (1988, 1994) model of a prolate spheroid to calculate body masses and surface areas of Mesozoic marine reptiles probably did not cause large errors in her estimates of relative swimming capabilities. Assuming a single general shape for ichthyosaurs and long-necked plesiosaurs may seem unreasonable; however, the present study, which uses more accurate body shape models aided by PaleoMass (Motani 2001), gave a similar result regarding the relative swimming capabilities as given by Massare (1988, 1994). This indicates that the variations in body shape do not affect the swimming capabilities as much as the differences among the efficiencies of swimming modes used. Also, there are mutual compensations between overestimated mass and surface area during calculation, as pointed out earlier. Therefore, most of Massare's (1988, 1994) discussions that concerned relative swimming capabilities are plausible.

The assumption that the correction factor  $\lambda$  is a constant (Hind and Gurney 1997) did not cause large errors in speed estimation; the

method approximated the optimal speeds of extant swimming vertebrates with reasonable accuracy. Therefore, it is likely that  $\lambda$  has a very limited range that does not affect the outcome of the present speed estimation very much. It is possible that  $\lambda$  scales with the Reynolds number within its limited range, and this may be one of the reasons why the speeds of larger swimming vertebrates were slightly underestimated. Although  $\lambda$  is useful in calculations, its theoretical relevance has yet to be fully established. As stated earlier, it is more reasonable to interpret  $\lambda$  as a correction factor for the entire equation (1), instead of narrowing down its role to the correction factor for the drag coefficient alone. It probably represents the combination of several factors, including the following: (1) contribution of thrusts generated by body parts other than propulsive organs (e.g., Wolfgang et al. 1999); (2) underestimation of body surface areas when calculating drag coefficients (Motani 2001); (3) use of a linear inviscid theory in estimating the magnitude of propulsive thrusts, and hence the drag coefficients—linear theory tends to overestimate thrusts even in relatively simple cases (Anderson et al. 1998; Streitlien and Triantafyllou 1998); and (4) elastic energy storage in muscles and ligaments during cyclic movements of propulsive organs (e.g., Altringham and Young 1991; Barclay 1994). Further investigation is necessary to scrutinize the theoretical establishment of  $\lambda$ . Until such is completed, researchers should always note the limitation of  $\lambda$ , which lacks theoretical support.

The present method can be improved in the future by refining the empirical constants used, by considering their variations across taxonomic and functional regimes. One of the simplifying assumptions concerns the value of aerobic efficiency of muscles, which was assumed to be constant. This variable, however, is known to vary with the speed of contraction (e.g., Heglund and Cavagna 1985; Curtin and Woledge 1993a,b) as well as size (Altringham and Johnston 1990; Altringham and Young 1991). It is desirable to incorporate these variations, which are expected to make the estimation range even narrower.

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#### Appendix

Another arithmetic error was introduced in Massare (1994), which assumed a uniform weight of 2000 kg for all taxa examined. The body lengths and surface areas of marine reptiles were calculated from prolate spheroids with a volume of 2 m<sup>3</sup> and fineness ratios (body length divided by depth) specific to each species. However, the radius and diameter were confused during calculation, and consequently the length was underestimated by a factor of 2.0, and the surface area by 4.0. For example, a 2000-kg *Ophthalmosaurus* was estimated to be 1.9 m long (polar radius of the spheroid), but it should have been 3.8 m (polar diameter of the spheroid). Conversely, a 1.9-m-long *Ophthalmosaurus* would weigh only 250 kg, when approximated to a prolate spheroid. It is simpler to follow this latter scheme and adjust weights to lengths and surface areas given by Massare (1994), rather than to calibrate the latter two measurements to match the weight. In this way, a uniform body mass of 250 kg for all taxa examined is assumed, and the metabolic rates given by Massare (1994) are overestimated by a factor of 4.76 (= 8<sup>0.75</sup>). This yields an overestimation of  $U_{crit}$  by a factor of 1.68 (= 4.76<sup>0.3333</sup>). In total, the speeds calculated by Massare (1994) are overestimated by a factor of 3.39 (= 1.68 × 2.02) on average.